

# The Segmentation of the Trilobite's Head.

By

Kai L. Henriksen.

---

As the Trilobites are typical Arthropods (having a segmented body, a cuticular exoskeleton, ecdyses, antennae and legs of the common Arthropodous type) the Trilobite's head must be composed by segments, and these segments are to be homologized with those of a typical Arthropod.

The primary segmentation of an Arthropod is an embryonic one (coelom sacs, neuromeres, embryonic limb-outgrowths), and the segmentation appearing on the body-wall of the adult animal as segmentally arranged sclerites and limbs must be regarded as only secondary — these are however the features according to which the segmentation practically must be judged, and most often are they the best criteria, for in reality the segmental limits can remain distinct and the segments thus appear separated in spite of coalescence of the ganglia.

Embryologic and comparative morphologic researches have shown that a typical Arthropodous head (i. e. the Crustacean head) is composed of the following elements, reckoned from the mouth backwards:

- 1) Labrum, situated just above the mouth opening. If the mouth is to be considered terminal, labrum will represent the foremost part of the head. It is however innervated from Tritocerebrum and is therefore commonly considered belonging to the antennar segment.
- 2) The ocular segment, innervated from Protocerebrum and bearing the eyes.
- 3) The antennular segment, innervated from Deutocerebrum and bearing the antennulae ( $A_1$ ).

- 4) The antennar segment, innerved from Tritocerebrum and bearing the antennae ( $A_2$ ).
- 5) The mandibular segment, bearing the mandibles (Mdb).
- 6) The maxillular segment, bearing the maxillulae ( $Mx_1$ ).
- 7) The maxillar segment, bearing the maxillae ( $Mx_2$ ).

To these may be added 1 or more thoracal segments, whose legs then will change in function and in their shapes and serve as maxillipeds (Mxp) in the nutrition, while the appertaining segments will merge into the primary head segments.

As to the Trilobites the question is now to interpret 1) the appendages of the head (which except the eyes all fix on the ventral side of the head), 2) the segmental limits, appearing as glabellar furrows and the occipital furrow on the dorsal side of the head, and the areae bounded by these. For this purpose 1) the morphological features in the different (adult) Trilobitous forms, 2) the more generalized segmentation of the known larval stages, will serve.

A labrum (in Trilobites commonly known as hypostome due to its ventral position) and eyes have been recognized for a very long time. They will be treated below.

The number of postocular appendages was recognized fairly well by WALCOTT (1881) in *Callymene*; but of special value were BEECHER'S investigations (1895) of *Triarthrus*, and WALCOTT'S (1918) of *Neolenus*. They all proved the existence of 5 pairs of appendages: anteriorly a pair of antennal organs, and behind them 4 pairs of leglike organs.

These 5 pairs of appendages are differently interpreted. The American investigators (BEECHER (1895), WALCOTT (1918), RAYMOND (1920)) cite them as homologous with  $A_1$   $A_2$  Mdb  $Mx_1$   $Mx_2$  of the Crustaceans; JAEKEL (1901) thinks that they represent  $A_2$  Mdb  $Mx_1$   $Mx_2$  Mxp, while KINGSLEY (1897) and ELSA WARBURG (1925) maintain that  $A_2$  has disappeared and the present appendages must be termed  $A_1$  Mdb  $Mx_1$   $Mx_2$  Mxp.

As well known  $A_1$  in the Crustacea differs from the common type of their other (biramous) appendages in being (primarily) simple, uniramous. The antennal organs of the Trilobites are setaceous and many-jointed, just as the typical

shape of  $A_1$  in the Crustaceans, and moreover they are simple to the very base. They must consequently be termed  $A_1$ .

JAEKEL (1901) objected to this interpretation and said, that the base of the antenna was not known with certainty and the possibility thus at hand that a little exopod could be present on it. This objection is of no value, partly because Trilobites being very generalized Arthropods showing distinctly biramous appendages, would also have shown a well developed exopod on the antenna, if an exopod belonged to the general organization of this appendage, and partly because later Trilobite specimens have been found (RAYMOND 1920) whose antennae do not show any exopod at all though the entire basal part is known with certainty. When JAEKEL also objects that the fixing point of the antenna is situated laterally to the mouth (off the middle of the lateral border of hypostoma) and an  $A_1$  is situated preorally, the answer may be that the segmental limits on the under side of the head are not known, and as the belonging segment on the upper side is crescentshaped it is rather probable that it is also crescentshaped on the under side and in such case the antennae may easily be interpreted as preoral.

The 4 posterior pairs of appendages are, just as those of the legs of the body, biramous, composed of an undivided sympod with gnathobase, a 6-jointed endopod and an exopod with a setal brim (branchial filaments sec. WALCOTT 1921). It is very curious that the sympod is undivided in the Trilobites while 3 joints can be counted in all recent Crustaceans (HANSEN 1925).

In *Calymmene*, *Ceraurus*, *Isotelus* and *Neolenus* the sympods of these 4 pairs of cephalic appendages are quite in accordance with those of the legs of the body. In *Triarthrus* however BEECHER figures a feeble specialization, the cephalic sympods being more flat and bootlike in outline.

The endopod in *Triarthrus* is plainly smaller and more slender on the cephalic appendages than on those of the body, while in *Cryptolithus*, which has a large and broad Trinucleid cephalon, they are considerably larger and stronger. In *Ceraurus*, *Isotelus* and *Neolenus* no distinct difference can

be seen between the cephalic and the body endopods. As to *Calymmene* different opinions have been set forth: WALCOTT maintains that the last pair of cephalic limbs were considerably stouter than the preceding ones, paddlelike, just as in Eurypterids, while RAYMOND is of the opinion that the 2 posterior pairs were of normal size, while the 2 preceding ones were smaller and more slender.

The exopod is in all the known instances (*Ceraurus*, *Cryptolithus*, *Neolenus*, *Triarthrus*) quite as that in the body legs; and those forms (*Ceraurus*, *Calymmene*, *Neolenus*, *Triarthrus*) which — according to WALCOTT — must be ascribed epipods on the body legs must also be ascribed epipods on the cephalic appendages.

As these 4 pairs of appendages are not so specialized that their interpretation can be made from their appearance only, we will turn to the dorsal side of the head and look at the transverse furrows present there.

Generally a deep and broad furrow, *the occipital furrow*, is found parallel with the hind border of the head, it is especially distinct on glabella and most often also distinct outwards through the fixed cheek.

The area of the head behind the occipital furrow, called *the occipital segment*, is at any rate on the glabellar part quite in accordance with the following (thoracic) segments: the hind edge overlapping the front edge of first body segment is endowed with a median spine or other sculpture, just as the body segments possess, etc. The ontogenetic development also plainly shows that this area (segment) is incorporated in the head at a much later stage and time than the preceding segments, which all belong to the primary head capsule. For instance in the Mesonacid *Elliptocephala* this segment has not yet been differentiated from the embryonal telson segment and is thus not in connection with the head in the young Protaspis stage (fig. 1 — Mxp). According to shape as well as to ontogeny this segment must be termed *a typical maxilliped segment*.

It must be granted that the last (4th) pair of biramous appendages is fixed to and belongs to this latter segment and

must thus be termed Mxp, and its shape does not disagree with that of a Crustacean maxilliped: it is principally built as the following thoracal segments, but is at the same time suited for the new purpose and therefore somewhat resembles the (preceding) mouth parts. As the anterior pairs of appendages, which at any rate must be the mouth parts, are

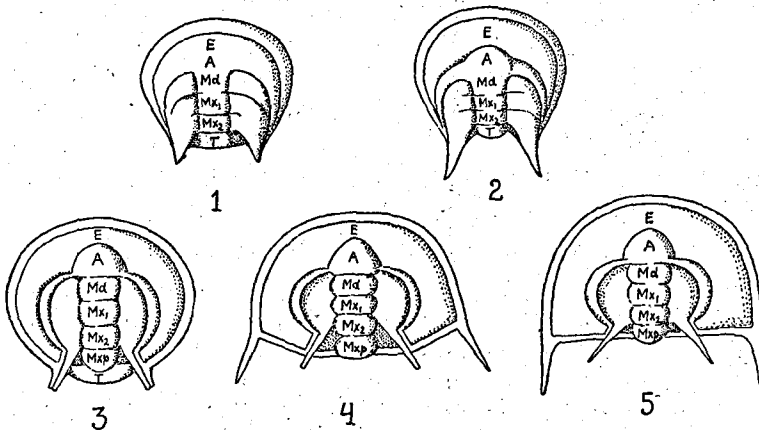


Fig. 1. Developmental stages of *Elliptocephala*.

1-3 Protaspis stages, 4-5 head of nepionic stages. E. eye segment, A. Antennar-segment, Md mandibular segment, Mx<sub>1</sub> maxillular segment, Mx<sub>2</sub> maxillar segment, Mxp occipital= maxilliped segment, T embryonal telson segment. (Walcott 1910).<sup>1)</sup>

not generally specialized in Trilobites, a specialization of the shape of the maxilliped cannot be expected. In *Triarthrus* mouthparts and maxillipeds are however a little — but equally — specialized.

Anterior to the occipital furrow glabella will show a varying number of transversal furrows or incisions, *glabellar furrows*. In many specialized forms, as *Megalaspis*, *Illaenidae* a. o. glabella is (as well as the axis of pygidium) glabrous and without furrows — even the occipital furrow may disappear (see f. i. fig. 14). Other forms, as *Dicellosephalus*, *Harpes* a. o. have only 1—2 more or less complete glabellar furrows (see f. i. fig. 18). A comparison with forms show-

<sup>1)</sup> In the following figures some other letters are used; viz.: a and p, anterior and posterior branch of the facial suture; h, hypostome; m, marginal suture; r, rostrum: (in Mesonacids and Paradoxids known as hypostome attachment).

ing more furrows proves that this low number does not mean that primarily few furrows (and segments) were present, but that they have arisen secondarily through the vanishing of furrows formerly present, and through coalescing of the corresponding segments. There are generally 3 transversal furrows, glabellar furrows, anterior to the occipital furrow (see f. i. fig. 22). These 3 furrows limit 3 lateral lobes and 1 frontal lobe of glabella, plainly corresponding to the 4 anterior pairs of appendages on the ventral side: posteriorly the  $Mx_2$ -segment, in front of this the  $Mx_1$ -segment; then the  $Mdb$ -segment, and on the frontal lobe the antennae were fixed. That each of these lobes is homologous through the Trilobite system, and always can be recognized when counting forward from the hind edge of the head is clearly affirmed — as SWINNERTON (1919) acknowledges — by the fact that the palpebral lobe in fully segmented forms, in adults as well as in larvae, always arises along the eye ridge on the last segment but five. This disproves BERNARD's opinion that the posterior part of the head is composed of a number of segments different in the different Trilobites.

As the eye segment and hypostome — as will be set forth below — follow direct in front of the frontal lobe, it will be seen that a complete accordance is established between the 4 glabellar lobes + the occipital segment and the 5 pairs of appendages. We did not find any  $A_2$  or  $A_2$ -segment, and we did not find any room for it.

Can such a disappearance of  $A_2$  be rendered probable? If not so, the possibility is still present that the 4 posterior segments must be termed  $A_2$ ,  $Mdb$ ,  $Mx_1$ ,  $Mx_2$ .

Such a disappearance of  $A_2$  is really known, and even in the generalized Lower Crustaceans, rather closely related to the Trilobites. In the freeliving Copepods, f. i. *Calanus*,  $A_2$  are small, much smaller than the very long setaceous  $A_1$ , and in the *Notostraca*  $A_2$  must be termed much reduced in size, in *Lepidurus productus* even quite evanesced.

Still more important is the fact that in several Mesonacids, f. i. *Calavia* (fig. 2), and in many choice genera belonging to various families, the area corresponding to the frontal

lobe in the just mentioned forms, is divided crossway by means of an extra (foremost) glabellar furrow; these forms thus possess a frontal lobe, 4 lateral lobes and the occipital segment, and thus space for all the segments typical of the generalized Arthropoda f. i. *Copepoda*, viz  $A_1$   $A_2$  Mdb  $Mx_1$   $Mx_2$   $Mxp$ .

Unfortunately the under side of the head and the belonging appendages are not known in any Mesonacid, most unfortunately as the *Mesonacidae* form the most generalized family of Trilobites which gives the key to the justification and understanding of so many facts in the other families. Thus it cannot be stated whether a *Callavia* possessed well-shaped  $A_2$  or whether they were reduced or even quite absent. This latter may very well have been the case. It is namely a well known fact that appendages can be reduced or quite disappear while the belonging segments are still present, I need only refer to the abdominal segments and their limbs in many Crustacean groups f. i. *Notostraca*.

Also in *Triarthrus* and *Neolenus*, whose number of limbs is well known — as set forth above — the separating furrow between the 2 antennar segments can still be seen. As to *Triarthrus* RAYMOND remarks, that the 2 foremost of the 4 transversal furrows are "exceedingly faint and the first of them is hardly ever visible." Whether  $A_2$  in these forms was quite absent or whether a diminutive rudiment could be demonstrated in the living creature is not possible to make out now.

When most of the Trilobites have reduced the number of glabellar lobes from 5 to 4 this can have taken place in 2 ways: the  $A_2$ -segment have been reduced more and more finally to quite disappear (then the frontal lobe will only represent the  $A_1$ -segment), or only the separating furrow has vanished, (then the  $A_2$ -segment is still present and the frontal lobe represents the combined  $A_1 + A_2$  segment). An examination of the different Trilobites does not show any form (known to me) which must be interpreted in the first-named manner; on the contrary, the different degrees of faintness found in the forms showing 5 glabellar lobes

favour the belief that the frontal lobe represents both segments, though appendages are only present on one of them.

Glabella only represents the axis-part of the mentioned segments. The belonging pleura are easily recognized: the pleuron of the antennal segment (the frontal lobe) is the palpebral lobe + the eye ridge, the pleura of the post-antennar segments are forming the fixed cheeks. In the adult Trilobites these latter will never show the furrows separating the composing segments, but in the protaspis stages of the generalized Trilobites f. i. *Elliptocephala* (WALCOTT 1910) and *Liostracus* (ELSA WARBURG 1925) these furrows are distinctly discernible at any rate towards glabella; in *Liostracus* even the pleura of the Mdb- and Mx<sub>1</sub>-segments will show a division in an anterior and a posterior part just as generally met with in the thoracal pleura of Trilobites.

The protaspis of *Elliptocephala* also gives information as to the intergenal spine commonly met with in the Mesonacids. In an adult Mesonacid this intergenal spine is placed so that it takes part in the longitudinal row of pleural spines of the thoracal segments, and it limits the pleuron of the occipital segment laterally. Thus it might be believed that this intergenal spine belongs to the occipital segment. In the protaspis it is however clearly seen that it advances from the Mx<sub>2</sub>-segment, even at that time when the Mxp-segment has not yet been differentiated from the embryonal hind-segment. That the palpebral lobe represents the pleuron of the antennal segment is also clearly proved by the *Elliptocephala*-protaspis.

Laterally to the facial suture of a common Trilobite the movable cheeks are found, on which the eyes are situated. That these movable cheeks represent the pleura of a pre-antennar segment is also clearly seen on the said protaspis, in which this segment is seen as an opisthocurv lunular space in front of the antennar segment where it keeps its place in spite of the increasing size and altering shape during the growth. As the eyes are found on this sclerit it must represent the eye-segment.



In an adult *Mesonacid* (fig. 2) the hind limits of the eye-segment are easily recognized when compared with the features in the protaspis. The limiting furrow takes its rise on the hind border of the head, runs obliquely forwards and inwards, and then in a laterally convex arch around the palpebral lobe and finally around and limiting the frontal lobe in front, where it joins the corresponding furrow of the other side. This furrow is evidently not a flexible soft-skinned connective membrane, but only a segmental limit which has kept its distinctness from protaspis to the adult stage. When found in the rock the head is never broken along this line, but always showing a whole upper side.

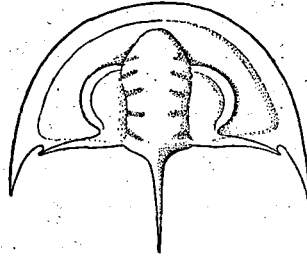


Fig. 2. Head of *Callavia Bröggeri* Walc., from above. (Walcott 1910).

The eye segment extends to the anterior and the lateral borders of the head and continues beyond these borders on the underside of the head as the so called doublure. As formerly stated only labrum in the Arthropods is situated between the eye-segment and the mouth.

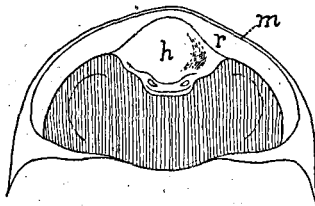


Fig. 3. Head of *Kjerulfia lata* Kjær, from below. (Kjær 1916).

Therefore it was to be expected that the hypostome (labrum) would fix direct on the doublure of the eye segment. MOBERG (1899) and KLÆR (1916) have however stated that the Mesonacids possess a large crescentshaped „sclerit“ inserted between the doublure and the hypostome, and KLÆR is inclined to regard this „hypostome attachment“, as it is termed (fig. 3 r), as representing a peculiar segment. But then the Trilobite's head would be composed by a more segment than otherwise believed. ELSA WARBURG, who refers to HOLMGREEN's brain-studies (1916), therefore does not admit this view, but she thinks, however,

that the hypostome attachment must be termed a primary well-circumscribed sclerit. Against ELSA WARBURG must be put forth that it is most improbable that so generalized Arthropods, as the Mesonacids are, should possess transversal furrows which are not to be interpreted as segmental limits, and the line which KLÆR interpretes as a segmental limit between the doublure (i. e. the eye segment) and the hypostome attachment is, as can be seen in the text as well as in the figures of KLÆR, a fold or crease on the doublure, along which this latter is folded back once more.

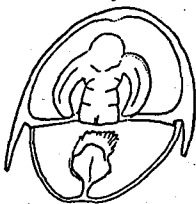


Fig. 4. Head of *Pædeumias*. Doublure and hypostom loosened along the marginal suture and turned round the hind corners of the head. (Walcott 1910).

It must, however, be admitted that the calcification along this line may be rather thin. The photo by KLÆR (l. c. pl. XI f. 2) shows along this line a rupture plainly caused by the pressure during the sedimentation of the surrounding stone, and the weakness along this line is not a mere chance. WALCOTT (1891) mentions that doublure + hypostome of *Callavia Brøggeri* are often found together in the rock, and he figures (1910) a head of *Pædeumias* showing the whole underside of the head including doublure and hypostome loosened

from the upperside along the borders and turned round the hind corners of the head (fig. 4). As SWINNERTON has clearly understood, this is the ecdysial mechanism of the head. In the Mesonacids the ecdyses have taken place just as in an *Apus* (or in the serpents) where the old skin loosens along the whole anterior border of the head, and the animal withdraws itself through this opening. It is this ecdysial line which KLÆR has seen and erroneously interpreted as a segmental limit. It may be termed *the marginal suture* though it can be submarginal or supramarginal as well as quite marginal — as will be seen from the following pages. In the Mesonacids it is submarginal. As the cuticula of the Mesonacids is rather thin the outline of the hypostome attachment is often seen impressed on the upper side of the head as preserved in the rock, and most often the hind limit

of it is especially plainly indicated as a line stretching backwards lateral to and rather parallel with the eye. This line has often been misinterpreted (f. i. by RAW (1925)) as a most peculiar shape of the facial suture (see about this latter below) partly on account of a misconception of the figure by HOLM (1887) where the upper surface of a large part of the

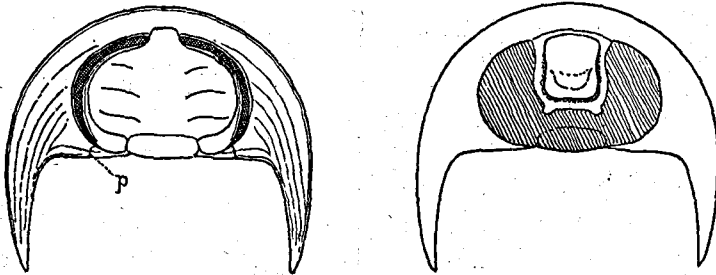


Fig. 5. Head of *Remopleurides radians* Barr. from above and from below. (Barrande).

left side of the head is dissected away to show characters of the under side.

Also in the family **Remopleuridae** (fig. 5), which is considered to be rather closely related to the Mesonacids, the hind limit of the eye segment is easily recognized. As the long, streak-shaped eyes lie close to the rather circular glabella, this limiting line is also found close to it.

Now it would be expected that the moulting took place as in the Mesonacids by means of a marginal suture, the broad flat head could be suggestive of that. It is, however, peculiar, that when Remopleurid heads are found in the rock it is generally glabella only (+ the very narrow fixed cheeks), which is preserved. The segmental limit behind the eye segment must thus have been so thin-skinned and fragile that the head could burst to pieces along it. That implies an important feature in the moulting, but then it seems rather improbable that the head of the new instar can force itself out through the rather small hole which is formed when glabella uncovers itself.

While the heads of the Mesonacids are always found rather whole in the rock, this is never the case with the

**Paradoxidae** (fig. 6), where always the cranidium and the movable cheeks are found separately. On the upper side of the head was thus established a soft-skinned line along which the head might break in two (p—a). This line is, just as in the Remopleurids, posteriorly (p) identic with the segmental

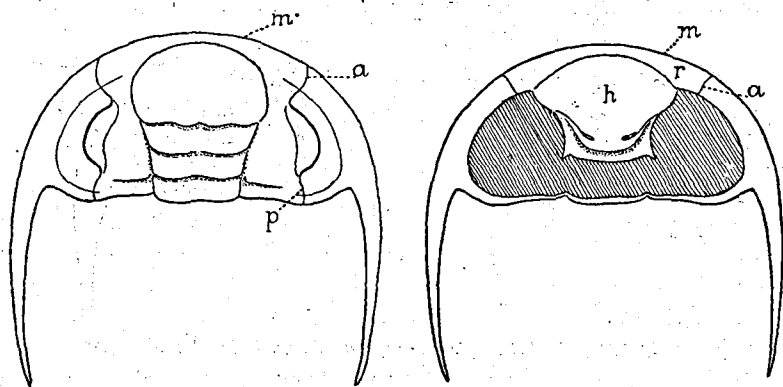


Fig. 6. Head of *Paradoxides bohemicus* Barr., from above and from below. (Barrande).

limiting furrow, running from the hind border of the head forwards and in between the eye and the palpebral lobe, but at the anterior corner of the eye it (a) turns outwards to the border of the head, continues on the under side of the head crossing the doublure to the edge of this latter, where it stops. Such a line along which the head is able to split up is, as well known, called *the facial suture*, and the shape as found in the Paradoxids is that commonly met with in the Trilobites.

At the outset it was most likely to think that the anterior (preocular) branch of the facial suture was running along the segmental limit, as is the case with the posterior (postocular) branch. But in that case the flat area around the glabella, the preglabellar field, has to be interpreted. And what is still more peculiar the central part of the eye segment seems to lack; the hypostome is fixed direct on the median part of the doublure which lies in continuation of the cranidium, and as the movable cheeks bear the eyes and thus are like the corresponding part in the Mesonacids to be

termed the pleura of the eye-segment they have no central part to fix upon.

This curious feature can be interpreted through an examination of the head of a Mesonacid. In these forms a rupture is very commonly seen (due to pressure) from the anterior corner of the eye and rather right-angled (the

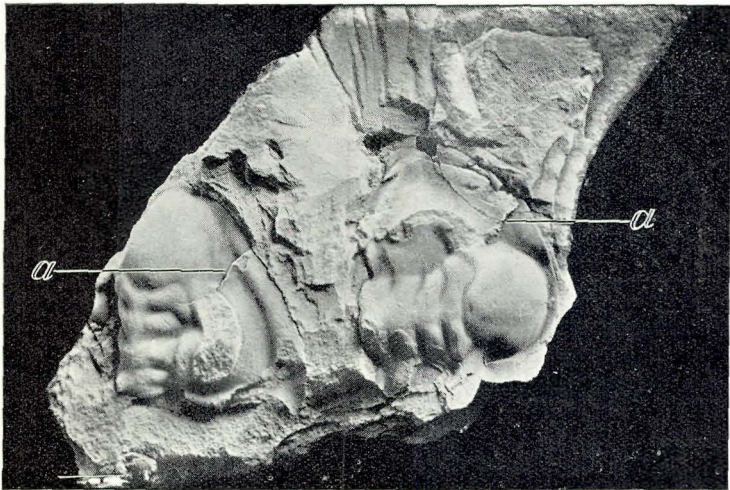


Fig. 7. Piece of rock with 2 heads of *Holmia Kjerulfi* L., showing ruptures (a) from the anterior corner of the eye outwards to the border. (Mineralogical Museum, Copenhagen).

shortest way) outwards to the border (fig. 7). Mag. CHR. POULSEN, who has drawn my attention to this fact, tells me that he has substantiated this rupture in all the specimens of Mesonacids kept in the Copenhagen Museum. It is in reality this short and fragile line together with the part of the limiting furrow between eye and antennal segment lying behind the said line, which become soft-skinned and form the facial suture of *Paradoxides*. The facial suture is thus a mixtum compositum; and the anterior part of the limit between eye and antennal segment is just as in the Mesonacids to be found along the eye ridge and around the anterior part of glabella, while the median part of the eye segment is the field in front of glabella including the doublure.

Such a soft-skinned suture having been established must be caused by something. There is no doubt — as generally admitted — that the facial suture plays its part at the moulting, thus being a splitting line along which the head opens, acting just as the marginal suture of the Mesonacids, but by no means homologous with this latter.

In *Paradoxides* and upwards in the system the eyes will become more and more important. They become larger and broader — while in the Mesonacids they were narrow streaks. During the moulting they cannot however be employed, during that time the animal is blind; therefore it has a great importance that the eyes may as quickly as possible get rid of the old cuticula, and this is established by the splitting line running immediately by the eye. And as the cuticula also must split at the anterior border in order that the animal can easily work its way out of it, the connecting rupture between the eye and the anterior border + doublure is established.

But of course the two facial sutures must be connected anteriorly to form the gap through which the animal can make its way out. It might be thought that this connection took place in the soft skin beneath the hypostome, which would effect, that the hypostome was thrown off together with the upper side cuticula of the head, while in the Mesonacids (just as in *Apus*) it is together with the under side cuticula.

Isolated hypostomes of *Paradoxides* are often found in Danish *Paradoxides*-beds as well as also in other places, and in all cases it will be remarked that such a hypostome shows a pair of broad angulate ears, and the earbearing part is separated from the narrower distal part through a curved furrow. An examination of a head's under side with hypostome extant will show that the said ear-bearing part forms the anterior part of the under side doublure. This means that the so-called hypostome consists of the real hypostome + the hypostome attachment. The median part of the doublure (laterally limited by the distal part of the facial sutures) (r) is thus always cast off together with the hypostome, the se-

parating furrow between hypostome attachment and hypostome being very firm and often rather evanescent, while a natural rupture line is present in the anterior border of the

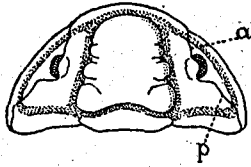


Fig. 8. Head of *Calymene Blumenbachi* Brongn., from above and from below (Barrande).

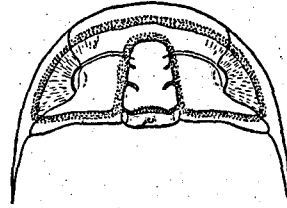
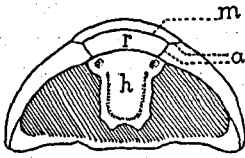


Fig. 9. Head of *Ptychoperia striata* Emmr., from above and from below. (Barrande).

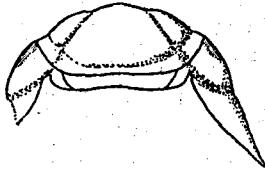
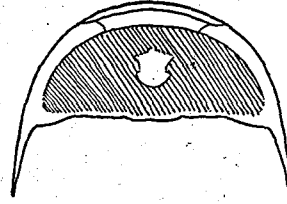


Fig. 10. Head of *Lichas conicotuberculatus* Nieszk., from in front. (Schmidt).

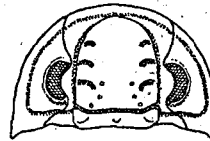


Fig. 12. Head of *Proetus bohemicus* Cord., from above and from below. (Barrande).



Fig. 11. Head of *Acidaspis crenata* Emmr., from below. (Barrande).

head, and when compared with the Menonacids this rupture line proves homologous with the marginal suture of these latter, in *Paradoxides* only shortened and here quite marginal — not submarginal, and agreeing with this the hypostome attachment is also shortened.

In a number of families *Proetidae*, *Ptychopariidae*, *Calymmenidae*, *Lichadidae*, *Odontopleuridae* (fig. 8—12)<sup>1)</sup> the facial sutures anteriorly as in *Paradoxides* turn separately down on the under side and go to the distal border of the doublure. Just as in *Paradoxides* we find a remainder of the primary marginal suture, however here not marginal, but as in the Mesonacids submarginal. Parallel to this and distal to it is found another deep and surely soft-skinned suture viz. that limiting the hypostome proximally. The hypostome attachment has thus been well and deeply limited on all sides, and is in that case known in the Trilobitous literature as *rostrum*, an identification which already KLÆR proposed, however without proofs.

As the furrow between rostrum and hypostome is not only deep and (surely) soft-skinned, but also rectilinear, the hypostome must have been movable in this suture.

Whether the moulting has taken place by splitting up along the uppermost or the nethermost of the 2 transversal furrows which limit the rostrum is questionable. As the upper parts of the facial sutures are converging also beneath the border and there continuing in the proximal transversal furrow (in which the splitting took place in the *Paradoxids*) we are inclined to think that this is the fact also here. But on the other hand again, in these families we never find rostrum and hypostome cast off together, so it surely means, that all the furrows around the rostrum will burst and the rostrum thus be quite removed.

In all the last mentioned families rostrum must thus be interpreted as only part of the central area of the eye seg-

<sup>1)</sup> The families *Zacanthoidae*, *Oryctocephalidae*, *Olenidae* and *Ellipsocephalidae* will most probably show the same characters as the above named families; only the upper side of their heads being known the matter cannot be stated with certainty. — The family *Lichadidae* is included among the above-mentioned families in accordance with the figures by SCHMIDT (1885 pl. III fig. 13 c and pl. IV fig. 12 b); it must however be mentioned that BARRANDE (1872 pl. X (fig. 12—14) has quite a different figure of another species of *Lichas*. — All the families are understood in the sense of SWINNERTON (1915).



ment, and not the whole eye segment, as JAEKEL believes.

In the family **Homalonotidae** (fig. 13) we find the same fundamental shape of the head as in the file of families just mentioned. It ought to be remarked that rostrum in a *Homalonotus* is so high, that it forms a real rostral shield which covers the protruding median part of the head above as well as below. Also in this family the splitting up during the ecdysis must have taken place along all the borders of the rostrum.

Also in the **Illænidae** (fig. 14) and **Bronteidae** (fig. 15), which are as to the head characterized by having glabella anteriorly very broad and inflated, we find a facial suture and a rostrum quite as in the foregoing families, but while in those families the furrows are deep and broad, they appear as faint lines in

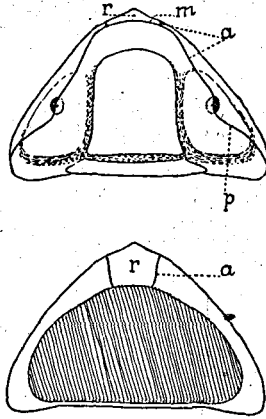


Fig. 13. Head of *Homalonotus Dekayi* Corda, from above and from below. (Barrande).

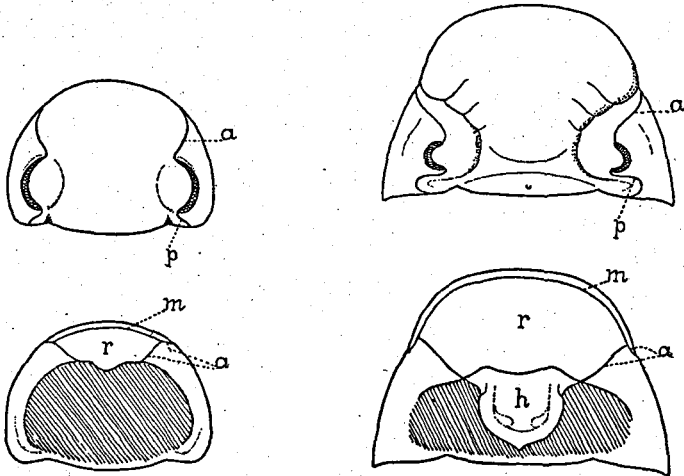


Fig. 14. Head of *Illanus Bouchardi* Barr., from above and from below. (Barrande).

Fig. 15. Head of *Bronteus campanifer* Barr., from above and from below. (Barrande).

Illæenids and Bronteids. In accordance with the broad glabella also rostrum is very broad; it is entirely lying on the under side, and as its shape is rather curvate, the mobility of hypostoma has surely been very much reduced. In *Bronteus planus* Corda (BARRANDE 1852 pl. 48 fig. 1) a. o. species we observe a well developed preglabellar field on the upper

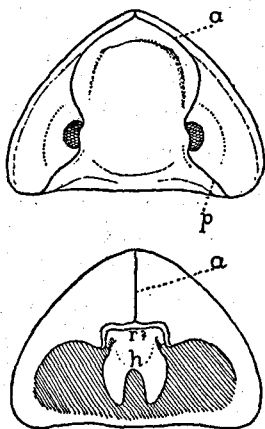


Fig. 16. Head of *Asaphus platycephalus* Stokes, from above and from below. (Barrande).

side, but in other species, f. i. *Bronteus campanifer* Barrande (BARRANDE 1852 pl. 44 fig. 1 and 3) (fig. 15) the glabellar inflation has been quite excessive, falling forwards beyond the original border and downwards to the limit of rostrum. We here see how an increasing glabellar cavity (probably on account of an increasing size of the stomach) can extend itself forwards and fill also the preglabellar field. Quite a parallel case is seen in the Phacopids, and in the Encrinurids the swelling has moreover passed on beyond the limiting transversal furrow and also made the movable cheeks inflated anteriorly.

In the family *Asaphidae* we find a very characteristic shape of the facial sutures in the genera *Asaphus*, *Ogygia*, *Megalaspis*, *Niobe* and allied (fig. 16). Anteriorly on the upper side of the head the 2 sutures are seen converging more and more, meeting in the median line and then as an odd sagittal furrow run forwards across the border through the doublure to the proximal border of the hypostome.

In *Niobe desiderata* Barr. BARRANDE (1872 pl. 4 fig. 6) figures 2 longitudinal furrows transversing the doublure, almost as in the under side of a *Homalonotus*. This might very well be interpreted as the starting point of the feature commonly met with in the Asaphids. Here is, however, a case where it must be permissible to doubt the exactness of the otherwise so splendid work of BARRANDE. Partly because

BARRANDE (ibid. pl. 9 fig. 11) also figures a younger specimen of the same species showing an unpaired longitudinal furrow, and partly because later on other *Niobe*-species have been figured f. inst. *Niobe primæva* (WESTERGAARD 1922 pl. 2 fig. 25) on the upper side of which the preglabellar field is seen tapering into an unpaired point which can only be interpreted as involving a sutural shape as in the genus *Asaphus*<sup>1</sup>).

The question is then: What has become of the central part of the eye segment? Is it only represented in the preglabellar field, or can a field also be found which may be homologized with a rostrum? This latter seems very probable. When examining an Asaphid hypostome (BRØGGER 1886 has figured a number of them) it will be observed that it possesses proximally a pair of lateral ears, and the Asaphid hypostome thus gets an amazing resemblance to a Paradoxid hypostome + hypostome attachment. Therefore the ears of the Asaphid hypostome may be interpreted as coalesced with rostrum. Quite surely ear-shaped processes are substantiated on the hypostomes of other Trilobites, f. inst. *Bronteus*, where besides these a separate rostrum is present. Thus the ears in a *Bronteus* cannot be identified as a rostrum, and that of course makes the interpretation in the Asaphids doubtful; and Asaphids which clearly point in a distinct direction are unknown to me. In the Asaphids however the ears have a much more rostrum-like appearance and the furrow between this basal part of the hypostome and the corpus proper of it is more accentuated than in the other forms having ears — as far as can be judged from the figures published. So I feel rather convinced that in these Asaphids rostrum has really been absorbed in the hypostome.

At the moulting the old cuticula of the head will clearly enough open owing to a Y-shaped splitting line, as the facial sutures of the 2 sides will loosen round a rather small median

<sup>1</sup>) The family *Dicellosephalidae* also shows a preglabellar field which is pointed anteriorly. It is therefore sure to be closely related to the Asaphids, but as the under side is not known (cfr. WALCOTT 1914) this cannot be stated with certainty.

area above, and then the sagittal joint line will start across the whole doublure; thus the hypostome (together with the possible rostrum) will be cast off separately.

The hypostome (+ rostrum) has been so firmly and deeply implanted in a bend in the doublure that the movability cannot have been great. BRØGGER suggests that the hypostome has been fixed and immovable, pressed against the under side of the head as a shelter for the viscera (stomach, ganglia) inside; if the 2 large, commonly well circumscribed spots on the Trilobites' hypostome is not to be interpreted as eyes, but as muscular fixing points<sup>1)</sup>, the muscles fixing on them may not have served in the movement of the hypostome, but assisted the masticatory stomach. But

<sup>1)</sup> LINDSTRÖM (1901) interpreted these two spots as ventral eyes, but this was contradicted by JAEKEL (1901) who compared their aspect with the muscular impressions of the Crustaceans especially the Ostracods with which they quite agree. HANSTRÖM (1926) has again taken up the view of LINDSTRÖM on account of the well proved presence of ventral eyes in the larva of *Limulus*. Though the interpretation should have been a valuable support to my views upon the descent of Merostomata and Arachnids, which I intend to give in a future paper and as to which I almost quite agree with HANSTRÖM, I must however say that the description and figures given by LINDSTRÖM do not convey to me the sure impression of their ocular nature, and the view of JAEKEL seems to me much more credible. It may also be mentioned that the ventral eyes of *Limulus* are innerved from protocerebrum, and in the Trilobites the case should have been the same; as the hypostome — being homologous with the labrum — must have been innerved from tritocerebrum, the nerves from the 1st segment should thus have acted on an organ in the 3d segment. I must however confess that such a case is really known, as HANSTRÖM has made out that in the Decapodous Crustaceans the eye-stalk possesses eye nerve (from protocerebrum) as well as a branch of Nervus tegumentarius (from tritocerebrum), but this turns upon very specialized Arthropods, and it is not just as likely that the most generalized Arthropods known, the Trilobites, will show similar secondary features. Nor do I venture to have a decided opinion of the significance of the proboscid eyes of the Cirripedious larvæ — referred to by LINDSTRÖM — as the Cirripedia is a highly specialized group of Crustaceans.

as the hypostome lies pressed firmly against the under side there would be no access to the mouth, but this is managed otherwise as the hypostome shows a deep median concavity inwards from the distal border — which would, if the hypostome was freely movable, affect the power of activity.

If the genera *Nileus* and *Symphysurus* (fig. 17) are to be retained in the Asaphids the actual shape of their furrows

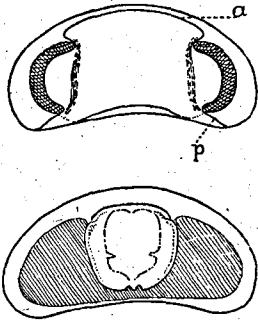


Fig. 17. Head of *Nileus armadillo* Dalm., from above and from below. (Barrande).

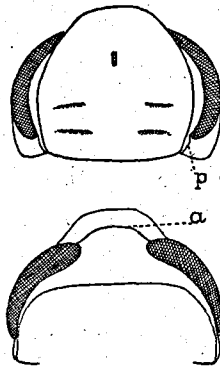


Fig. 18. Head of *Aeglina sulcata* Barr., from above and from below. (Barrande).

must be interpreted as arisen through disappearance of the sagittal furrow and thus only a transverse splitting line is retained which runs in a bow round glabella without being pointed anteriorly. The movable cheeks are thus fused together. The hypostome has not the same shape as in the above treated genera, the ears are not so distinct. It is therefore much more possible that rostrum has quite disappeared in these genera than in the preceding.

The family *Æglinidae* (fig. 18) which is characterized in having very large eyes and a swollen large glabella on the thick and rather globular head shows a shape of the splitting furrow just as in *Nileus* or *Symphysurus* viz. a connecting furrow running between the front parts of the eyes around the front part of glabella. I think it also most probable that the large crescentshaped anterior doublure of

the head, as proposed for *Nileus* and *Symphysurus*, only represents the fused movable cheeks while rostrum has disappeared from it.

If *Æglina* is not to be interpreted in this way the said connecting furrow can only be interpreted as a segmental limit just as in the Mesonacids (and Remopleurids) but this

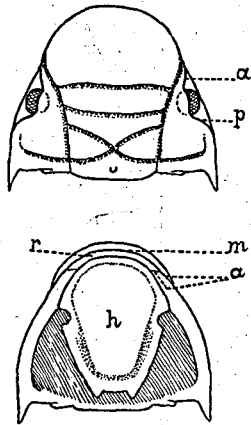


Fig. 19. Head of *Cheirurus gibbus* Beyr., from above and from below. (Barrande).

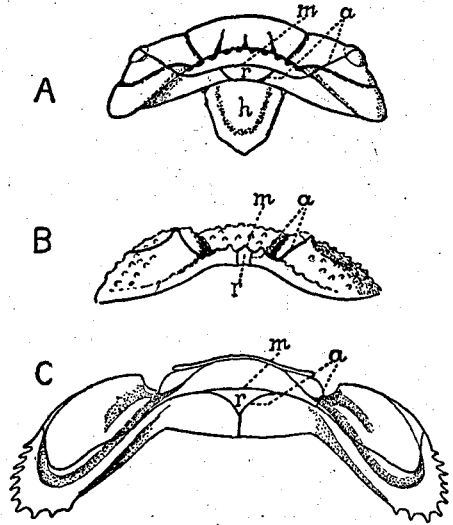


Fig. 20. Head of A *Pliomera Fischeri* Eichw., B *Cybele bellatula* Dalm., C *Placoparia grandis* Barr., all seen from a front. Hypostome is only preserved in A. (A and B Schmidt, C Barrande).

does not seem likely considering the general shape of the body (non-flat head, few body segments etc.) which does not prove a near relationship between *Æglinids* and Mesonacids.

When we pass on to the Proparian families we find in the family **Cheiruridae** a rostrum typically present. In the genus *Cheirurus* (fig. 19) it is large and broad, filling most of the limbus anteriorly. In *Pliomera* (fig. 20 A) it has become smaller and narrower than the hypostome, in *Cybele* (fig. 20 B) it is a narrow median stripe between the movable cheeks, and in *Placoparia* (fig. 20 C) it loosens the connection with the hypostome and draws back in a much reduced size; in this latter genus it is recognized as a trian-

gular sclerit lying against the large glabella, while the movable cheeks are meeting below it, without fusing together however.

At the moulting the old cuticula will clearly enough split along the proximal of the transversal furrows which lies in a mere continuation of the upper part of the facial sutures. Whether rostrum entirely loosens, as is proposed for the Proetids etc. cannot be made out with certainty. *Placoparia* however has a heavy armature of spines on the movable cheek, and an enlargement of the rupture was perhaps desirable in this genus; it is interesting that just in this genus we find a sagittal line connected with the above mentioned, so that a Y-shaped rupture can take place as in the Asaphids.

In the family **Encrinuridae** (fig. 21) we find a diminutive rostrum, which as in *Cybele* forms a narrow sclerit stretching between the transverse splitting line formed by the upper parts of the facial sutures and the distal border of the doublure.

As mentioned above, the swelling of the anterior part of the glabella has become so extensive that it has extended itself not only over the preglabellar field but also farther forwards on the anterior parts of the movable cheeks. At the moulting the movable cheeks are removed separately as also the lateral sutures of the rostrum open.

In the family **Phacopidae** (fig. 22) we find a further development of the features found in the Cheirurids (and Encrinurids) as the movable cheeks have fused together in front of the splitting furrow, and the rostrum is not recognizable; when we compare the said families, we are inclined to think that in the Phacopids it has been so much reduced that it has quite evanesced. It will easily be seen that the furrows present in the Phacopids run just as in *Nileus* or *Æglina*. As however the Phacopids are nearly

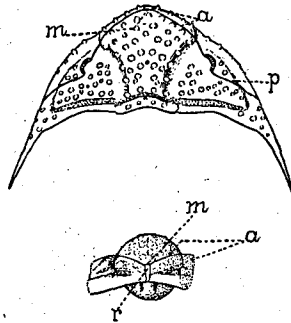


Fig. 21. Head of *Encrinurus punctatus* Wahlb., from above and from in front. (Barrande, Schmidt).

related to the other Proparian families and not — as far as can be ascertained — to the forms named above, I feel convinced that the interpretation given here is the correct one; and the conformity in the two files is only due to convergence. It must however be stated that in a few species

the trace of a crescent-shaped line parallel with the proximal edge of the hypostome may be recognized, which might indicate the presence of a (broad) rostrum coalesced with the doublure.

Just like in the Bronteids we also in the Phacopids find species (of *Phacops* and *Dalmanites*) in which a distinct preglabellar field is found in front of the anteriorly inflated glabella, and others (of the same genera) in which the swelling has extended forwards to the splitting line the preglabellar field thus disappearing.

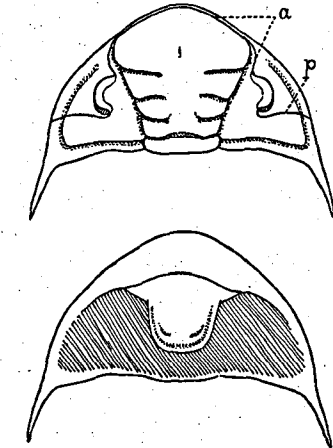


Fig. 22. Head of *Dalmanites socialis* Barr., from above and from below. (Barrande).

While in the Cheirurids the proximal limit of the hypostome is rather straight-lined, and the hypostome therefore surely must have been movable, the corresponding furrow in the Phacopids is curved and the hypostome has therefore certainly been rather immovable.

In the foregoing only the anterior branch of the facial sutures, from the eye and forwards, has been treated. Their posterior branch needs only a few words. As is well known it may run from the hind corner of the eye to the hind edge of the head (*Opisthoparia*), or to the hind corner of the head (*Calymmenidae*), or to the lateral edge of the head (*Proparia*). For the animals it is only important that this branch is posteriorly placed so much outwards that the new instar can at the moulting withdraw itself through the whole rupture. Thus, if it is necessary for a Trilobitous form to



have a spinous hind corner of the head (due to inheritance or fitting of the biology) it plays no part whether this spine takes its rise from the movable cheek as a real genal spine (*Opisthoparia*) or from the cranidium (*Proparia*) in which latter case this spine must have quite another origin, as placed on quite another head segment, and must be homologized with the intergenal spine of the Mesonacids, as WALCOTT (1910 p. 237) and REED (1916 p. 172) correctly recognized it.

Among the Trilobites more families contain genera which are quite blind, i. e. without eyes, and as the facial suture, as set forth above, is of special importance as to the moulting of the eyes it is clearly seen that a facial suture cannot be of the same importance in these blind forms, while however an ecdysis must, of course, take place as in other Arthropods.

In the family **Raphiophoridae** (fig. 23), the forms of which are all blind, we find well developed facial sutures on the upper side of the head which bear a witness of their descent from oculate forms. The head, especially glabella, is strongly projected in the middle and this also affects the course of the suture on the under side, where, just as in *Ægina* or *Nileus*, only a transverse furrow, here proconvex, is present. BARRANDE (1872 pl. 2 fig. 33) for certain figures a pair of sutures from this furrow posteriorly to

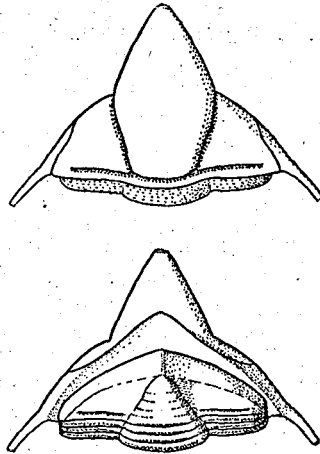


Fig. 23. *Ampyx (Lonchodomas) Portlocki* Barr., an enrolled specimen, from above and from below. (Barr.).

the hind edge of the doublure indicating a rostrum of large size. Mag. CHR. POULSEN who has prepared specimens belonging to the Copenhagen Mineralogical Museum has kindly called my attention to the fact that this is due to an error, the doublure posteriorly to the transversal furrow does not show any further furrow. In contradistinction to BARRANDE RAY-

MOND (1917 pag. 205 fig. 2) has figured the shape correctly.

I think it most probable that the Raphiophorids just as the Æglinids are related to the Asaphid genera *Nileus* and *Symphysurus* but the most peculiar specialization of the *Ampyx*-type makes it very difficult to decide it with any certainty.

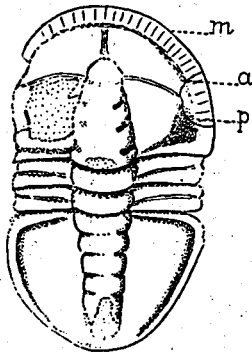


Fig. 24. *Pagetia bootes* Walc., from above. (Walcott).

Also the Cheirurid genus *Placoparia*, which is mentioned above together with the other Cheirurids has retained the facial sutures and shows thus that it descends from oculate forms.

The other blind families show features quite different to those of *Ampyx* and *Placoparia*.

To the family Agnostidae a number of differently shaped genera of very heterogeneous contents are reckoned. I will confine myself to

mention the genera *Pagetia* and *Agnostus*.

*Pagetia bootes* (fig. 24) which was described by WALCOTT (1916) shows on the upper side of its flat head two long eye ridges which from the anterior part of the glabella bend outwards (and somewhat backwards). Fairly near the side margin the eye ridge shows a little palpebral lobe and here it joins the (real) facial suture which as an arc limits the small movable cheek, and anterior as well as posterior to this reaches the border of the doublure. Thus the eye segment here shows movable cheeks (laterally), as well as (frontally) a large preglabellar field limited behind by the eye ridge. The preglabellar field shows a very distinct sagittal furrow which cannot, of course, be homologous with the sagittal furrow of the Asaphids, as in these latter it is formed through the meeting of the eye pleura while the central part of the eye segment is displaced, and in *Pagetia bootes* the line runs along the median line of the central part of the segment while the eye pleura lie far from another laterally on the head. The splitting of the old cuticula at the moulting will then take place along a line combined by the

2 anterior branches of the facial sutures and a line along the border between these two, this latter as in the *Paradoxids* a. o. representing the original marginal suture. — The other species of *Pagetia* described by WALCOTT, viz. *clytia*, only differs from *bootes* in the missing eye ridge. The facial suture quite agrees with that of *bootes*.

In *Agnostus* the interpretation is more difficult, as no movable cheeks are present at all, and at the same time no trace of an eye ridge can be observed. BEECHER (1897) however proposed that facial suture and movable cheeks were to be found on the under side of the head (and according to this he created the systematic group *Hypoparia* parallel with *Opisthoparia* and *Proparia*). BEECHER however gave no evidence of this interpretation, and RAYMOND, who (1917) maintains the same on account of a find made by him, has in reality not seen any facial suture, but rather a (submarginal) ecdysial line, which has at any rate nothing to do with a facial suture but is quite of the same type as that of the *Mesonacids*, thus being a marginal suture (fig. 25)<sup>1</sup>). Thus it will easily be seen that *Pagetia* and *Agnostus* belong to different lines of descent.

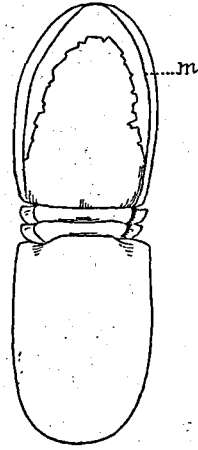


Fig. 25. *Agnostus nudus* Beyr. The specimen mentioned by Raymond (Raymond).

In the family *Conocoryphidae* (fig. 26) neither any trace of eye nor facial suture is present. But on the other hand a

<sup>1</sup>) Moreover it does not perhaps turn upon the head, but upon the pygidium. RAYMOND certainly terms the part in question the head, but head and pygidium of the investigated form (*Agnostus nudus* Beyr.) are quite alike one another, and the form and the overlapping of the thoracal segments favour the interpretation as pygidium. (It may be mentioned that RAYMOND for the sake of conformity also rebaptizes head and pygidium of the figure of *Agnostus integer* Barrande (1852 pl. 49), but a glance at this figure shows this to be still more incredible.

marginal suture just as that of the Mesonacids can very easily be recognized, and in the forms showing „genal“ spines, f. inst. *Conocoryphe Sulzeri* Schloth. (fig. 26), the marginal suture is seen rounding the genal angle above the spine, which latter thus proves to belong to the doublure.

BARRANDE (1852 pl. 14 fig. 8) figures a well-developed rostrum on the doublure of *Conocoryphe Sulzeri* Schloth., but this cannot be correct. As a rostrum implies the presence of

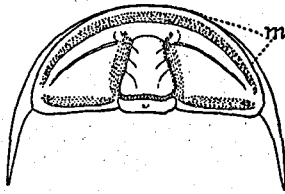


Fig. 26. Head of *Conocoryphe Sulzeri* Schloth., seen from above. (Barrande).

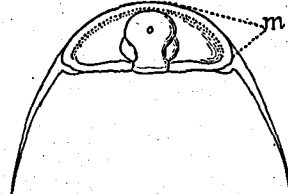


Fig. 27. Head of *Trinucleus Reussi* Barr., from above. (Barrande).

both the marginal suture and the facial sutures acting together, and only the first named is present in a *Conocoryphe*, the drawing by BARRANDE cannot be correct.

In the family **Trinucleidae** (fig. 27) also a marginal suture is easily observed, just as in the Conocoryphids, and just as in this latter family the most primitive Trinucleids, f. inst. *Trinucleus Reussi* Barr. (BARRANDE 1872 pl. 5 fig. 15-16) (fig. 27) clearly shows that the „genal“ spine belongs to the doublure, as the ecdysial suture is seen transversing the hind corners of the head above the spine. Nor can in this family apparently any trace of facial suture be observed no more than an eye ridge.

RUEDEMANN (1916) has however on the cast of the head shield of *Cryptolithus tessellatus* Green observed a raised line on each cheek which he calls facial suture; it is forming an acute angle with its apex pointing inwards and here forming a little tubercle which RUEDEMANN interprets as a rudimentary eye. The entire feature is too doubtful to give a well-founded interpretation, for one thing because the species in question is a highly specialized one (broad brim

etc.) and the more generalized forms do not show these features, f. inst. *Trin. Reussi* Barr., and in other forms the course of the said lines is such that to interpret it as a facial suture is not a matter of course.

In the family **Harpedidae** the ecdysis must as in the Trinucleids have taken place along the margin of the head, the marginal suture thus being in use. As in the above mentioned families this line has commonly been termed facial suture, but as eyes (reduced to 2—3 stemmata) and eye ridges are present and these lie far from the splitting line (while they are always connected when the question is upon a real facial suture) the interpretation as a facial suture is clearly enough wrong.

Thus in *Agnostus*, *Conocoryphidae*, *Trinucleidae* and *Harpedidae* only the primary ecdysial line, the marginal suture, is present and acting, indicating that the relationship of these forms is not to be sought for in the oculate specialized families, as facial sutures then surely were to be recognized, but in the generalized families, such as the Mesonacids, with which they agree as to the broad flat heads.

In the families **Burlingiidae**, **Solenopleuridae**, **Bathyruridae** and **Shumardiidae** the underside sutures are not known, and the upperside sutures do not allow us to conclude anything with certainty as to the features on the under side; therefore I dare not range these families into the files treated on the preceding pages.

At last I must say a few words upon the dorsal (frontal) eyes not hitherto mentioned by me. HANSTRØM (1926) ascribed to the Trilobites — just as *Limulus* — three visual areas viz. a dorsal, a lateral and a ventral, furnished respectively with median eyes, compound eyes and hypostomic eyes. The compound eyes have been sufficiently treated in this paper, and my hesitation in interpreting the hypostomic maculae as eyes is given on pag. 20.

Finally the dorsal eyes: HANSTRØM is surely right in ascribing to the Trilobites median eyes, homologous to the nauplius eye of the Crustaceans — eyes which surely have

been of the inverted type. HANSTRØM refers to the observations of RUEDEMANN (1916) as to the structure of the median tubercle on glabella which is stated to be present in *Cryptolithus (Trinucleus)* as well as in many other chance genera<sup>1)</sup>. RUEDEMANN substantiated that this tubercle showed a rather thin cuticula indicating the presence of an internal organ beneath, and the tubercle is not developed in the early forms (Mesonacids, Paradoxids, Olenids, Conocoryphids) where only circular transparent spots are present on glabella, but best developed in the later ones — which may all very well agree with the nature of the eye as a subdermal inverse one.

Though I think that RUEDEMANN and HANSTRØM are right in this interpretation I must say that it is curious that the tubercle (or transparent spot) when present is always found so far behind on glabella that the median eye, which according to its neural rise must belong to the eye segment (there is no reason at all to believe that the Trilobites have differed from the recent Arthropods in this respect) should have wandered backwards in all forms, and not a single one of the more generalized families will show a median eye tubercle situated on the eye segment.

The dorsal eye is described as unpair where a tubercle is present (just as the nauplius eye of the Crustaceans appears unpair), and when but spots are seen, these are present in a number of two. In the very specialized form *Æglina* an unpair tubercle as well as two spots are present. For more details see HANSTRØM (1926).

Almost all the figures accompanying this paper have been redrawn from the works of BARRANDE and SCHMIDT. Of course I have — as far as possible — stated the correctness upon the material present in the Geological-Mineralogical Museum of Copenhagen, and therefore more of the figures are not mere copies, but are modified as to details.

<sup>1)</sup> I do not consider the cases where the tubercle or impress is due to a broken spine, f. inst. in *Trinucleus Reussi* Barr. (see BARRANDE 1872 pl. 5 fig. 16—17).

At least I wish to express my thanks to mag. sc. CHR. POULSEN Esq. with whom I have discussed the matter set forth above, as the discussion has been of great value to me.

Copenhagen in June 1926.

### Cited literature.

- BARRANDE, JOACHIM: Systeme Silurien du Centre de la Bohême. Vol. I Trilobites 1852 935 pag. — Suppl. au vol. I 1872 648 pag.
- BEECHER, C. E.: Further Observations on the Ventral Structure of Triarthrus. Amer. Geol. XV 1895 p. 91—100.
- BEECHER, C. E.: Outline of a Natural Classification of the Trilobites. Amer. Journ. of Sci. (4) III 1897 p. 89—207.
- BRÖGGER, W. C.: Ueber die Ausbildung des Hypostomes bei einigen skandinavischen Asaphiden. S. G. U. Ser. C. No. 82 1886 78 pag.
- HANSEN, H. J.: Studies on Arthropoda II. Copenhagen 1925 176 pag.
- HANSTRÖM, BERTIL: Das Nervensystem und die Sinnesorgane von Limulus polyphemus. Lunds Univ. Årsskr. N. F. Avd. 2 Bd. 22 Nr. 5. 1926 78 pag.
- HANSTRÖM, BERTIL: Eine genetische Studie über die Augen und Sehzentren von Turbellarien, Anneliden und Arthropoden (Trilobiten, Xiphosuren, Eurypteriden, Arachnoiden, Myriapoden, Crustaceen und Insekten). K. Sv. Vet. Akad. Handl. (3) IV. 1. 1926 176 pag.
- HOLMGREN, NILS: Zur vergleichenden Anatomie des Gehirns von Polychæten, Onychophoren, Xiphosuren, Arachniden, Crustaceen, Myriopoden und Insekten. Kungl. Sv. Vet. Akad. Handl. Bd. 56 No. 1 1916 304 pag.
- JAEKEL, O.: Beiträge zur Beurtheilung der Trilobiten I. Zeit. deut. geol. Ges. Bd. 53 1901 p. 133—171.
- JAEKEL, O.: Über die Agnostiden. Zeit. deut. geol. Ges. Bd. 61 1909 p. 380—401.
- KINGSLEY, J. S.: The Systematic Position of Trilobites. Amer. Geol. XX 1897 p. 33—38.
- KLÆR, JOHAN: The Lower Cambrian Holmia Fauna at Tømten in Norway. Videnskapsselsk. Skr. Mat.-naturv. Kl. 1916 No. 10 140 pag.
- LINDSTRÖM, G.: Researches on the Visual Organs of the Trilobites. Kongl. Sv. Vet. Akad. Handl. Bd. 34 No. 8 1901 86 pag.
- MOBERG, J. C.: Sveriges äldsta kända Trilobiter. Geol. Fören. Stockh. Förh. XXI 1899 p. 309—348.
- RAW, FRANK: The Development of Leptoplastus salteri (Callaway) and of other Trilobites (Olenidæ, Ptychopariidæ, Conocoryphidæ,

- Paradoxidæ, Phacopidæ, and Mesonacidæ). *Quart. Journ. Geol. Soc.* vol. LXXXI 1925 p. 223—322.
- RAYMOND, P. E.: Beecher's Classification of Trilobites, after Twenty Years. *Amer. Journ. of Sci.* vol. 43 1917 p. 196—210.
- RAYMOND, P. E.: The Appendages, Anatomy, and Relationships of Trilobites. *Mem. Connect. Acad. Arts. a. Sci.* VII 1920 169 pag.
- REED, F. R. COWPER: Notes on the Genus *Trinucleus* Pt. IV. *Geol. Mag. Dec. 6.* vol. III 1916 p. 118—123, 169—176.
- RUEDEMANN, RUDOLF: The Presence of a Median Eye in Trilobites. *New York State Mus. Bull. No. 189* 1916 p. 127—143.
- RUEDEMANN, RUDOLF: The Cephalic Suture Lines of *Cryptolithus* (*Trinucleus* Auct.). *N. Y. St. Mus. Bull. No. 189* 1916 p. 144—148.
- SCHMIDT, FR.: Revision der ostbaltischen Silurischen Trilobiten.  
I. Phacopiden, Cheiruriden und Encrinuriden. *Mem. Acad. Imp. Sci. St. Petersb. (7)* XXX No. 1 1881.  
II. Acidaspiden und Lichiden. *Ibid. (7)* XXXIII No. 1 1885.  
III. Illaeniden (von Gerh. Holm). *Ibid. (7)* XXXIII No. 8 1886.  
IV. Calymmeniden, Proetiden, Bronteiden, Harpediden, Trinucleiden, Remopleuriden und Agnostiden. *Ibid. XLII* No. 5. 1894.  
V. Asaphiden. *Ibid. (8)* VI No. 11 1898.  
VI. Allgemeine Übersicht mit Nachträgen und Verbesserungen. *Ibid. (8)* XX No. 8. 1907.
- SWINNERTON, H. H.: Suggestions for a Revised Classific. of Trilobites. *Geol. Mag. N. S. Dec. VI* vol. II 1915 p. 487—496, 538—545.
- SWINNERTON, H. H.: The Facial Suture of Trilobites. *Ibid. Dec. VI* vol. VI 1919 p. 103—110.
- WALCOTT, CH. D.: The Trilobite: New and old evidence relating to its organiz. *Bull. Mus. Comp. Zool. Harvard.* VIII 1881 p. 192—224.
- WALCOTT, CHARLES D.: 10th Ann. Rep. U. S. Geol. Survey 1891 p. 638.
- WALCOTT, CHARLES D.: *Olenellus* and other Genera of the Mesonacidæ. *Smithson. Misc. Coll. Vol. 53* No. 6 1910 p. 231—422.
- WALCOTT, CHARLES D.: *Dikelocephalus* and other Genera of the *Dikelocephalinæ*. *Ibid. vol. 57* No. 13 1914 p. 345—412.
- WALCOTT, CHARLES D.: Cambrian Trilobites. *Ibid. vol. 64* No. 5 1916 p. 307—456.
- WALCOTT, CHARLES D.: Appendages of Trilobites. *Ibid. vol. 67* No. 4 1919 p. 115—216.
- WALCOTT, CHARLES D.: Notes on Structure of *Neolenus*. *Ibid. vol. 67* No. 7 1921 p. 365—456.
- WARBURG, ELSA: The Trilobites of the Leptæna Limestone in Dalarne with a Discussion of the Zoological Position and the Classification of the Trilobita. *Bull. Geol. Inst. Univ. Upsala XVII* 1925 p. 1—446.
- WESTERGÅRD, A. H.: Sveriges Olenidskiffer. S. G. U. Ser. Ca No. 18 1922 205 pag.
-