THE ONTOGENY OF *OLENUS GIBBOSUS*

BY

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WITH ONE PLATE

Introduction.

When collecting in the alum shales at the Evjeviken[1] in the parish of Ringsaker during the summer of 1925, the author found a quite small loose piece of fine-grained black limestone, which showed on its surface the cranidium of an *Olenus*. By chiseling up the piece, there was found a number of cranidia, free cheeks and pygidia of the same form (pl. fig. 14 a—c), which proved to be the Upper Cambrian species *Olenus gibbosus* (WAHLENB.), agreeing with the description and illustrations given by WESTERGÅRD l. c.[2]. In Norway BRØGGER has cited this form from the Langesund—Skien District, (1882 l. c. p. 373, 1884 l. c. p. 257).

On examining the material by means of a binocular microscope, there was further found a rather great number of well preserved embryonal specimens, some of which are depicted and described in the present paper. Judging from the fact that only the species mentioned is represented among the mature specimens of the rock, and further from the succession of stages demonstrated below, one may safely conclude that also the embryonal forms belong to this species.

The present little study has been carried out in the Paleontological Museum, Oslo. To Professor J. KIÆR, Director of the Museum, and to Professor O. HOLTEDAHL the author wishes to express his heartiest thanks for valuable advice and help during the work.

[1] On the situation of this locality see KIÆR l. c., the sketchmap text fig. 1.

[2] See References p. 329.

Description of the larval specimens.

1. Pl. fig. 1.

The outline is circular, the length 0,35 mm from the anterior margin to the end of the occipital lobe. The body is rather strongly convex, and is provided with an axis, which is limited by distinct dorsal furrows, and by transverse furrows divided into five lobes. The frontal lobe widens anteriorly and passes at the front into tapering ridges. At each side of the frontal lobe, just behind the ridges mentioned, another ridge runs in a curved line, reaching the margin as far backwards as the first furrow of the axis. It is obvious that those are the eye ridges, which fact is clearly shown from the later stages. The three following lobes have a somewhat square outline, they are almost equal in size, each of them being smaller than the frontal lobe. The occipital lobe is small, tapering posteriorly. It is to be remarked that no rim has been found along the margin.

2. Pl. fig. 2.

The length from the anterior margin to the end of the occipital lobe is 0,37 mm. The outline and shape of the body agree with those of the preceding stage; the posterior part, however, shows different characters. From the occipital lobe there runs to each side a ridge in a strongly backwards directed curve, meeting the posterolateral margin at a pointed angle and continuing in a fine downwards directed spine. Behind the occipital lobe there is still another lobe almost of the same size. The postcephalic part surrounding this lobe is curved strongly downwards between the posterior angles.

3. Pl. fig. 3 a & b.

The outline of the cephalon is circular except at the posterior border. The length is 0,40 mm. The cephalon is not evenly convex, especially its anterior and anterolateral parts being curved down. The anterior part of the frontal lobe continues at each side in a tapering, quite short process. The eye ridges in this stage follow the margin in their lateral parts. The ridge marking the posterior termination of the cephalon turns backwards

at a rather marked angle, proceeding into a pair of spines directed downwards at about 45°. From the said angles another ridge runs along the margin for about half the length of the cephalon. The postcephalic part of the animal is lying in the plane of the two spines. It is provided with an axis, which seems to be divided into two lobes.

4. Pl. fig. 4 a & b.

In this and the following stages only the cephalon is found. The outline is circular or ovate, except at the posterior border, which is straight. The length is 0,43 mm. The anterior and anterolateral parts curve strongly down. The frontal lobe shows an impression at the midst of the anterior margin and a pair of frontal furrows, dividing the lobe into two parts but not meeting across the middle part. The anterior part of the lobe does not, as in the preceding stages, pass into tapering processes, but has a distinctly marked lateral margin. Along the anterior margin of the cephalon, at both sides of the frontal lobe, there is seen a very narrow ridge, which is of even width. There is no indication of a ridge in front of the axis. The eye ridges commence just anterior of the frontal furrows, they are stronger than the ridges in front of them. In the inner parts they run parallel to the ridges mentioned above and the area lying between, in the outer parts they follow the margin. The posterior termination is marked by a rather strong ridge; at the posterior angles there are strong spines lying in the plane of the cephalon. The ridges at the posterolateral margin reach as far forwards as the midst of the second lobe. The test has a punctuate sculpture upon the cheeks.

5. Pl. fig. 5 a & b.

The cephalon, or as it is now to be termed, the cranidium, free cheeks being without doubt developed, has an outline rather similar to that of the adult with a straight anterior margin, which is, however, rather narrow. The length is 0,52 mm. The axis is strongly convex, especially in the middle lobes. The frontal lobe is similar to that of the preceding stage, but narrows only slightly posteriorly. The first furrow of the axis

is shallower than the two behind it. The eye ridges and the ridges along the anterior margin at each side of the frontal lobe agree in general with those of the preceding stage. The posterior margin curves backwards at the sides, from the posterior angles proceed very fine spines. The greatest width is found about one third of the whole length anterior of the posterior end; the ridges along the posterolateral margins run for the same distance.

6. Pl. fig. 6.

Length 0,53 mm. The width of this specimen, and especially the width of the axis, is much greater than in the preceding stage. Furthermore the present stage, and also the following ones, differ in showing no spines at the posterior angles.

7. Pl. fig. 7 a & b.

Length 0,63 mm. As in the preceding stages especially the anterior and anterolateral parts of the cranidium are curved down. The occipital lobe not taken into consideration, the axis narrows anteriorly, a feature in which this stage differs from the smaller ones. The frontal lobe is provided with frontal furrows, the impression at its anterior margin is also still seen. The first furrow of the axis is shallower than the two behind it. The anterior border of the cranidium is curved slightly forwards; there runs a ridge along the entire margin. The front of the axis approaches very closely to the said ridge. The nicely curved eye ridges thicken in their lateral parts to form eye lobes. The posterior border curves as usual backwards at the sides; the cranidium attains its greatest width outside the third furrow of the axis. At the posterior angles there is a flattened area.

8. Pl. fig. 8.

Length 0,70 mm. The specimen agrees with the one just described fairly well in shape, but shows in some features distinguishing characters. The cranidium is somewhat more convex. The axis narrows more strongly towards the front. The occipital lobe is strongly pointed and protrudes rather far behind the posterior margin. The posterior border furrows are now rather marked; at the posterior angles there are flat brims, which grow narrower inwards and forwards.

9. Pl. fig. 9.

Length 0,71 mm. The cranidium is yet more convex than that of the precedingstage. The axis is broadest in the second lobe, narrowing both to front and back. There is no impression at the anterior margin. Frontal furrows are present. The three following furrows are directed backwards from the sides of the axis, and are shallower in the middle part. The posterior of them is most deeply impressed. The axis approaches very closely to the anterior border of the cranidium, which is curved forwards. The eye lobes are more flat and broad than in the two preceding stages. The posterior border curves backwards towards the sides; the greatest width of the cranidium is now found just in front of the posterior angles, outside the midst of the first axial lobe.

10. Pl. fig. 10.

Length 0,94 mm. The cranidium is strongly convex, like in the specimen just described; the cheeks are now highest at some distance from the dorsal furrows. The axis is limited by almost parallel sides and is gently rounded in front. The frontal lobe is short. The front of the axis is retreated from the anterior border, leaving a preaxial field, which is strongly curved down and is also convex from side to side. Also in this specimen the anterior border is curved forwards and the posterior borders are curved backwards at the sides. The greatest width of the cranidium is found, however, between the very posterior angles.

11. Pl. fig. 11.

Length 1,00 mm. The cranidium is strongly convex in the cheeks, but in the other parts it is less convex than the specimen described just above. The axis narrows towards the front. The frontal furrows are present inside the eye ridges. The three furrows of the axis turn backwards from the sides of the latter and grow progressively fainter from the back to the front pair. In the middle part they are shallow. The occipital furrow is as always straight and distinct. The anterior border of the cranidium is straight, and the preaxial field is developed as an almost flat brim. The eye ridges are separated from the axis by the deep dorsal furrows and are swollen in their middle part. The

strongly curved eye lobes are long and distinctly marked out from the cheeks. The posterior borders are as before directed backwards at the sides, the border furrows widen strongly outwards. The test has a punctuate sculpture on the cheeks, like in all stages from stage 4, but the axis is as always smooth.

While the development of the head is shown rather well from the stages described, nothing is found to demonstrate that of thorax and pygidium. A single fragment is present, (pl. fig. 12), showing three segments, probably from the pygidium, as they narrow posteriorly. They have a strongly convex axis; and each of the pleurae has a broad furrow, running parallel to the margin.

Larval hypostoma are found, the smallest of which is about 0,45 mm long and 0,30 mm broad (pl. fig. 13). It has an ovate posteriorly narrowing central body, which is separated from the marginal brim by a furrow. The brim is narrow at the sides and widens posterior of the central body, where it is curved rather strongly down. It is surrounded by a marginal ridge. The hypostoma of the adult is very strongly convex, the furrow being almost obliterated (pl. fig. 14 d).

Summary of the larval development.

The stages of development in trilobites are usually divided into the protaspis stages, the nepionic and neanic, ephebic and gerontic stages. Of the stages described above, the three first belong to the protaspis, probably also the fourth one. As nothing is known of the development of the thorax, it cannot with certainty be decided to which stages the following are to be referred; perhaps the specimens 5 to 9 belong to the nepionic, while 10 and 11 belong to the neanic stages.

Making a brief summary of the development in the different parts, the following features may be emphasized.

The anterior border is made out in the three first stages by the frontal lobe and the ridges proceeding from its anterior part. In stage 3 these processes are very short, and in stage 4 we have narrow ridges of even width at both sides of the distinctly limited frontal lobe. In the the same stage,

it is to be noted, the frontal furrows and the impression upon the frontal lobe appear. In the stages 5 and 6 there are the same conditions, while in stage 7 and the following ones there is a complete anterior border also in front of the axis. — One may suppose that the parts which are to form the anterior border, were bent downwards to the ventral side in the first stages and remained bent down for a longer time in front of the axis; perhaps they were also quite soft in the first stages, where the processes from the frontal lobe serve to strengthen the margin. When the evenly wide ridges at the sides of the frontal lobe first appear in stage 4, they are much less strong than in later stages.

The eye ridges are present from the very first stage; they differentiate into the interior parts, taking more and more a straight outward direction, and the exterior parts, making the broad, curved eye lobes. A swelling of the ends of the ridges is seen for the first time in stage 7. The long eye lobes of stage 11 are remarkable in contrast with the short ones of the adult. When a pair of frontal furrows are present, the eye ridges commence in front of them.

The axis is in the first stages characterized by the anteriorly widened frontal lobe, in stage 6 all the lobes are of even width; the frontal lobe is longer than the others in all the stages just mentioned. In the stages 7 and 8 all the lobes are of almost equal length, the axis, except the occipital lobe, narrows towards the front; in stage 9 the second lobe is the broadest. Finally, in the stages 10 and 11, the axis has assumed somewhat the same shape as in the adult, being yet longer in proportion to the width. Here the frontal lobe has grown short, and at the same time a rather broad preaxial field has appeared. The preaxial field seems to get broader, while the axis becomes shorter in proportion to width, its anterior part being reduced. In the adult the eye ridges are directed slightly forwards, a fact which may indicate a backward move of the anterior margin of the axis.

The facial sutures are quite absent in the two first stages. In the stages 3 and 4 at least their first traces are seen. The anterolateral margins of the cephalon are here strongly

curved downwards, and in their outer parts the eye ridges run along this curved-down margin. The posterolateral margins are provided with a ridge. Perhaps this ridge was continued on the free cheek; it is at least possible that free cheeks were present. In the following stages the posterior ends of the facial sutures move more and more backwards. In stage 6 the marginal furrows run for a good distance in front of the posterior angles of the cranidium. In stage 9 the sutures still seem to commence a little in front of the posterior angles, as the posterolateral margins of the cranidium also here have an inward direction. In the stages 10 and 11 the posterior ends of the suture finally reach the posterior angles of the cranidium, and the free cheeks probably take the same form as in the adult.

The occipital segment shows a very rapid growth in the stages 2—4, in the last of which a straight posterior margin has been formed. In all stages up to stage 9, the posterior margin is still narrower than the part of the cranidium lying anterior of it, while in the stages 10 and 11, as in the adult, it is the broadest part of the cranidium. The intergenal spines are present in the first stages, except in the very earliest; in stage 5 they are faint and then disappear, but their loci are marked by a pointing backwards of the posterior angles.

Comparison to some other forms.

The structure and development of the trilobites has been recently discussed, with a summary of the hitherto known facts, in the works of ELSA WARBURG and F. RAW. In the following the present writer will compare the forms described above with some previously known.

Of *Liostracus Linnarssoni* larvae were depicted by Prof. BRØGGER (1875 l. c., p. 580, pl. 25), some protaspis stages of the same form have been described and figured by E. WARBURG (l. c.p. 24—25, text-fig. 6). They are quite similar to those here described, only it seems that the processes from the frontal lobe and the eye ridges are united to make what Dr. WARBURG calls the larval ridge. The said author mentions how in the specimens depicted in text-fig. 6 b & c_1 the inner posterior

parts of the larval ridges are more swollen than the other parts, and are also separated from the frontal lobe; and then continues: "and in some specimens it looks as if, at least near the glabella, there were indistinct furrows in front of them." These swollen posterior parts of the larval ridges, separated by the indistinct furrows, seem to represent the eye ridges.

Of the larvae of *Leptoplastus Salteri* described by RAW l. c., those of degree 1 (pl. XVI fig. 1 & 2) correspond in some respects with the stage 6 here described; the axis is said to reach the front of the cephalon, while in degree 3 there is a distinct marginal rim in front of the axis. In the structure of the axis, the first degrees of RAW correspond with the stages 7 and 8 here described. In degree 7 (pl. XVII fig. 11—13) the frontal lobe is very short and there is a distinct preaxial field, as is the case in the stage 10 here described.

The larvae of various olenids figured by Prof. HOLTEDAHL l. c. seem to agree with those of the stages 7—9 of this paper.

CHR. POULSEN (l. c. text-fig. 22) has figured larvae of *Peltura scarabæoides*, the protaspis form of which is remarkable in being quite different from those of the olenid form above described.

Remarks on the phylogeny of Olenus.

In the stages 7 and 8 it is interesting to note that the axis is rather similar to that of a *Strenuella*. In both instances the frontal lobe is somewhat of the same length as the other lobes and the axis narrows anteriorly, being rather long and slender, if yet more so in the larval forms just mentioned. But in general, a *Strenuella* form, as those from Tömten described by Prof. KIÆR (l. c. pl. IV & V), shows the same structure of the axis as these *Olenus* larvae. This fact may perhaps be of value in a discussion of the phylogeny of the *Olenidae* and related forms.

Summary of the contents.

The present paper deals with some embryonal forms of *Olenus gibbosus*, found in a piece of limestone from Ringsaker, Norway.

11 larval stages are described, which give a fairly complete information of the development of the cranidium.

A summary is made of the changes taking place in the different parts, thus is demonstrated the development of the anterior border and the eye ridges, of the axis and the preaxial field, and of the facial sutures and the occipital segment with the intergenal spines.

A comparison is made with embryonal forms of some related species.

Finally, a phylogenetical significance is suggested for the stages 7 and 8, because of their similarity to *Strenuella* in the structure of the axis.

Paleontological Museum, Oslo, Nov. 1926.

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Printed, March 8th, 1927.

Explanation of the plate.

The figures are photographed or drawn by the author, the photographs have been retouched by Miss L. MONSEN.

The originals are all in the Paleontological Museum, Oslo.

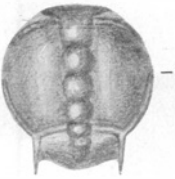
Olenus gibbosus, (WAHLENB.).

Fig. 1. Larval specimen stage 1, × 40.
» 2. » — » 2, × 40.
» 3 a. » — » 3, × 40.
b. » — » × 30.
» 4 a. » — » 4, × 40.
b. » — » × 30.
» 5 a. » — » 5, × 30.
b. » — » × 30.
» 6. » — » 6, × 30.
» 7 a. » — » 7, × 30.
b. » — » × 25.
» 8. » — » 8, × 25.

Fig. 9. Larval specimen stage 9, × 25.
» 10. » — » 1,9 × 15.
» 11. » — » 11, × 12,5
» 12. Larval segments ca. × 25.
» 13. Larval hypostome × 30.
» 14 a—d. Adult.
a. Free cheek, somewhat defective at the inner side × 3,3.
b. Cranidium × 3,1.
c. Pygidium, with one spine broken. × 3,3.
d. Hypostome × 3,2.

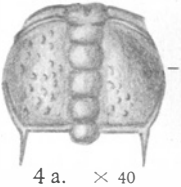
1. ×40

2. ×40



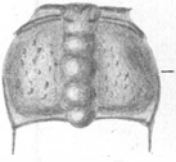
3 a. ×40

3 b. ×30



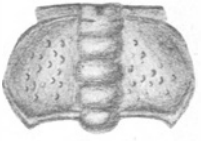
4 a. × 40

4 b. ×30

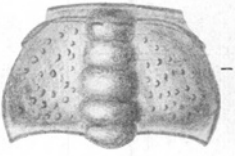


5 a. ×30

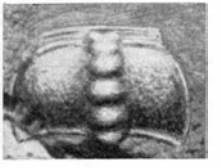
5 b. ×30



6. ×30



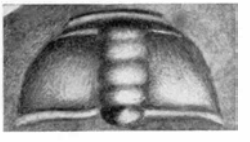
7 a. ×30



7 b. ×25

8. ×25

9. ×25



10. ×15

12. ca. ×25

11. ×12,5

13. ×30

14 a. ×3,3

14 b. ×3,1

14 c. ×3,3

14 d. ×3,2

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