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Development of Squilla oratoria de Haan.
I. Change in External Form.

By

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With Plate XVIII and 3 Text-figures.

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Introduction.

The development of the Stomatopoda has never been described. This seems to be rather a striking fact, bacuse, first, among the whole of the Malacostraca only the rare and peculiar Anaspidacea shares with that order such a situation, second, the animal belonging to that order is by no means uncommon in any part of the tropical, subtropical and temperate seas in the World, and third, the larval stages have been familiar to us for a fairly long time. This study was undertaken to fill this gap and to contribute something to our knowledge of this interesting group of the Crustacea. The present note deals chiefly with the change in the external form of the embryo, and this will be followed by another concerning the internal change. My best thanks are due to Professor S. Goto of the Tokyo Imperial University who suggested this work to me and also to the staff of the Fishermen's Association of Koyasumura, Yokohama, who helped me in getting material.

Material and Methods.

The material used in this work was obtained from *Squilla oratoria* de Haan caught in Tokyo Bay by men of Koyasumura, a fishing village at the east end of the city of Yokohama during June 7-30, 1918. The mantis-shrimp lives in great abundance in that bay, and the fishermen of the villages around the bay go out throughout the year to catch them together with plaices, swimming crabs and various kinds of shells with a certain kind of fishing implement somewhat like a dredge. They then send the shrimps to the markets in Tokyo and Yokohama where people eat them fried or boiled, which is one of the best sea-grills. While I was staying in the office of the Fishermen's Association of that village to collect the material for my research, more than two hundred fishing boats used to go out every morning, and they brought me back the egg-clusters in the evening, whenever they happened to fish mantis-shrimps carrying eggs, and thus furnished me with the material.

As Giesbrecht (1910) mentions, the egg-cluster of *Squilla* is of the shape of a flat disc, about 10 cm. across, the eggs being arranged in three to five layers. By weighing several small portions of a cluster and counting the eggs in each portion, I could estimate roughly the number of the eggs in the whole cluster to be 43,000-50,000, which number approximates the 50,000 given by Giesbrecht. The mother shrimp keeps the cluster on her ventral side, holding it with her three posterior pairs of maxillipeds, until the larvae hatch out. Such shrimps begin to appear in that bay usually in the middle of May, and increase in number toward the end of the same month and are fairly abundant in June. They become rarer at the beginning of July and they are usually no longer found at the end of the same month, although, according to some of the fishermen of the village, mantis-shrimps carrying eggs may be caught from time to time in August.

The egg of *Squilla* measures about 0.5 mm. in diameter and is covered with a fairly tough chorion. All the eggs in the same cluster are nearly of the same stage of development. No aquarium with running seawater supply being accessible to me there, I tried several measures to develop the eggs obtained, but in vain: therefore I could not get any exact idea of the length of the embryonic period. But, as far as could be judged from the time of the appearance of the youngest larvae in plankton in the bay and the neighboring seas, the period seems to be 4-6 weeks, which is shorter than the 10-11 weeks given by Giesbrecht for *S. mantis* of Naples.

The egg-clusters brought by the fishermen were cut into small pieces and fixed with hot or cold acetic sublimate solution, boiled water, Kleinenberg's solution, picro-acetie or picric acid saturated aqueous solution. Of all these, the hot acetic sublimate solution gave the best results. Especially for removing the chorion, which is necessary for further treatments, this reagent, or boiled water is the most effective. When eggs, fixed with either of these methods, are put from 70-90 percent alcohol into water, water instantly penetrates in through the chorion, filling the space outside the egg-body, and makes it easy to prick off the chorion with needles. The chorion having been removed, the eggs were stained with diluted Delafield's hematoxylin, clarified in clove or cedar oil, and mounted in balsam. The stain gave a clearer figure of the embryo than borax-carmine.

In the whole course of the embryonic development of *Squilla* the following features seem to be the most noteworthy of all the facts observed in toto:

1. that, on account of the large amount of yolk contained in the egg, the embryo is in its early stages quite flattened;

2. the presence of a distinct egg-nauplius stage;

3. the presence of a stage with seven pairs of appendages—five cephalic and two thoracic;

4. that the thoracico-abdominal region of the body is kept turned over on the ventral side throughout the embryonic stages;

5. the absence of the "dorsal organ".

In showing these features in the embryonic stages, the Stomatopoda approache the Decapoda, Schizopoda and Nebaliacea. With the Decapoda it shares the first four (1-4) features' with the Schizopoda the first two (1, 2.) and with the Nebaliacea all except the fourth (1, 2, 3, 5) features. This fact evidently shows that the Stomotopoda is more closely related to these orders than to the remaining orders of the Malacostraca, namely, Isopoda, Amphipoda and Cumacea. Especially noteworthy is the resemblance between the Stomatopoda and the Nebaliacea; and this affords another support for the opinion of Grobben (1919), who gives special emphasis to the affinity of these two orders. Further discussion as to the systematic position of the Stomatopoda will be deferred to the concluding chapter of the next paper.

Stage 1 (Blastula stage, Text-fig. 1).

No egg in the segmentation stage came under my examination. The earliest stage obtained was the blastula-stage, in which the whole surface of the egg had been divided into 200-300 cells and no nucleus was found in any deeper region. The surface of the egg looks alike everywhere, showing no differentiation whatever.

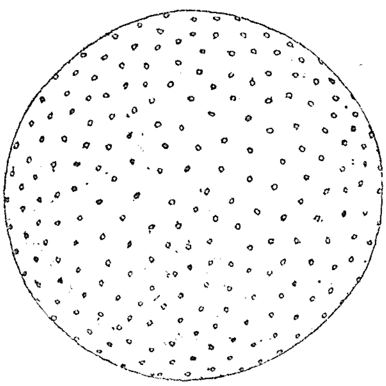
Stage 2 (Text-fig. 2).

The number of the nuclei is soon multipied by division. This process goes on more actively on one side of the egg than on the other, so that the former soon comes to be more densely nucleated than the latter. At a point in the periphery of this more densely nucleated hemisphere, a disc-shaped gathering of nuclei becomes apparent—this is the first ruaiment of the thoracico-abdominal plate (*th. ab*). Here, especially at the center of the disc, one can observe some nuclei situated somewhat beneath the surface of the egg. From this rudiment of the thoracico-abdominal plate forward, there soon appears a pair of band-like gatherings of nuclei diverging at an angle of 60 degrees, so that the embryonic rudiment looks like the letter V.

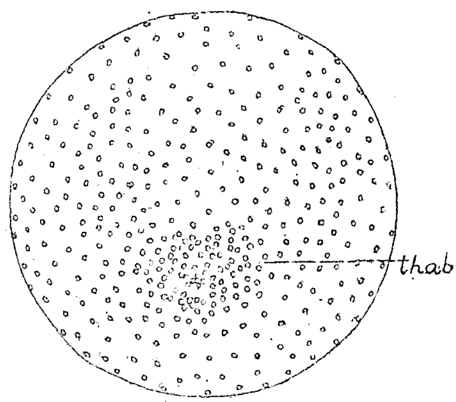
Stage 3 (Pl. XVIII, Fig. 1).

The anterior end of each arm of the V becomes densely nucleated and marks out the optic disc (*op*). In the meantime the thoracico-abdominal plate becomes more and more densely nucleated. One can observe by regulating the focus that the central part of the plate is two or three cell thick. This part evidently represents the blastopore of other crustacean eggs, but no invagination occurs in this case. The embryonic area is the largest in extension in this stage, occupying almost the whole hemisphere of the egg; soon afterwards it begins to contract, and keeps on doing so to the egg-nauplius stage.

In each arm of the V, just in front of the thoracico-abdominal plate, appears the first rudiment of the mandible (Figs. 1, 2, *md*) as a



Text-fig. 1. Stage 1.
Blastula-stage. ×100.



Text-fig. 2. Stage 2.
Rudiment of thoracico-abdominal plate formed. ×100.

gathering of nuclei a little denser than in the region either in front of or behind it. This appendage is the first to be formed of the three pairs of appendages of the egg-nauplius.

Stage 4 (Fig. 2).

Soon there appear in each arm of the V, between the optic disc and the mandible, the rudiments of the antennule (*an. 1*) and antenna (*an. 2*) almost at the same time, but the former a little earlier. The optic discs are connected by a transverse agglomeration of nuclei, which transforms the V into a triangle. Meanwhile the embryonic area has been contracted a little.

Stage 5 (Fig. 3).

The embryonic area keeps on contracting, while the nuclei multiply by division very rapidly. As the result of these two changes going on hand in hand, the entire embryonic area comes to be crowded with nuclei and the triangle becomes solid. On the median line of the embryo, on the level between the antennules and antennæ, appears a crescent-shaped depression with the concave side directed forward—this is the stomodeal depression (*st*).

Stage 6 (Egg-nauplius stage, Fig. 4).

The embryo is now in the "nauplius" stage. The embryonic area having continued to contract to this stage, the embryo is now more or less smaller in size than at any of the preceding stages. It looks very much like the embryo of the Decapoda (Reichenbach, 1888, Herrick, 1891) of the same stage. The embryo is provided with a pair of eyes (*op*) and three pairs of appendages, namely, antennules (*an.* 1), antennæ (*an.* 2) and mandibles (*md*). The eyes are directed obliquely forward, the appendages more or less backward, the antennules the least and the mandibles the most. They are all simple and stump-like in appearance. The stomodeal depression (*st*) is defined now very clearly. The thoracico-abdominal plate (*th. ab*) is roughly square in shape, with its posterior margin a little longer than any of the other margins. The anterior margin is elevated slightly above the surface of the egg, on account of the thoracico-abdominal fold developing underneath. At a short distance behind this margin, on the median line, is shown the anus as a clear spot (*a*).

Stage 7 (Fig. 5).

The antennules and antennae increase in length rapidly and become spatulate, while the mandibles remain small and rather indistinct. The mouth is transferred backward to the level slightly behind the base of the antennæ and its anterior lip begins to form the labrum. The thoracico-abdominal plate is elongated considerably by the division of the cells at its posterior end, until the length of the embryo comes to cover the entire hemisphere of the egg. At the same time the fold grows deeper and lifts up the whole plate above the surface of the egg.

Stages 8 (Stages with 7 pairs of appendages, Fig. 6);
Stage 9, (Figs. 7 a-c).

The eyes, which were about of the same size as the appendages in the egg-nauplius stage, grow rapidly and become much stouter than any of the appendages. The terminal part begins to be differentiated into the primordium of the corneal region, while the basal part becomes the rudiment of the ganglion (*p. c*). The antennules and antennae are elongated and curved backward. The mandibles are now low mammiform processes (Figs. 7 b & c, *md*). Behind these appendages are the rudiments of the first and second pair of maxillæ (*mx. 1, mx. 2*) and of the first and second pair of maxillipeds (*mxP. 1, mxP. 2*). The first maxillæ are likewise mammiform and lie close to the mandibles. All of the remaining three pairs of appendages are situated near the topographically hind end of the body. The second maxillæ are very small at the beginning of this stage; but soon they grow up nearly to the size and shape of the first maxillæ; only they are a little more slender. The first and second pairs of maxillipeds are about equal in size, sausage-shaped; the first pair are directed laterally and the second anteriorly. The thoracico-abdomen shows some segmentation, which change is apparently initiated at the basal end and proceeds towards the distal. One can distinguish about eight segments altogether (Fig. 7, b). The distal end is furcated.

To describe some of the internal structures which can be observed in toto preparations, the heart-tube has begun to develop along the median line of the thoracico-abdomen. The three anterior pairs of ganglia belonging to the optic, antennnlar and antennal segment are going to form together the cerebral ganglion; they are to be called protocerebrum, deuterocerebrum and tritocerebrum respectively according to Reichenbach's terminology (1888) (Pl. XVIII Fig. 6, Fig; 7 a, *p. c, d. c, t. c*). These ganglia are all square-shaped, more or less irregular. The autennal ganglion on either side is connected backward with the ventral nerve-cord. The latter is swollen into a ganglion in each segment at the base of the appendage; and between the ganglia of the same segment is a transverse strand connecting them with each other, so that the ventral nervous system is ladder-shaped. In addition to the ganglia present in each segment, there is a pair of similar ganglia situated just behind the mouth and in front of the mandibular ganglia. The mandibular ganglia are the largest of all the ganglia found in the ventral cord. The ganglia of the last three pairs of appendages lie close together near the topographically hind end of the body.

As the embryo develops, its length comes to cover more than the hemisphere of the egg. The eyes become very prominent pear-shaped bodies. In each eye one can distinguish four parts, of which the corneal region forms the most distal part. I call this more advanced stage, Stage 9.

Stage 10 (Figs. 8 a-c).

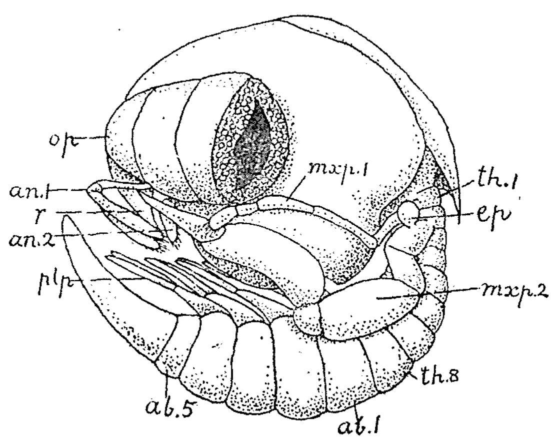
The eyes become strikingly large, and pigment appears in the center of the corneal region, forming a distinct crescentic shape. Between the eyes on the median line, is a process of the shape of a wedge with the apex truncated and turned backward—the rudiment of the rostral spine (*r*). Behind it and a little in front of the center of the procerebrum, there is an ocellus (*oc*) formed by the union of the two halves, one belonging to each side. The antennule (*an.* 1) increases in length; it consists of a protopodite made up of two short segments and an exopodite and an endopodite. The distal end of the exopodite is notched, which evidently marks the division of the exopodite into two flagella in the larval and adult stage. Some setae have developed on the apices of the exo- and endopodite. The antenna (Figs. 8 a & c. *an. 2*) is much longer than the antennule; it consists of four segments, of which the ultimate segment is the longest and spatulate in shape, the penultimate very short, the basal two somewhat longer and about equal to each other. Behind the antennæ and in front of the mouth, is the labrum, now clearly defined. The mandibles and two pairs of maxillæ are grouped together behind the mouth, and all are of the shape of a plate. Both the maxillipeds have grown a great deal. The first maxilliped (*mxp.* 1) is five-segmented; the basal segment is the shortest of all, and the second to fifth are of about the same length; the fifth segment is pointed something like a claw. The distal segments lie nearly parallel with the distal part of the antenna. The second maxilliped (*mxp.* 2) is by far the largest of all the appendages; six segments may be distinguished: the basal the shortest, the second a little longer, the third very much longer, the fourth very short, the fifth the longest and stoutest, and the sixth of medium length and pointed like a claw.

In the thorax one can distinguish eight segments, and in the abdomen five; the latter bear four pairs of pleopods, (Figs. 8 a-c, *plp*) each with a broadened and bifurcated apex.

The telson (*t*) reaches the level very close to the antennæ. On the antero-dorsal side of the thorax, the rudiment of the carapace may be discriminated.

Stage II (Text-fig. 3).

This is the last embryonic stage ready to hatch out. It is almost the same in appearance as Giesbrecht's "Propelagisches Stadium 1."—



Text-fiig. 3.
Stage II. Last embryonic Stage.
×100.

ab. 1.	First abdominal segment.
ab. 5.	Fifth abdominal segment.
an. 1.	Antennule.
an. 2.	Antenna.
ep.	Epipodite.
mxp. 1.	First maxilliped.
mxp. 2.	Second maxilliped.
op.	Eye.
plp.	Pleopod.
r.	Rorstral spine.
th. 1.	First thoracic segment.
th. 8.	Eighth thoracic segment.

the first larval stage. The yolk has been much reduced; still the anterior part of the body is hump-like owing to the pretty large amount of yolk contained. The carapace is provided with a rostral spine (*r*) with the tip turned antero-ventally and also with a postero-median acute spine directed posteriorly. The thorax comprises eight well-defined segments. In the abdomen the anterior four segments are already well differentiated; the fifth (*ab. 5*) is still only half as long as the preceding segment and the sixth is closely attached to the telson, and can be distinguished only in clarified material.

The pigment in the corneal region has increased a good deal; the ommatidia have been developed fairly well. In the antennule (*an. 1*) the peduncle has become more slender; it is now divided into three segments. The antenna (*an. 2*) is segmented more definitely than in the preceeding stage.

Of the maxilliped, the first (*mxp. 1*) has been elongated considerably; it is now five-segmented, the last segment of the preceding stage having been divided into two; the second segment is the longest of all the five. The basal segment of the second maxilliped (*mxp. 2*) has developed an epipodite (*ep*). Each of the four pairs of pleopods (*plp*) consists of a protopodite, an exopodite and an endopodite, all well developed.

August, 1923.

Explanation of Plate XVIII.

LIST OF ABBREVIATIONS.

a.	Anus.	*oc.*	Ocellus.
ab.	Abdomen or Abdominal segment.	*op.*	Eye.
an. 1.	Antennule.	*p. c.*	Protocerebrum or Optic ganglion.
an. 2.	Antenna.	*plp.*	Pleoped.
d. c.	Deuterocerebrum or Abdominal ganglion.	*r.*	Rostral spine.
h.	Heart.	*st.*	Mouth.
md.	Mandible.	*t.*	Telson.
mx. 1	First maxilla.	*t. c.*	Tritocebrum or Antennal ganglion.
mx. 2.	Second maxilla.	*th.*	Thorax.
mxp. 1.	First maxilliped.	*th. ab.*	Thoracico-abdominal plate.
mxp. 2.	Second maxilliped.		

(All figures enlarged 100 times natural size).

Fig. 1. Stage 3. Optic discs and rudiments of mandibles formed.

Fig. 2. Stage 4. Rudiments of antennules and antennae formed.

Fig. 3. Stage 5. Embryonic area has been contracted; rudiment of mouth formed.

Fig. 4. Stage 6. Egg-nauplius stage.

Fig. 5. Stage 7. Later egg-nauplius stage.

Fig. 6. Stage 8. Stage with 7 pairs of appendages.

Figs. 7, a-c. Stage 9. Later stage with 7 pairs of appendages. (a) View with mouth in front. (b) View with thorax and abdomen in front, c. Side-view.

Figs. 8, a-c. Stage 10. Embryo with pigment in eyes. (a) View with cerebrum in front. (b) View with thorax and abdomen in front, c. Side-view.

Fig. 1.

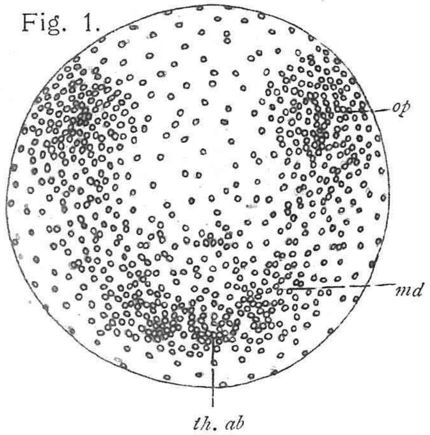


Fig. 2.

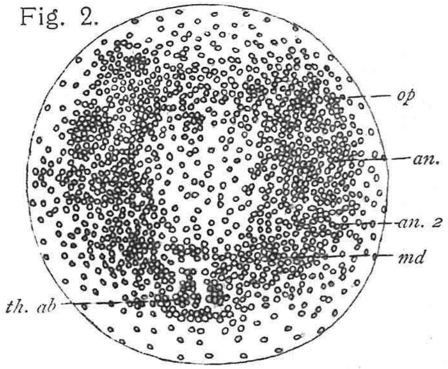


Fig. 3.

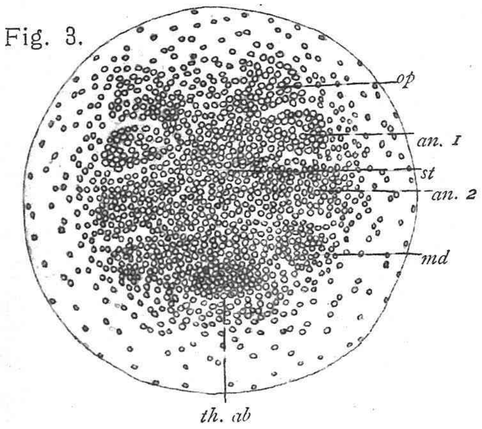


Fig. 4.

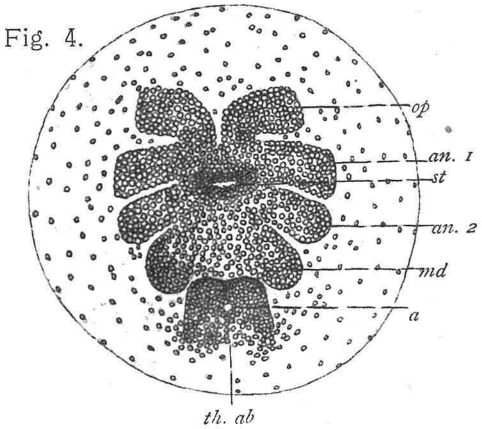


Fig. 5.

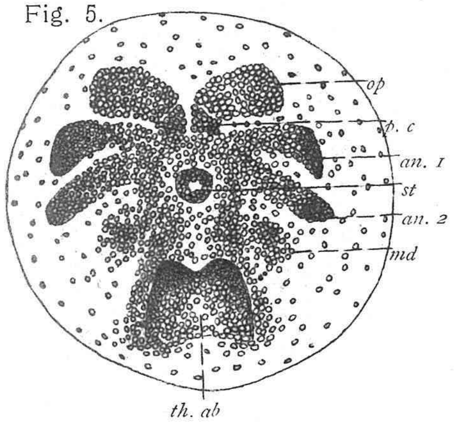


Fig. 6.

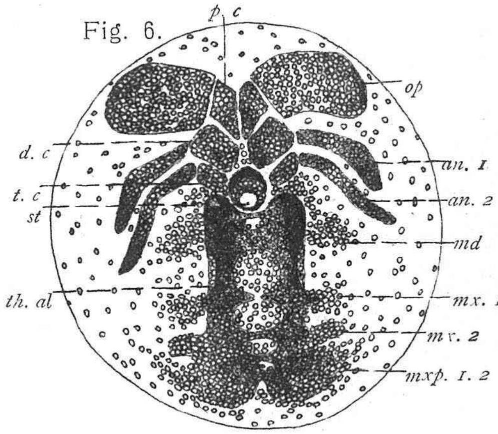


Fig. 7. a

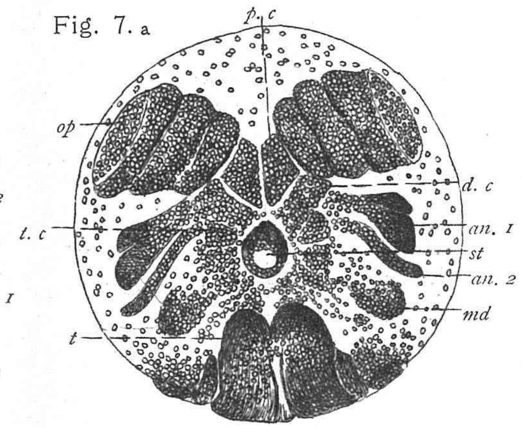


Fig. 8. b

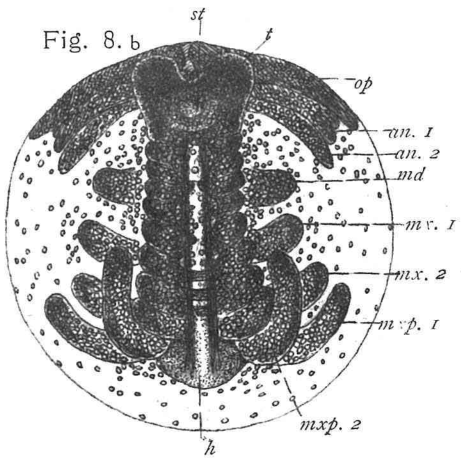


Fig. 7. c

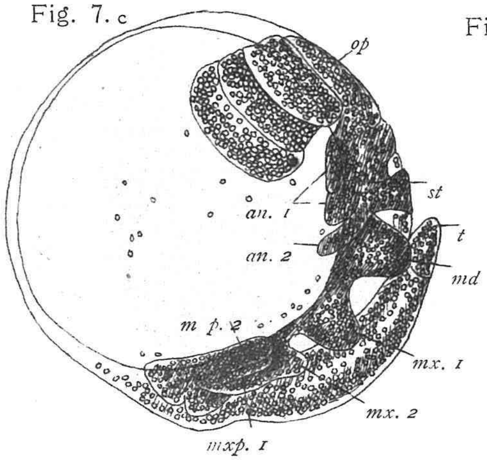


Fig. 8. a

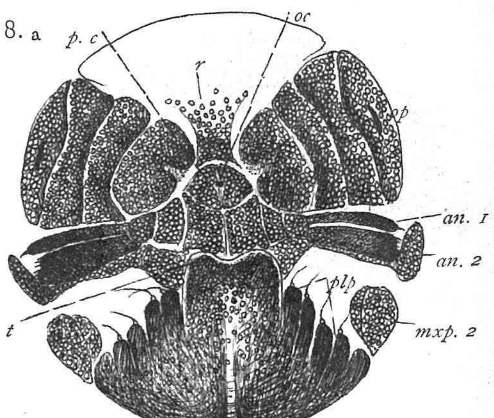


Fig. 8. b

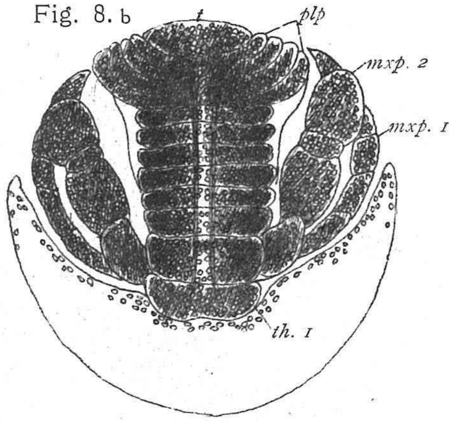
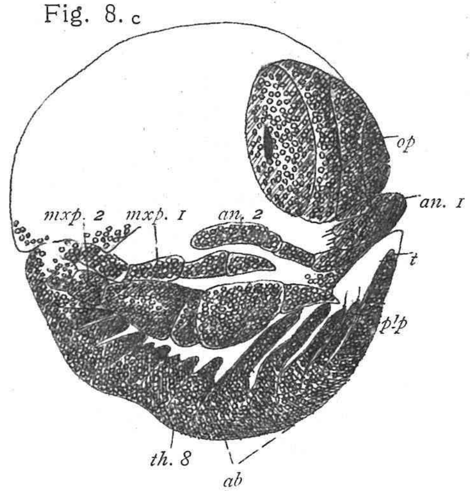


Fig. 8. c



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T. Komai: Development of Squilla.