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Reorganization in Regenerating Pieces of Coeloplana.

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With Plate XVIII and 16 Text-figures

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Contents

Introduction

In 1880 EIMER reported that Beroë has no regenerative power, and the theory that the adult Ctenophore has no power to regenerate missing parts has since been as widely accepted among zoologists as the fact that the development of its egg is of mosaic character. However, CHUN (1892) and MAYER (1912) have pointed out that some Ctenophores possess regenerative power, and MORTENSEN (1913) has confirmed it in *Bolina infundibulum* and *Pleurobranchia pileus* as well as in *Beroë cucumis*. According to MORTENSEN the regeneration of such essential organs as the statocyst and the tentacles is as easy a task for Bolina as the regeneration of other parts of the body. But still more astonishing is the fact that when the animal is divided into two parts, whether in the longitudinal or in the transverse direction, each half regenerates the other half and gives rise finally to a complete new animal, including the missing number of comb-plates. Quite recently ZIRPOLO (1930) has carried out the same sectioning experiments on a Neapolitan Ctenophore, *Lampetia pancerina*, and found that when the animal is divided into two parts by a transverse section, it is only those apical pieces bearing the statocyst that regenerate properly while the oral pieces are generally less regenerative. In any case, these experimental results of MORTENSEN and ZIRPOLO are sufficient to correct the erroneous presumption that Ctenophores have no regenerating power. Nevertheless, if incompleteness of regeneration in Ctenophores is still maintained, it can be deduced from the facts of their embryonic development that this must be connected with that of the comb-plates.

It may well be supposed, therefore, that regeneration of Coeloplana, which lacks the comb-plates in the adult state, will be more perfect than in any of the ordinary forms. In nature, this aberrant Ctenophore actually lacerates the periphery of the body, perhaps for the purpose of asexual proliferation. In this case it goes without saying that complete regeneration must take place. According to KREMPF (1921), the piece can complete its regeneration on condition that a part of the ectoderm is present with the endoderm. The regeneration of Coeloplana at this time does not proceed in an epimorphic way; it forms first a small disc by closing the cut surface. A morphalaxis then follows, complete reorganization of the internal structures taking place in a limited quantity of the material. The reconstruction of tissues or organs need not be considered as performed at the same time in every part of the disc, but the phenomenon, as has been pointed out by OKADA (1931), would commence at the place where the cut surface is closed, and spread out from there to the more distal parts. OKADA states that the tentacle that first appears is always situated on the line of fusion of the cut edges in the regenerating piece and the other tentacle is given rise to afterwards at the opposite side. So it is highly probable that the process of regeneration starts around the line of fusion and spreads out from there to the more distal parts. It would be also a natural consequence, therefore, that we should have an unequal development of the paired structures on each side of the piece. This interpretation does not agree with KREMPF's idea which supports CHUN's old theory of the bilateral symmetry of Ctenophores. OKADA has gone into this subject in some detail.

The present work is the outcome of a suggestion made by Prof. Yô K. OKADA that I should devote my first thesis in Zoology to the elaboration of his opinion on the regeneration of Coeloplana.

The experiments and some observations on living specimens were made at the Seto Marine Biological Laboratory from the end of May to the beginning of September, 1930, and other work mostly on the histological side was done in the laboratory of this institute.

Before going further, I wish to acknowledge my great indebtedness to Prof. Dr. Yô K. OKADA for his kind guidance and constant encouragement. I am also deeply indebted to Prof. Dr. T. KOMAI, and further thanks are due to other gentlemen of the laboratory.

Material and Method.

At Seto, Coeloplana is represented by four species viz., *C. willeyi* ABBOTT, *C. mitsukurii* ABBOTT *C. bocki* KOMAI and a species which distinctly differs from the other three, and to which (ref. the next pub.) I give the name *C. echinicola*, since it is found always in close association with an Echinus *Toxopneustes pileolus* LAMARCK. Of those four species *C. willeyi* ABBOTT and *C. mitsukurii* ABBOTT are the most common and can be obtained in sufficient numbers in any season, but the other two are found only on rare occasions from June to August.

The specimens used for the experiments were collected among the sediment washed off such sea-weeds such as Ecklonia, Sargassum and other brown algae, to which the first species adhere abundantly. *C. bocki* was simply separated with forceps from the stock of Alcyonaria belonging to the genus Dendronephtya. They were then transferred into small glass vessels filled with clean sea-water from the littoral zone. The stock material was thus preserved in this artificial condition.

To obtain regenerating pieces, a part of the periphery was isolated from the animals while in an extended state by cutting with a sharp knife on a glass-plate covered with a thin layer of paraffin. When it was necessary to have a certain limited region of the body, however, the part was lifted up by means of a micro-pipette and cut off with a glass-needle. The operated fragments were kept in several glass vessels of smaller size filled with particularly cleaned sea-water, and the water was changed more than twice a day. In my own experience, the best regeneration results were obtained in water of ph. 8.4 at 22–27°C.

Of the pieces thus prepared some were used for direct observation in the living state, while the rest were fixed for internal examination in sections. As fixative, BOUIN's picro-formol was used. The pieces were first placed between two cover-glasses to prevent their contraction, and the solution after being slightly warmed was poured instantly upon them while they were extended. After 30 minutes the preparations were transferred into alcohol, first 50% and then 70%, till the picric acid was dissolved completely out. After this treatment the percentage of alcohol was gradually lowered to zero, the specimens still being kept in their original state between the two cover-glasses. Finally each specimen was put into 70% alcohol and carefully freed from the pressure of the cover-glasses. By this method specimens well fixed in an extended state were obtained. They were then preserved in 70% alcohol till needed. The sections were cut by the ordinary paraffin-method, and stained with HEIDENHAIN's haematoxylin and Eosin, or simply with BORAX carmine *in toto* before embedding.

General Organization.

Coeloplana, differing from the ordinary ctenophore, has a peculiar mode of creeping on the substratum. But at night, it may come up to the surface, and this character is especially developed in specimens that are regenerating; we may sometimes find them floating during the night especially when it is very dark.

In shape the animal is like a flat-worm and the upper and the lower side can be distinguished, the former being represented by the presence of the sense-organ and the latter by the mouth. The tissues are transparent and quite fragile, but the mesogloea and muscle-fibres seem to be more developed than in the ordinary ctenophore. Although the structure and arrangement of various organs in Coeloplana have been dealt with in considerable detail by KOMAI (1920) and KREMPF (1921), those two descriptions are too extensive for the present purpose. It may, therefore, be useful to summarize them to such an extent as I think practically helpful for the present study. The epidermal structures are nearly the same as in the ordinary ctenophore with the exception of the aboral sense-organ, the margin of which is divided into lobes at least in *C. bocki* and *C. echinicola*.

A pair of tentacles stretch out on each side of the transverse axis of the body from their proper sheath. The elastic stem bears many thread-like accessory branches along its entire length as in the ordinary case, but the basis is horizontal instead of vertical.

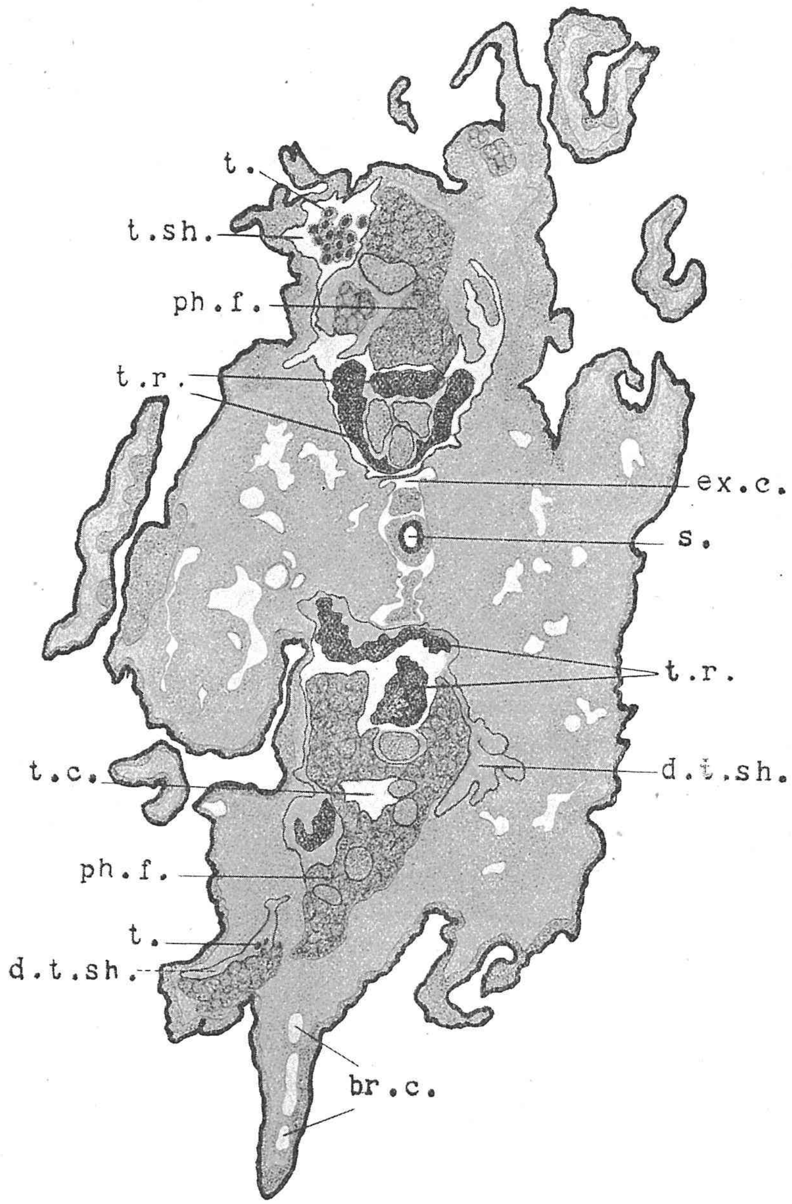

Fig. 1.

Semi-diagrammatic illustration of the inner structure of Coeloplana in horizontal section.

The tentacular sheath shows a peculiar modification, having a dorsal and a ventral compartment. There are many short protuberances on the dorsal surface of the body. They are called dorsal tentacles, but they are nothing more than an outgrowth of the branches of the gastro-vascular canals on that surface. The number of these protuberances varies in different species.

It is hardly necessary to say that Coeloplana has no comb-plates.

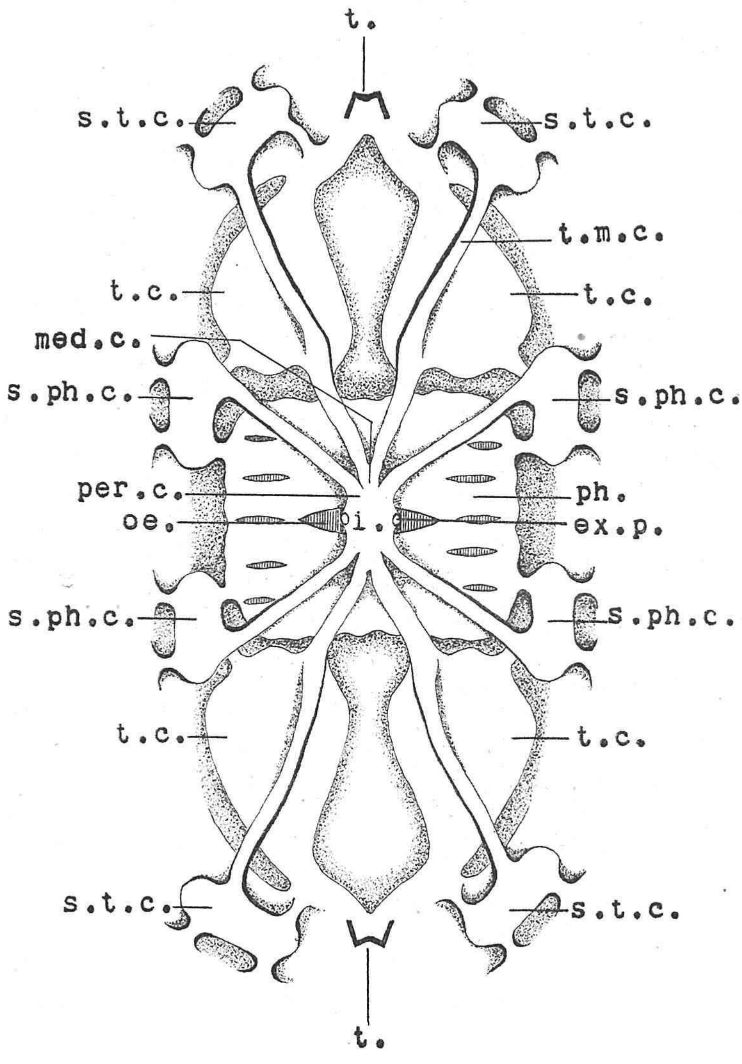

fig. 2.

Diagram of the gastro-vascular system.

The main part of the gastro-vascular system (fig. 2) is nearly identical with that of the ordinary ctenophore; the mouth opens in the middle of the ventral surface, and other organs such as the pharynx, oesophagus, and infundibulum follow one after another in a vertical direction. From the infundibulum (fig. 2 i) a pair of perradial canals (per. c.) depart in the plane of the tentacular axis as in the ordinary way, but each of them divides almost instantly into two side canals and a median short one. The paired canals which correspond to the meridional canals of the ordinary ctenophore represent here the subpharyngeal canals (s. ph. c.). The unpaired median canal (md. c.) bifurcates also very soon into two branches close to the tentacular root, each expanding to a large sac representing the tentacular canal (t. c.), from which a canal homologous to the tentacular meridional canal of ctenophores (t. m. c.) arises on and along its dorsal side. This latter makes the origin of the subtentacular canal (s. t. c.). Besides these there are the excretory canals, situated in the sagittal direction and open to the exterior at the centre of the dorsal surface of the body (ex. p.).

Coeloplana is hermaphrodite; the sexual elements are produced in the dorsal wall of the subpharyngeal and subtentacular canals which have just been mentioned.

From the above description we may easily suppose that the organization of Coeloplana is due to depression of the ordinary ctenophore on the median axis, but according to KOMAI the flatness of the animal and the distinctness of its dorsiventrality have not been brought about simply by the reduction of the main axis, but are partly due to out-spreading of the outer half of the pharynx in the original cydippid form.

External Changes in Regenerating Pieces

Without any particular reason but for the sake of convenience, I cut from the periphery of the animal pieces of about a millimetre in size, and these pieces were left to regenerate.

The first phenomenon observed was the closing of the wound by confluence of the cut edges. This process continued for more than one half hour. During this time the regenerating pieces moved slowly about on the bottom of the glass vessel (fig. 3 A–E). After about three hours the pieces completed the wounded closure by fusing the original cut edges, but the direction in which the fusion took place was left as the future tentacular axis. The ectoderm became gradually thickened in this direction (fig. 3 G), and about 15 hours after cutting, the anlage of one tentacle was layed down. The sheath was then formed at its basis (fig. 3 K). However, the tentacular apparatus was not differentiated *in situ* but derived from the ectodermal cells that have been brought into at the time of the closure of the wound.

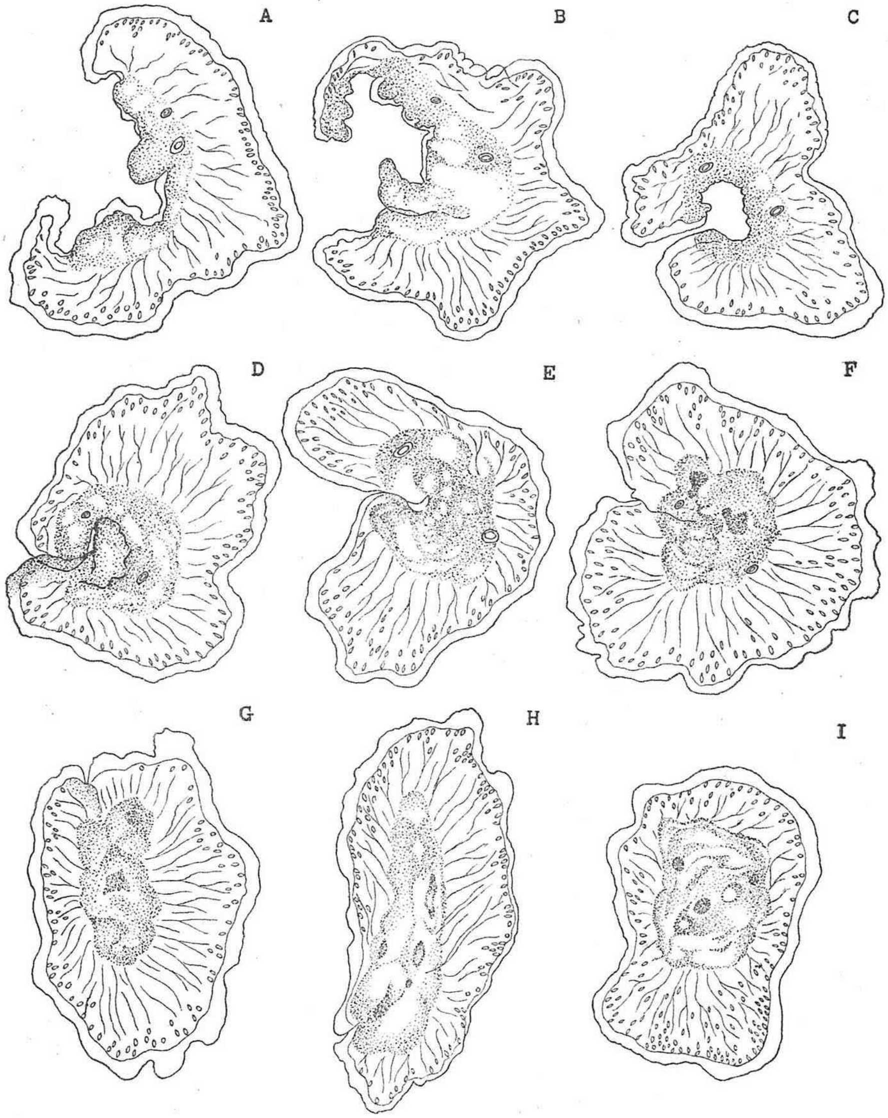

Fig. 3. a

Changes of shape in regenerating Coeloplana (dorsal view). A) About 5 minutes, B) 20 minutes, C) 40 minutes, D) 1 hour, E) 1 hour and 40 minutes, F) 3 hours, G) 4 hours, H) 5 hours and 30 minutes. I) 8 hours.

I shall return to this subject later on and describe the process more precisely.

Simultaneously with these internal changes, the regenerating pieces, which had been moving actively on the bottom, became sluggish or

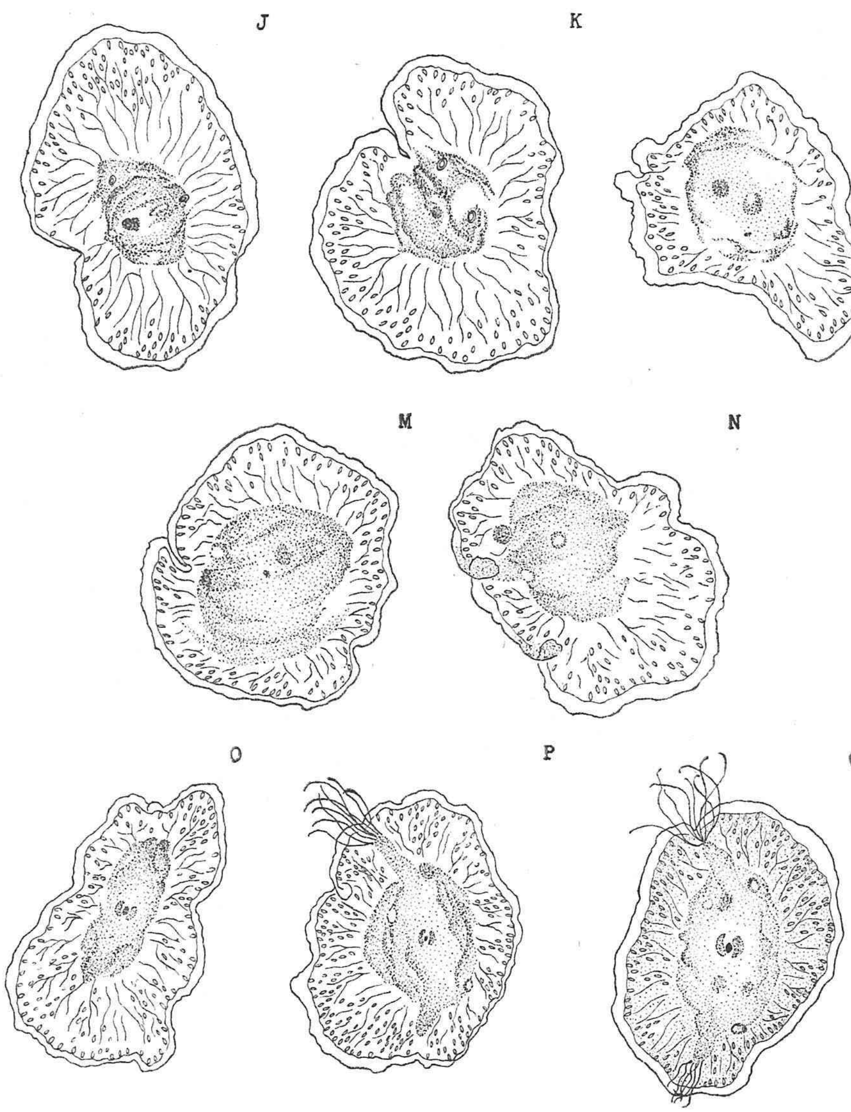

Fig. 3. b

J) 14 hours, K) 18 hours, L) 20 hours, M) 27 hours, N) 28 hours, O) 50 hours, Q) 72 hours after operation (L-N in quiescent state).

even did not creep any more; this state continued for about 20 hours. While they were in this quiescent state, the main part of the gastro-vascular system was reestablished, and most of the mesogloea was dissolved away.

After about 25 hours the anlage of another tentacle made its appearance opposite the one already regenerated, and at the same time just in the middle of their bases, the dorsal ectoderm invaginated (fig. 3, M). It turned next into a deep depression in which the aboral sense-organ was formed about 5 hours still later or 30 hours from the beginning of the experiment (fig. 3 N).

On the other hand, a larger invagination took place on the ventral side, and the mouth was formed. By this time the main part of the gastro-vascular system was reestablished, and the regenerating pieces began to creep again.

After about 50 hours the polar plates and the complete tentacular apparatus were distinct (fig. 3 O), and after 65 hours the larger tentacle, i. e. the one which appeared first, attained a length of 10 times that of the body, and was observed frequently stretching and contracting (fig. 3 P). After about 70 hours, the regeneration of the pieces was complete except for the formation of gonads (fig. 3 Q).

According to OKADA (l. c.) the pieces require about 5 days to recover their original structure, but in my own case it was completed in 70 hours only (at a water-temperature of 22–26°C). But at a temperature of 29°C. (at the beginning of August) pieces require more time for regeneration, and at this time I have got complete regeneration only after 100 hours i. e. 4 days. From those facts the time required by the pieces to complete their regeneration seems to differ according to the experimental condition, especially the temperature of the water.

As has been mentioned, Coeloplana frequently lacerates itself in nature, and this phenomenon is especially well observed in *Coeloplana mitsukurii* from the beginning of June to August, when the water temperature of the littoral zone varies from 22 to 29°C. After the middle of the latter month, the water is often warmer than 32°C., and the animal disappears completely from the shore. With descent of the temperature in Autumn the animal reappears, but this time it does not perform asexual reproduction by means of laceration. Before closing the description of this section I shall give here one example of my observations on the behavior of living Coeloplana reared at the beginning of August.

DATE	CHANGES IN ANIMAL	W. TEMP.	pH
4 th.	An individual, with the longer diameter about 7 mm.	28.5	8.4
6 th.	4 pieces broken off.	28.5	8.4
7 th.	2 pieces do.	29.0	8.4
8 th.	3 pieces do.	28.5	8.4
9 th.	1 piece do.	30.5	8.4
10 th.	1 piece do.	30.5	8.4
11 th.	No laceration.	31.0	8.4
12 th.	No laceration.	30.5	8.4
13 th.	No laceration.	31.5	8.4
14 th.	No laceration.	31.5	8.4

Internal Reorganization

1) **TENTACULAR APPARATUS**

The regeneration of the tentacular apparatus can be well studied in transverse sections of the pieces. It begins with the appearance of the tentacular basis.

As mentioned already, the wound of the fragments is closed by the coming together of the cut edges from each side. By this process of confluence a small area of the ectoderm is rolled inside. This part of the ectoderm is then separated from the general surface and massed up to be carried gradually to the more central part of the body (fig. 4 ect. schema B t. r); This is the origin of the tentacular apparatus on one side, and the track along which the ectodermal mass has moved back indicates the further direction of its development. The ectodermal mass in question grows gradually, and when it attains a certain size a layer of proliferating cells departs from its distal side towards the

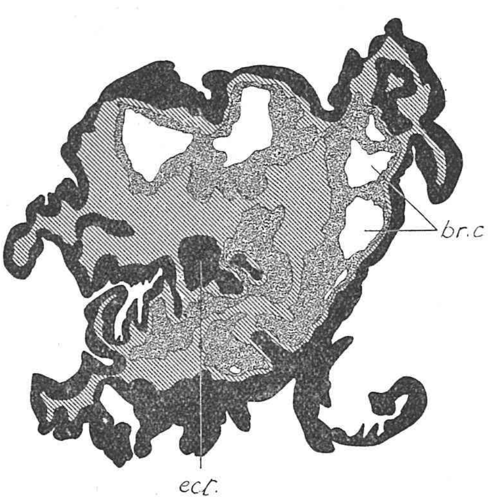

Fig. 4

Horizontal section of 5 hour specimen, showing the separation of the ectoderm (*ect.*) for the tentacular apparatus.

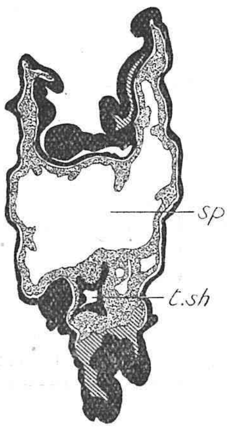

Fig. 5

Horizontal section of 13 hour specimen, showing a large central space (*sp*) derived from damaged gastro-vascular system.

periphery, keeping, however, a regular single arrangement. Thus it soon constitutes a bag-like structure, the inner surface of which is lined with short cilia (fig. 6 t. sh. schema D). The hollow structure grows further in length and becomes finally closely attached to the surface ectoderm. The latter is perforated from inside out. Thus the ectoderm for the tentacular apparatus, that has been brought inside, becomes again connected with the surface. It can be easily understood without further explanation that the aperture of the hollow structure represents the opening of the future tentacular sheath and the cavity itself the inner cavity of the sheath. The same structure grows also to the proximal side always carrying the original ectodermal mass at its base. Or this phenomenon may be regarded as due to a backward movement of the cell-mass itself, in which the stem and base of the tentacle subsequently differentiate. The tentacular stem elongates along the inner surface of the sheath, the distal and the proximal parts taking, however, a different course. This difference in development of the stem is principally due to the fact that nearly at the same time or a little earlier the sheath is divided into two parts, one for the basis (ventral compartment, see fig. 7 a, v. t. sh) and the other for the stem (dorsal compartment). They are both disposed horizontally, instead of vertically owing to the flatness of the piece. Later (about 50 hours after operation) the ventral compartment is further divided into three parts as shown in figure (fig. 13 v. t. sh. 1. 2. 3).

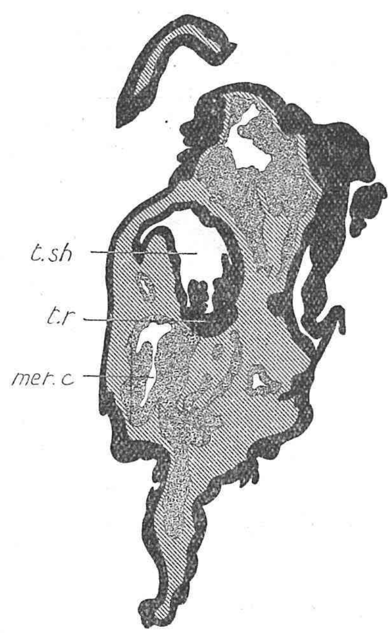

Fig. 6.

The same horizontal section as before in a 15 hour specimen. The ectodermal mass shown in fig. 4 differentiates now into the tentacular sheath (*t. sh*) and the root (*t. r*).

Next the accessory branches are produced along the entire length of the tentacle one after another from the base to the end. Thus at about 30 hours after the piece has been cut off, the tentacular apparatus on one side is almost complete (fig. 8a 10a schema E).

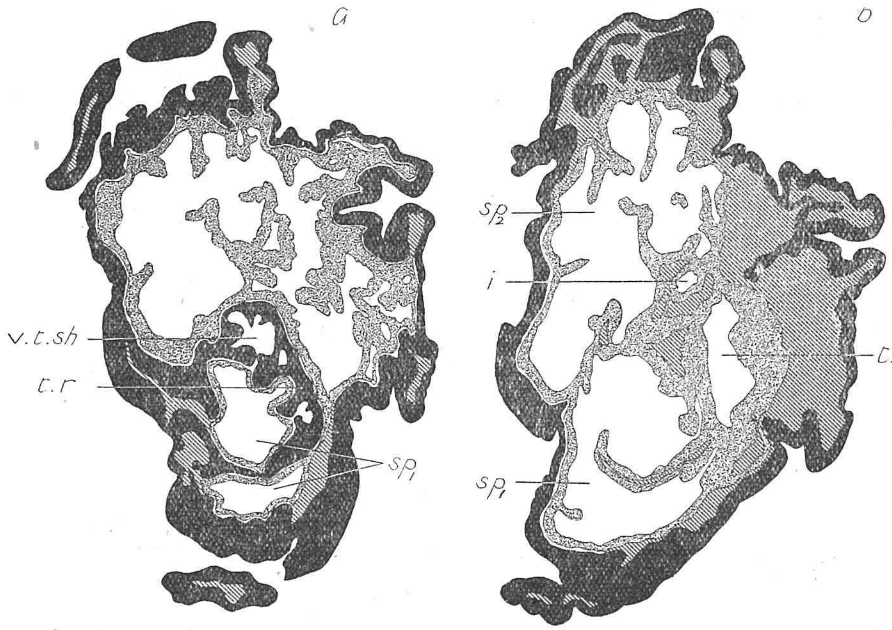

Fig. 7.

Two horizontal section from a 17 hour specimen. In a) the tentacular sheath is further divided into two parts and the ventral compartment alone is shown (*v. t. sh*). In b) the central space is separated into Space I and Space II. The infundibulum appears (*i*).

The tentacle on the opposite side is also derived from the same (central) mass of ectoderm that has been brought inside at the time of the closure of the wound, i. e. from the basis of another tentacle. At about the time when the mouth begins to be formed (30 hours after operation) a layer of cells detaches from the proximal end of the ventral compartment of the first tentacular sheath. It soon divides into two branches and surrounds the outer surface of the stomodeal invagination to appear in the other side of the piece (fig. 11 12b t. r_2). After passing this part of the stomodeum the branches join together into a single mass which extends just in the opposite direction to the first tentacle, and thickening takes place at the distal end (schema E).

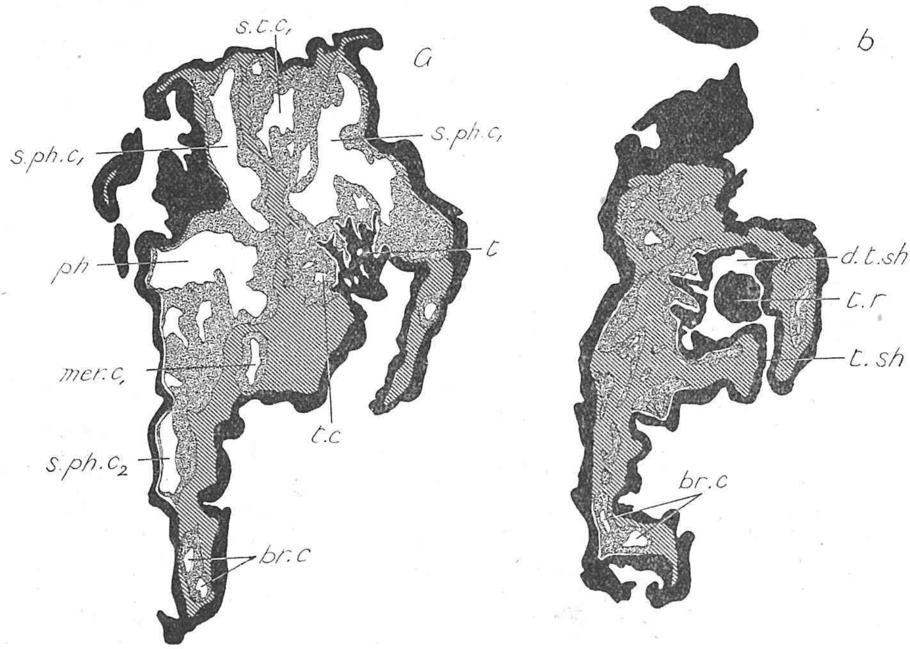

Fig. 8.

Horizontal section of a 28 hour specimen. In a) the second subpharyngeal canal (*s. ph. c 2*) is already derived from Space II; in b) the first tentacular apparatus is almost complete.

This is the anlage of the second tentacle, and when the thickening becomes great enough, the sheath with the dorsal and ventral compartments and the stem differentiate after the same manner as in the case above considered. Further development of the second tentacle is also the same as we have already seen in the first tentacle, except that the growth is in the opposite direction (fig. 13 t. r_2).

By the time the connection between the first and second tentacles is cut off, the cellular remnant between them is taken into the walls of the pharyngeal part of the stomodeum. Owing to this addition the thickness of the walls of the latter is considerably augmented. Sometimes there are specimens in which the cellular connection between two tentacles remains till quite late. But in any case it is destined to be broken off, and the entire tentacular apparatus is complete by 65 hours after operation (fig. 15b schema F).

The regeneration of the tentacular apparatus has a close connection with that of the gastro-vascular system to which we shall come soon.

2) ABORAL SENSE-ORGAN

The origin of the aboral sense-organ is a deep depression of the dorsal surface of the regenerating piece just above the stomodeal invagination. In a sagittal section of a 30 hour specimen it is however seen to be more or less widened in the transverse direction. The bottom of the depression thickens in the middle part, and in 40 hour specimens we can distinctly recognize an otolithic mass in this place (fig. 14 s).

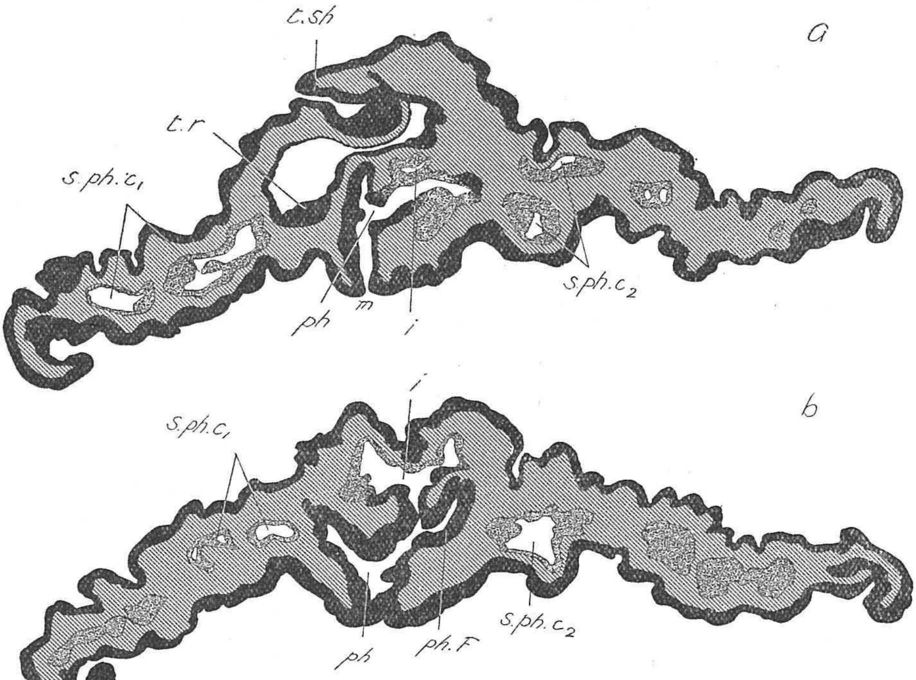

Fig. 9.

Cross sections of a 30 hour specimen showing the formation of the mouth (*m*) and pharynx (*ph*).

3) MOUTH PART

As early as after about 30 hours the mouth opens (fig. 9a). It is represented by a simple but large invagination of the ventral surface like the aboral sense-organ in the dorsal surface. Nearly at the time when one of the tentacles is completed, the ectoderm in the middle of the ventral surface invaginates over a considerable area, and this invagination becomes gradually deeper until it comes to have a direct

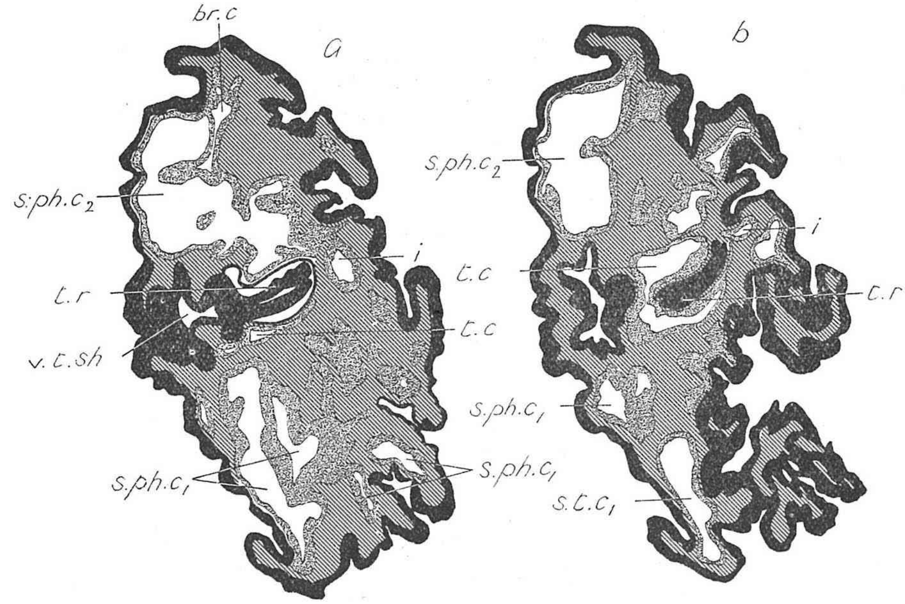

Fig. 10.

Horizontal sections of a 34 hour specimen. In a) the tentacular apparatus and in b) the principal part of the gastro-vascular system including the subpharyngeal (*s. ph. c*) and subtentacular (*s. t. c.*) canals are shown.

communication with the infundibulum, which has been established by this time in the central part of the piece by reorganization of the remaining gastro-vascular spaces (fig. 7b 9a i).

4) **GASTRO-VASCULAR SYSTEM**

The general constitution of the gastro-vascular system has been mentioned at the beginning of this work. We shall now proceed to show how this system is reestablished after being completety destroyed. In a horizontal section of pieces which have completed the closure of the wound, a large space is always observed at the central part of the piece, instead of the network of the branched canals. Such a figure possibly results from reduction of the mesogloea and fusion of the separated canals in the regenerating pieces (fig. 5 schema B sp). The walls of the space are not uniformly thick everywhere but the part surrounding the basal end of the tentacle is exceedingly hypertrophied and a particular space may appear in it at quite an early stage in the reorganization (fig. 7b i). This space makes the centre of the regeneration of the gastro-vascular system (schema C), and gives rise later to the infundibulum.

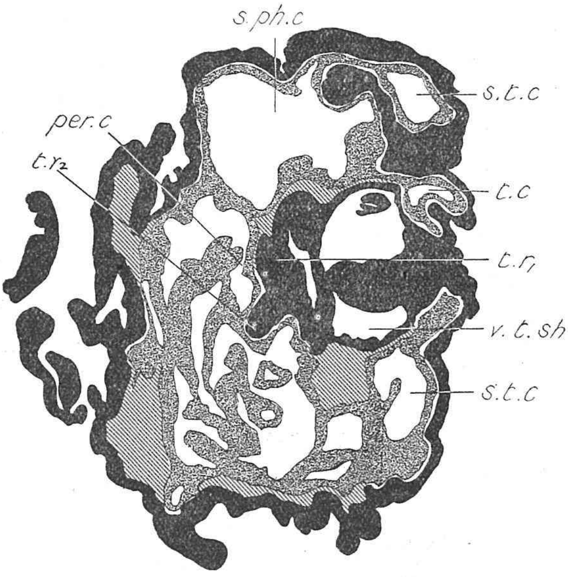

Fig. 11.

Horizontal section of a 42 hour specimen showing the beginning of the second tentacle (*t. r. 2*) from the proximal end of the first one (*t. r. 1*).

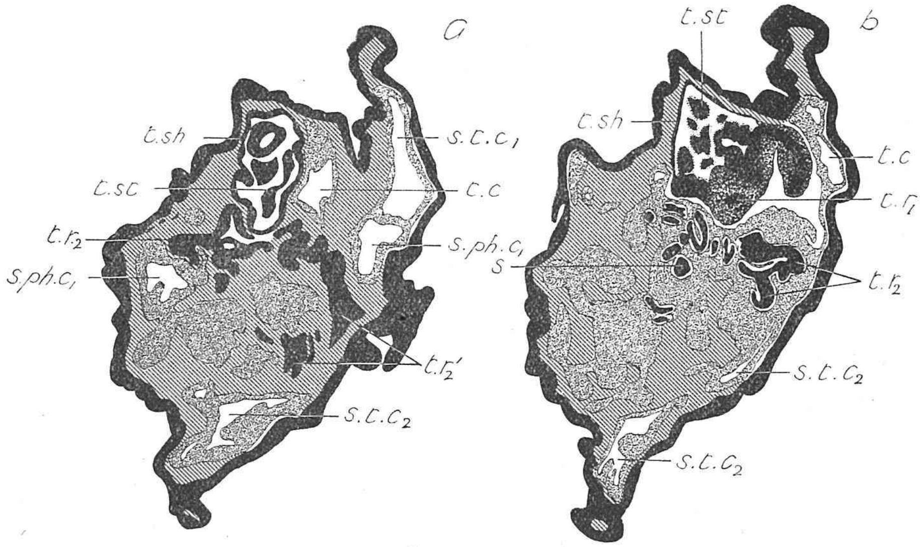

Fig. 12.

Horizontal sections of a 52 hour specimen showing the further differentiation of the second tentacular mass dividing into two branches *t. r. 2.* and *t. r.' 2*; *s* represents the invagination of the sense-organ.

On the other hand cellular strands grow out from the inner surface of the central space at several points, and a septum is soon established in one of them. The space is now divided into two compartments, one for the developing tentacle, while the other is reserved for another tentacle which does not yet appear at this time. For the sake of convenience, I shall denote these compartments hereafter Space I and Space II respectively : sp_1 & sp_2 (fig. 7b, schema C).

Space I differentiates in company with the differentiation of the tentacle on the same side; when the sheath appears on the latter, the space, which is always more closely associated with its ventral side, puts out two canals, namely the future tentacular canals, without,

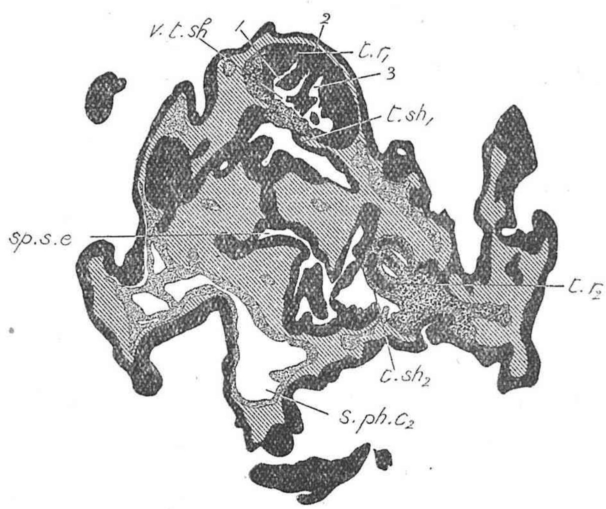

Fig. 13.

Horizontal section in a 54 hour specimen showing the second tentacular apparatus (*t. r. 2*) almost complete; The ventral compartment of the tentacular sheath of the first tentacle is divided into three compartments (*t. sh. 1, 2, 3*).

however, losing its connection with the infundibulum at the opposite side (fig. 7b 8a 10a t. c). After giving off the tentacular canals, Space I separates itself into two parts, one on each side of the tentacular base, and each of them is further sub-divided into two canals by a transverse septum. Thus four canals in two pairs are established in a plane (fig. 10 s. ph. c & s. t. c). Of these canals, two are always situated farther out than the other two, both, however, making a symmetrical pair on each side of the tentacular axis or the future transverse axis of the body (schema E). From the 1st pair develop the subtentacular canals, and from the 2nd pair the subpharyngeal canals. In the same way, but of course at a later stage of regeneration, Space II differentiates on the opposite side of the piece in company with the appearance of the second tentacle. It produces first the tentacular canals, and next the subpharyngeal and snbtentacular canals as has been described (fig. 15a t. c_2, s. ph. c_2, s. t. c_2). They are also arranged symmetrically with reference to the transverse axis of the body which is represented by a plane passing through both tentacles.

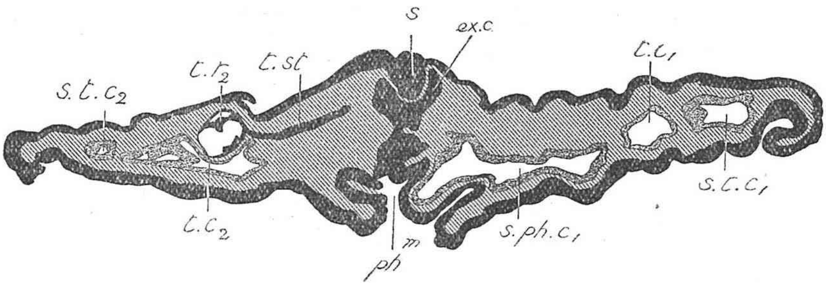

Fig. 14.

Cross section of a 54 hour specimen showing the formation of the sense-organ (*s*) and the excretory canals (*ex. c*).

Now coming back to the central part, after the connection between the mouth and the infundibulum has been well established, the pharyngeal and the oesophageal part differentiate in the latter and at the same time parts of the canals depart towards the dorsal direction to communicate with the exterior through respective pores on each side of the aboral sense-organ. These are the excretory canals (fig. 14, 16 ex. c).

The regeneration so far as described requires about 70 hours from the beginning, when the main part of the gastro-vascular system is almost complete, and the vascular networks begin to be formed around the pharynx by the branches of the subpharyngeal canals. KREMPF ('21) claims that he can distinguish a "réseau méridien", "réseau gonadien" and "réseau pharyngean" in the canal-system of Coeloplana, but we can not see any such distinction in regenerating pieces, and it seems that Coeloplana is without pharyngeal canals. Indeed there has been observed no structure which can be referred to the pharyngeal canals of the ordinary ctenophore in any stage of regeneration.

Unfortunately, I could not make out from what part or parts of the canals, and in what way the sexual elements were produced

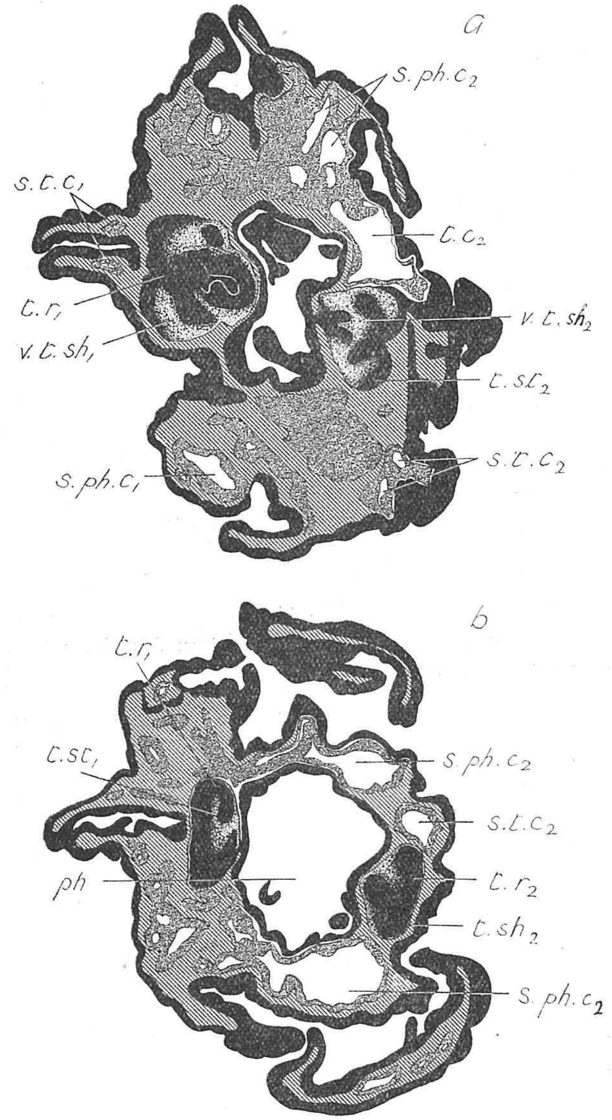

Fig. 15.

Horizontal sections of a 62 hour specimen showing the complete reorganization of the internal organs, especially the reconstruction of the gastro-vascular system ; *t. c.* tentacular canals, *s. ph. c.* subpharyngeal canals, *s. t. c.* subtentacular canals etc.

in regeneration. They are probably be produced from the entire length of the subpharyngeal and subtentacular canals, but of course I have no authentication of this statement.

Problem of Symmetry

As has been pointed out by OKADA (l. c.) the bilateral symmetry in regenerating and regenerated Coeloplana is determined by the direction in which the original cut surface has closed, one of the tentacles being always formed in it. This line of fusion represents the transverse axis of the body. The formation of new organs also takes place with reference to this axis; the antagonistic elements situated symmetrically on each side are regenerated at the same time, but not the elements lying in the longitudinal direction. The sagittal axis of the animal is, therefore, secondarily determined after the appearance of a tentacle.

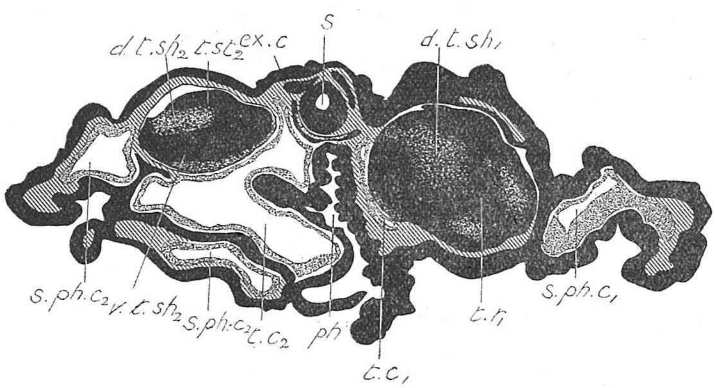

Fig. 16.
Cross section of a 70 hour specimen.

KREMPF (l. c.) considers this disharmony of time in the regeneration of the "foyer dorsal" and the "foyer ventral" as representing an ideal form having one tentacle and one gastro-vascular system as in *Thoë paradoxa* of CHUN (1880). He seems to be of the opinion that ctenophores are animals which have lost their radial symmetry, and in place of the original radial harmony have acquired a new harmony around a single centre, which results in their present bilateral symmetry. I can not understand very well the meaning of his terms "foyer dorsal" and "foyer ventral". The dorsal surface of Coeloplana corresponds to the whole surface of the ordinary ctenophore, while the ventral surface is produced by the outspreading of the pharynx. I am inclined to interpret his "foyer dorsal" as connected with the anlage of one of the tentacles and the "foyer ventral" as the origin of the gastro-vascular system, from the standpoint of my own observations in regenerating Coeloplana. At any rate I recognize the principal results of KREMPF's experiments, but I can not agree with his explanation as to the nature of the asymmetrical appearance of paired antagonistic elements such as the tentacles. OKADA has already discussed this subject, and according him as well as to my own account the time-difference in the regeneration of those antagonistic elements is not due to atrophy of the elements on one side but rather to the fact that regeneration starts at one side and ends at the other, i. e. spreading out from the place where the wound first closed to the more distant parts. Therefore, it would be a natural consequence that unequal development should occur in such organs as form pairs on each side of what is called the sagittal axis of the animal.

It may be mentioned that MORTENSEN (1911) homologizes the tentacular axis of the ctenophore with the sagittal axis of the bilateral animal, but this idea has been much disputed from several points of view. At any rate in regeneration the tentacular axis is first determined and the paired organs and systems are reestablished asymmetrically with reference to this axis.

Summary

1) After recovery of form, severed pieces of Coeloplana regenerate the missing organs by means of internal reorganization. The process commences at the place where the wound first closed and is propagated towards the more distal parts. These regenerating animals are, therefore, of an asymmetrical constitution.

2) One of the tentacles is always formed on the line of fusion and the other is then derived from its base, following the same process of development.

3) The aboral sense-organ is produced from a depression in the median dorsal surface between two tentacles. A similar but still wider depression appears nearly at the same period in the ventral surface for the pharynx.

4) The infundibulum and other parts of the gastro-vascular system are derived from a large central space produced by a fusion of the canals broken in the original piece.

5) Regeneration of the gastro-vascular system takes place also asymmetrically, following the same order of differentiation as the tentacles. The central space is divided by a septum into Space I and Space II, the former for the side where the tentacle is regenerating and the latter for the other side where the other tentacle will be formed.

6) The canal networks around the pharynx are derived from the side branches of the subpharyngeal canals. The excretory canals open to the exterior a little after the connection between the stomodeal invagination and the infundibulum is established.

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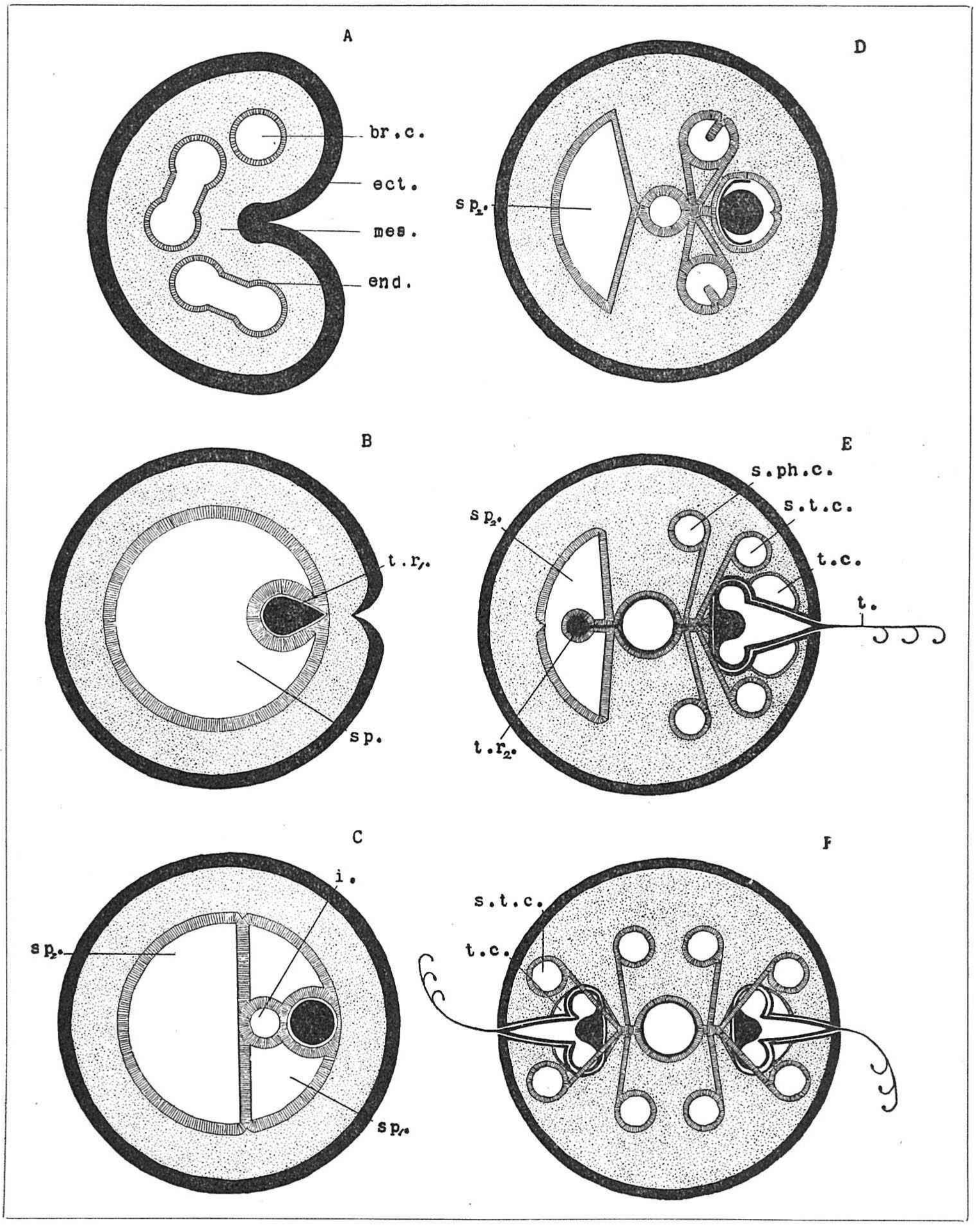
Abbreviations in Figures

a. f. . . . . Accessory filament of tentacle.
b. p. . . . . Body parenchyme.
br. c. . . . . Branches of canal-system.
d. t. or d. p. . . . . Dorsal protuberance.
d. t. sh. . . . . Dorsal compartment of tentacular sheath.
ect. . . . . Ectoderm.
end. . . . . Endoderm.
ex. c. . . . . Excretory canal.
ex. p. . . . . Excretory pore.
i. . . . . Infundibulum.
m. . . . . Mouth.
oe. . . . . Oesophagus.
ot. . . . . Otolithic mass.
per. c. . . . . Perradial canal.
ph. . . . . Pharynx.
ph. f. . . . . Pharyngeal fold.
s. . . . . Aboral sense-organ.
sp. . . . . Space.

sp I. . . . . Space I.
sp II. . . . . Space II.
s. ph. c. . . . . Subpharyngeal canal.
s. t. c. . . . . Subtentacular canal.
t. . . . . Tentacle.
t. b. . . . . Tentacular basis.
t. c. . . . . Tentacular canal.
t. r. . . . . Tentacular root.
t. sh. . . . . Tentacular sheath.
t. st. . . . . Tentacular stem.
v. t. sh. . . . . Ventral compartment of tentacular sheath.

Schema A–F Diagrams illustrating the reorganization and reconstitution of the internal organs in regenerating pieces of Coeloplana.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H. TANAKA.