

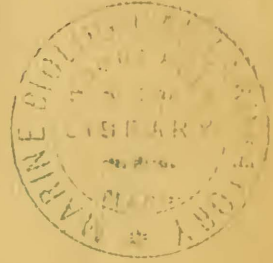
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STUDIES ON TWO ABERRANT CTENOPHORES,
CŒLOPLANA AND GASTRODES

BY

TAKU KOMAI



WITH NINE PLATES

KYOTO, JAPAN, JUNE, 1922.

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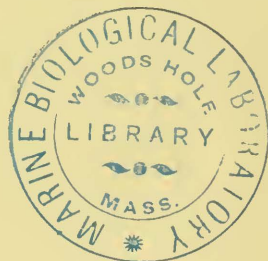
STUDIES ON TWO ABERRANT CTENOPHORES,
CŒLOPLANA AND GASTRODES

BY

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INTRODUCTORY.

Although ABBOTT's works on *Coeloplana* which appeared in 1902 and 1907 shed a great deal of light on the structure of that interesting animal, yet much has remained to be elucidated, especially as regards its development. In fact, the embryology of the animal has never been studied. As a consequence, there still exists a difference of opinion among authors with respect to the systematic position to be assigned to the animal, some of them regarding it as a transitional form in the stages of evolution from the Ctenophora to the Turbellaria, while others believe its striking resemblance to the latter group to be nothing more than an instance of convergent adaptation.

In 1916 I took up the study of *Coeloplana* with the intention of verifying the accounts given by ABBOTT and to fill up, if possible, some of the gaps in our knowledge of the animal. Fortunately enough, a fairly plentiful supply of material for my use could be obtained at Misaki. This enabled me to realize my intention in a measure. Especially a fortunate circumstance was that material was securable on which to undertake a study of the development. Some of the results of my researches have already been given in a preliminary report published in 1920 (a). The present paper embodies a fuller account of the results in regard to the anatomy and development of the animal.

During the whole course of the study, I was quite unaware of that KREMPF also had been engaged in the same research. But, when I saw his work published, I was glad to find that, there was no great discord between our studies, at least as far as important points are concerned. I have been able to refer to his results in the present work, and as to the points of disagreement, I have dealt with them somewhat in detail.

The facts about *Gastrodes* given in the second part of this paper are, so to speak, by-products of the research in *Coeloplana*. While consulting literature necessary for that work, my attention was attracted to the existence of another peculiar form called *Gastrodes* which had been referred to the Ctenophora with some doubt, and in the hope of making out the nature of that animal, I was waiting for the opportunity of studying it. And it was again my good luck that a plenty of material was obtained soon afterwards at Misaki and enabled me to ascertain without difficulty that the animal is unmistakably a ctenophore and moreover a form most probably referable to the group *Platyctenea*

to which *Coeloplana* also belongs. My preliminary account about the animal appeared in the number of *Annotat. Zool. Japon.* that contained the paper on *Coeloplana* mentioned above.

Most of the following ^{see}research-works were carried out at the Zoological Laboratory of the Tokyo University during the years 1916-1919. I am greatly indebted to the late Professor IJIMA for his kind guidance and untiring encouragement all through the work. I owe also Professors WATASE, GOTO and YATSU much valuable advice. Further, Mr. OKUBO, a friend of mine, favoured me with a gift of many fine specimens of *Coeloplana* which he had collected and fixed at Misaki. Finally, I should not fail to mention the kind assistance I have received from Professor OKA of the Tokyo Higher Normal School, Dr. MORTENSEN of the Zoological Museum of Copenhagen, Dr. ONO of the Tokyo University and Dr. TERAOKA of the Imperial Fisheries Institute of Tokyo in getting literature necessary for the study. To all these gentlemen my sincerest thanks are due.

STRUCTURE AND DEVELOPMENT OF COELOPLANA.

Historical Remarks.

In 1880, KOWALEVSKY read before the Sixth Assemblage of the Russian Naturalists and Physicians a paper on a remarkable animal which he discovered in the Red Sea and named *Coeloplana metschnikowii*. A short abstract of the paper was given by A. BRANDT in the "Zoologischer Anzeiger" (p. 140) of the same year. The animal was stated to be perfectly alike a planarian, but it showed some features characteristic of the Ctenophora, so that the author regarded it to be an intermediate form between the Coelenterata and the Planariae. In the following year, 1881, appeared the author's second work that contained a somewhat fuller account of the animal, as well as a fine sketch of its general habitus. However, probably owing to its having been published in Russian and in a journal of difficult obtainment, the work seems to have remained unknown to many subsequent writers. The material which formed the basis of both the papers consisted of a single specimen, and this seems to have been examined only in a superficial way. Anyway the papers deal mainly with external features of the animal, and are not without passages which seem to rest on insufficient or erroneous observations. They remained, however, the only original records of the peculiar animal down to the time of the appearance of ABBOTT's papers.

Apropos of his argument on the phylogeny of the Polyclada, LANG ('84) regarded *Coeloplana*, known to him from BRANDT's abstract in the "Zoologischer Anzeiger", regarded *Coeloplana* as a form representing an intermediate stage in the evolution of the Turbellaria from the Ctenophora. It appears that this work of LANG's made *Coeloplana* widely known to all zoologists as a remarkable form of high interest in its systematic position.

In 1902 ABBOTT wrote a preliminary account of two Japanese species of *Coeloplana* obtained at Misaki, which he described under the names of *C. willeyi* and *C. mitsukurii*. In 1907 the same author published a fuller paper on the animals especially dealing with their internal anatomy in detail. This paper brought many new important facts to light, thus greatly supplementing our knowledge of the genus derived from KOWALEVSKY. Nevertheless, there still remained many points in the morphology of the animal requiring further investigation. Recently, in 1920, the present author (KOMAI, 20, a) published a preliminary

description of *C. bocki*, a third species occurring plentifully in the waters near Misaki, giving at the same time a short sketch of its development which he was able to study. In the same year, another new species, *C. gonactena*, was described by KREMPF ('20, a-c, '21) from Annam, with a series of works on the structure and development of the animal published during the year and the next.

Turning our attention to other forms which evidently stand in close relationship to *Coeloplana*, there come into question the three genera, *Ctenoplana*, *Tjalffella* and *Gastrodes*.

Ctenoplana was first described by KOROTNEFF ('86) from the eastern coast of Sumatra, and afterwards by WILLEY ('96) from the Eastern Archipelago of British New Guinea. It is represented by three species, namely, *C. kowalevskii* KOROTNEFF, *C. korotneffi* WILLEY and *C. rosacea* WILLEY. In both external and internal features they bear a far-reaching resemblance to *Coeloplana*, but differ from this, above all, in being furnished with comb-plates by means of which WILLEY's specimens were observed to swim.

Tjalffella (*T. tristoma*) is a very singular animal which was described from the western coast of Greenland by MORTENSEN. ('10, '12, a-c). It is sessile in habit, and is in external appearance very unlike any of the genera mentioned. It has been made clear that the species passes through a typically cydippid larval stage.

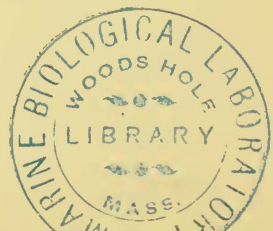
Gastrodes (*G. parasiticum*), finally, is a parasitic animal living in the body of *Salpa*. It was discovered in 1888 by KOROTNEFF, who regarded it at first as a narcomedusa but afterwards as an actinian ('91), whereas, HEIDER ('93) referred it to the Ctenophora. Recently ('20, b) the present author has shown that it is distinctly a ctenophore evidently to be assigned to the same group as the three genera mentioned above.

As to the name given to the group, BOURNE ('00) introduced "Platyctenea", which was adopted by most of subsequent writers either without or with an alteration in the ending of the word.*

Material and Methods.

The material which formed the basis of this study were all secured in the littoral of Misaki mostly by myself at several occasions during

* "Platyctenida" or "Platyctenidae". For the same group the term "Archiplanoidea" was proposed by WILLEY ('96); but this is not preferable, since it conveys a somewhat inadequate conception about the systematic position of the group.



the years 1916-1919. They were observed alive or as fixed and sectioned preparations. Owing to the extremely delicate texture of the body, it is a rather difficult matter to secure good results in killing and fixing *Coeloplana*. Of various fixing reagents tried for the purpose, FLEMMING'S strong solution was found to be the best suited. A reagent consisting of 100 parts of saturated aqueous solution of corrosive sublimate and of 3 parts of glacial acetic acid or 10 parts of formalin gave also fairly good results, but the object must not be allowed to remain too long in it. Double imbedding in paraffin and celloidin after SAMASSA'S prescription ('92) has proved to be the most reliable method for sectioning with histological purpose. But tolerably good results may be obtained by the simple paraffin method too, and for anatomical purpose this method was quite sufficient. For the staining of the material fixed with FLEMMING'S solution, iron-haematoxylin and safranin have proved to be the best, while for the corrosive-sublimate material I have employed with preference DELAFIELD'S haematoxylin combined with eosin. Narcotization of the animal always led to discouraging results, since the tissues are very apt to become disintegrated thereby.

External Features and Life-habits.

Coeloplana is represented in the waters of Misaki by three distinct species, viz. *C. willeyi* ABBOTT, *C. mitsukurii* ABBOTT, and *C. bocki* KOMAI. All the three species are found in the littoral, *C. willeyi* and *C. mitsukurii* on various sea-weeds, but most commonly on certain species of *Sargassum*, and *C. bocki* on stocks of an alcyonacean of the genus *Dendronephthya*. All the species are rather common and may be collected without difficulty. Examples of *C. willeyi* and *C. mitsukurii* may be obtained by searching carefully among the sea-weeds at all seasons of the year, but the winter is, in my experience, the most favourable time for collecting the material in plentiful supply. The frequency of their occurrence seems to be subject to considerable fluctuations in different years and seasons. In 1916 I found *C. willeyi* to be very common especially from January to April, when a day's search yielded fifty or more individuals of it without much difficulty, while in the summer of the same year, ten individuals of the same were about the utmost that could be collected in a day. *C. mitsukurii*, which may be found on the same frond of sea-weed together with *C. willeyi*, is of a rarer occurrence. This was particularly the case with during those

winter months, when only a few specimens of it were secured during a period of time in which more than a hundred specimens of the other species were collected. In the year following, both the species were strikingly rarer, and that to an extent that I searched on occasions strenuously for them in vain for days in succession.

The third species, *C. bocki*, is quite common on the *Dendronephthya* sp., that thrives in the littoral of the neighbourhood of Misaki. It occurs in adherence to any part of the surface of the stock of the alcyonacean either to the stalk or to the crown (pl. 1, fig. 1), and may be found in such abundance that I have secured as many as fifty or sixty, and sometimes even more than a hundred, specimens from one and the same stock of a moderate size.

It is by no means difficult to keep the animals alive in a jar provided the water is fairly pure. To detach them from the substratum to which they adhere, it is necessary to use a pipette, otherwise the specimens will always suffer damage.

The three species (Pl. 1, figs. 2-4) may be readily distinguished by their colours, though this is subject to a certain degree of variation within each species. The colour variation is especially pronounced in *C. willeyi* and *C. bocki*. The former (fig. 2) may be of a deep purple, a pale rosy or a reddish colour, or of a colour intermediate between any of these. The peripheral margin of the body and the base of "dorsal tentacles" are marked with scattered yellowish-white spots, a feature which never obtains in the other two species. The latter (fig. 4) shows a coloration which is about as much, or even somewhat more widely variable. This species is characterized by exhibiting a rather conspicuous marking on the ground colour. The marking consists of a number of branching and anastomosing stripes, which on the whole run along the tentacular axis and may be deep vermilion, dark red, brick-red, pinkish, orange or greyish in different individuals. The stripes number a dozen or more in large specimens; they may be discontinuous and irregularly streaky in small ones. In all cases the marking grows indistinct towards the margin of the body. The ground colour of the body is usually similar to that of the stripes, though very much lighter in tone. Rarely it is of a colour which more or less contrasts with that of the stripes, for instance, I have found some cases of individuals, in which it was of an orange hue while the stripes were vermilion. The stripes constitute a feature peculiar to the species; it is found in neither of the remaining two species, both of which being rather uniformly

coloured, excepting the yellowish-white spots mentioned above of *C. willeyi*. *C. mitsukurii* (fig. 3) is generally light yellowish-brown, though not always same in tone, this species showing the least colour variation. Whether or to what extent an adaptive significance is involved in the variability of the coloration, I can not say for certain, but it may be mentioned as a fact that individuals of various coloration may occur side by side amidst the same surroundings. But, there is an undeniable tendency among individuals having similar coloration of occurring close by. This, in my opinion, is due to division of the animal by accidental damage and subsequent regeneration of lost parts.

The three species show very close resemblance with one another as regards both their external and internal features, and it is not necessary to deal with the morphology of the three separately. The data recorded in the present paper may be regarded to have reference alike to all the species, unless special references are made to a particular species. However, since *C. willeyi* and *C. bocki* are by far the commoner species, these naturally have formed the chief material for my study.

The animals, as they adhere to the sea-weeds or to the alcyonacean stock, might easily be mistaken by the unaccustomed eye for a planarian or perhaps for a small nudibranch. When detached from the substratum and placed in a jar with sea-water, they soon stretch out on the bottom and assume a thin film-like appearance, in which condition they may appear not unlike a kind of encrusting bryozoa or of compound ascidians. The body in such an extended state may be said to be almost shapeless; but when contracted, it is generally of an oblong outline. The size of the animal varies considerably in different individuals and of course also in different states of contraction of one and the same individual. Roughly speaking, it generally measures 0.5–1 cm., more rarely 2 cm., in diameter in a moderately contracted state, and 1.5–3 cm., sometimes even as much as 5 or 6 cm. in diameter when fully extended. On the whole, *C. bocki* is smaller than the other two species; it is commonly 1–1.5 cm., exceptionally 3 cm. in diameter in the fully extended state, and may contract to a size of 0.5 cm. or somewhat less across.

The dorsal surface of the body shows a small round unpigmented area at the centre, indicative of the situation of the aboral sense-organ as well as of the excretory pores (Pl. 1, fig. 4, *s*). On either side of the sense-organ, along the longer median axis of the body, occurs a tentacular apparatus (Pl. 2, fig. 1, Pl. 1, figs. 3, 4), which constitutes one of the most prominent organs of the animal. It consists of a basal part

enclosed within a sheath and of the tentacle proper which can be stretched out to such a length as may exceed twenty times that of the body diameter. Besides, there exist "dorsal tentacles" (Pl. 2, fig. 1, Pl. 2, fig. 4; *d. t*), which are the outgrowths of the gastro-vascular canals on the dorsal side. Some ten to forty (commonly twenty to thirty in *C. willeyi*, and ten to twenty in *C. mitsukurii* and *C. bocki*) of them may occur in an individual, arranged along the course of the canals representing the meridional canals of ordinary ctenophores. Their shape does not differ in different species in the manner pointed out by ABBOTT ('02, '07). In all the species they may be said to be usually of a simple club-like, and exceptionally of a divided or digitate, shape.

As regards the mode of locomotion, ABBOTT ('02, '07) has made so full and correct a record that I have but little to add. The ventral surface of the body appears to be highly thigmotrophic, as indicated by the active manner in which the animal creeps right over a foreign object it may come across during locomotion on a hard substratum or on the surface of water, instead of avoiding it.

Freshly captured animals kept alive in a glass jar, are often seen to discharge from the mouth pellets of about 1 mm. diameter. These always prove to be undigested parts of the food taken, as well as some other objects which happened to enter the mouth and consist generally of some vegetable and animal matter agglutinated together by slime. They usually contain diatoms in several forms, fragments of sea-weeds, pieces of exoskeleton of small crustaceans, etc. Not infrequently even small pieces of the tentacle of the animal were met with among the ingredients. It was also observed that an empty but nearly perfect skeleton of a certain isopod or amphipod was discharged from the mouth. On this connection it may be mentioned that I have often come across little pieces of striped muscles, apparently of some crustacean, imbedded in the plasm of endodermal cells in the canal-system. Above observations give an idea of what the animal subsists on. It seems after all that *Coeloplana* takes nearly the same food as pelagic ctenophores or *Tjalffella* (MORTENSEN, '12).

Anatomical and Histological Features.

It will be convenient to give a brief account of the structure of the body before entering into a detailed description of its parts. As already mentioned, the body of *Coeloplana* is extremely changeable in

shape, but generally takes an oblong shape when contracted. At the centre of the dorsal surface, lies the aboral sense-organ (Pl. 2, figs. 1 & 4, *s*); directly below it and on the ventral surface, is situated the mouth (*m'*). The two organs just mentioned determine the main axis of the body. The vertical plane determined by this axis and by either the long or the short diameter of the oblong body may be called the "perradial" planes, of which one is the "transverse" or "tentacular" plane and the other the "sagittal" or "pharyngeal" plane, distinguished according to their including the long or the short body-diameter respectively. The two planes intermediate between the perradial planes and forming with these an angle of 45° may be called the "interradial" planes.

The tentacular apparatuses (*t*), which lie in the tentacular plane, are nearly identical in structure with those of cydippid ctenophores, excepting for the fact that, both the tentacle-basis (*t. b*) and the tentacle-sheath (*t. sh*) are placed horizontally instead of vertically as in those forms. The mouth leads dorsally into a spacious pharynx (*ph'*) of a depressed form, which is succeeded dorsally by the oesophagus (*oe*) shaped like a compressed tube. Both the pharynx and the oesophagus are clothed with an epithelium of ectodermal origin. The oesophagus opens aborally into the infundibulum (*i*) situated immediately beneath the sense-organ and forming the centre of the entire canal-system. The canal-system is arranged essentially in the same way as in ordinary ctenophores:— A pair of perradial canals (figs. 2 & 4, *per. c*) proceed from the transverse wall of the infundibulum, and each of them divides at once into three branches, of which the lateral two (*s. ph. c*) represent the subpharyngeal meridional canals of ordinary ctenophores and the median (*t. c*) the trunk of tentacular canals. This latter soon divides into two branches which accompany the tentacular apparatus on its ventral side. Each of these two branches gives rise dorsally to a canal (*s. t. c*) which represents the subtentacular meridional canal of ordinary ctenophores; the canal runs nearly parallel to the transverse axis of the body along either side of the tentacle-sheath. All the canals mentioned above, excepting the perradial, give rise to several branchlets that divide and anastomose and bring about the extensive canalar network of the peripheral parts of the body (*br. c*). The infundibulum further sends out from either of its sagittal sides a narrow canal, the "excretory" canal (*ex. c*), which proceeds dorsally to open externally without dividing unlike the same of ordinary ctenophores. The gonads develop from the dorsal wall of the eight canals representing

the meridional canals, the ovary (*ovy*) as a continuous tract of egg-cells and the spermary (*te*) as a series of certain numbers of compact sperm-cell masses.

Not infrequently there are met with anomalous individuals in which the two body halves on either side of the sagittal plane are quite unequally developed as regards both the external shape and the internal structure. Indeed, it may be said to be rather exceptional when those two body halves are perfectly symmetrically developed. MORTENSEN ('12) has made a similar observation in *Tjalfiella* and has regarded the asymmetry to be due to an incomplete regeneration of parts lost by accidental damage. In this I fully agree with him. Unfortunately, I could not ascertain how and to what extent regeneration takes place in *Coeloplana*. But according to KREMPF ('20, '21), even a very small piece of the body can grow into a perfect individual provided the piece possesses both ectoderm and endoderm.

Epidermis.

The epidermis of *Coeloplana* is in structure essentially ctenophoran. It is in a highly differentiated state and consists, as in all ordinary ctenophores, of gland cells and interstitial cells. The former are distinguishable into two kinds, the granular and the clear.

On the dorsal surface of the body (Pl. 4, fig. 1), the epidermis may be said to be made up very largely of the gland cells (*c. g.*, *g. g.*). These are arranged very close together, restricting the occurrence of the interstitial cells, so that these are found mostly in the deepest parts of the epidermis (*i. c.*). The two kinds of gland cells occur in about equal frequency in the dorsal epidermis.

The granular cells ("Körnerzelle", CHUN, '80; "Drüsenzelle", HERTWIG, '80;? "Drüsige Deckzelle", SCHNEIDER, '02; "Stadium C," SAMASSA, '92) (*g. g.*) are generally broadly columnar in shape and not of a swollen appearance. The cell-body includes in the distal parts a crowd of spherules, while the basal parts may remain in a clear and homogeneous state. The spherules measure 2-3 μ in diameter and are polygonal in form as the result of mutual pressure. They exhibit strong affinity for eosin; they also take up deeply certain other dyes, such as, acid fuchsin and orange G, as well as iron-haematoxylin. The basal part of the cells often presents a basophilous reaction.

The clear gland cells ("Glanzzelle", CHUN, '80; "Deckzelle",

HERTWIG, '80; "Stadien A & B", SAMASSA, '92; "Schleimzelle", SCHNEIDER, '02) (*c. g.*) vary both in size and appearance to a certain degree. Those which occur predominantly in the dorsal epidermis are of a swollen appearance, being filled up with a homogeneous-looking matter which shows affinity for basis dyes such as haematoxylin and safranin. Superficially and wedged in between the ends of gland cells, there is a scattered occurrence of a peculiar kind of clear cells (*c. g'*) which present a shrunken appearance and take up dyes more strongly than the ordinary clear cells. These evidently represent senescent stages of the clear gland cells after the discharge of their contents.

The interstitial cells (*i. c.*) form an irregular layer in the basal parts of the epidermis. The nuclei are of a somewhat oval shape, measuring $3\ \mu$ by $2\ \mu$, and are provided each with a nucleolus situated in the centre. In the peripheral half of the thickness of the epidermis, one meets but seldom with nuclei referable to the interstitial cells.

The dorsal epidermis is structured similarly in all parts of the body, except in the part forming the dorsal tentacles as well as the part about the aboral sense-organ to be dealt with later.

On the dorsal tentacles, the epidermis is made up principally of the interstitial cells, the glandular elements being found only in a scattered distribution. At the tip of the dorsal tentacles, the epidermis, as also the entoderm directly underlying it, is reduced to a very thin layer which takes up stains but faintly and shows at intervals some flattened nuclei.

In the surface view of fresh specimens (Pl. 4, fig. 4), the dorsal epidermis presents an appearance not unlike that of vegetable parenchyme, all the constituent cells being of a distinctly polygonal shape. The distinction between the two kinds of gland cells is quite manifest. Those of the one kind are filled with yellowish refringent granules (*g. g.*), while those of the other kind are of a clear appearance. Closer examination of the latter kind shows that, this is again divisible into two sorts, namely, the larger with a swollen and perfectly clear appearance (*c. g.*) and the smaller of a somewhat irregular shape and translucent appearance (*c. g'*). These two sorts correspond without doubt respectively to those two kinds of clear cells of the dorsal epidermis described above, one to the ordinary kind and the other to that of the senescent stage.

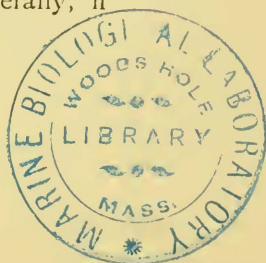
As regards the thickness of the epidermis, some topographical differences are to be found. In the central parts of the dorsal

surface the epidermis is generally 20–25 μ thick, while in the peripheral parts it is somewhat thicker, measuring 25–30 μ . As is pointed out by ABBOTT ('07), it is thinnest (10–18 μ) in the parts directly over the tentacle-sheath.

The ventral epidermis (figs. 2, 3) differs somewhat from the dorsal epidermis in its histological character. It consists of the gland cells and of the ciliated cells. Of the gland cells, one can distinguish the same two kinds that we have seen in the dorsal epidermis. The granular cells (*g. g.*) are more rarely found in the ventral epidermis than in the dorsal. Moreover, there occurs a fairly larger variation in the size of the spherules contained in them: some granular cells may show spherules quite as large as those found in the granular cells of the dorsal epidermis, while others (fig. 2, *g.g.*) may contain much finer spherules measuring only 1–1.5 μ in diameter. The clear cells (*c. g.*) are rather commonly found in the ventral epidermis and are usually of size and of staining reaction standing between the two kinds of the clear cells in the dorsal epidermis. They stain fairly well with basic dyes and enclose in the cell-body a strongly stainable network of fibrils. Some of the clear cells were observed to have been fixed just in the process of the discharge of the inclusion. The matter discharged, which is probably mucous substance, is frequently seen covering the ventral surface of the body. SAMASSA ('92) is of opinion that, all the kinds of gland cells in the epidermis of ctenophores are no more than different phases of one and the same kind of cell. This view was accepted by many subsequent writers including ABBOTT ('07). Evidently, however, some, at least, of the clear cells of *Cocloplana* secrete their inclusion actually, without changing into the granular cells. Direct evidence for this is given just above. Moreover, this seems to be supported by the fact that, on the ventral surface of the body which is extremely slimy, the clear cell is found much more commonly than the granular cell.

The ciliated cell (*c. c.*) is usually columnar in form, showing the nucleus at varying point of its height, in parts where the cell-body is broadest. The appearance of the nucleus resembles closely that of the interstitial cell in the dorsal epidermis. In the surface view of fresh material (fig. 5), the ventral epidermis shows ciliation everywhere, which obscures the existence of gland cells.

At the margin of the body skirt, the ventral epidermis is thickest, the thickness exceeding somewhat that of the dorsal epidermis at the same place. In all other parts, the ventral epidermis is generally, if



not always, thinner than the dorsal epidermis, measuring 18–25 μ in the peripheral parts of the body, and somewhat less in the central. In regions neighbouring the mouth aperture, the thickness of the ventral epidermis scarcely exceeds 10 μ . The epidermis is thinnest in parts directly under the tentacle-sheath, where it is as thin as 5 μ on the average.

There exists nothing like a basement membrane under the epidermis, although its presence is maintained by ABBOTT ('07).

Aboral Sense-organ.

The aboral sense-organ is situated at the centre of the dorsal surface of the body directly above the mouth-aperture. In living specimens, the situation of the organ is indicated by a small roundish unpigmented area readily recognized from the surrounding parts. In the surface view under the microscope (Pl. 4, fig. 6), the organ presents itself as a deep depression somewhat elongate in the transverse direction and containing an otolithic mass in the centre. On either sagittal side of the entrance into the cavity of the depression, there is an area shaped semilunar and covered with cilia, apparently to be identified as the polar plate (*p. p*). In minute points in the structure of this part, *C. bocki* differs somewhat from the other two species, *C. willeyi* and *C. mitsukurii*. In *C. bocki*, the part is raised into a rather tall crest-like prominence, of which the inner side is formed by ciliated epithelium and the outer by ordinary epidermis. Evidently, the entire ciliated part represents the polar plate. The free margin of the prominence is generally divided into from two to five lobes of various sizes (figs. 6, 7), although it is by no means rare, especially in small specimens, that the margin is quite even and lacks lobation entirely: the prominences of the two sides seldom keep up a strict symmetry. In *C. willeyi* and *C. mitsukurii*, the lobation of the polar plates does not occur even in the largest individuals, the entire area being of a simple semilunar shape.

As in ordinary ctenophores, the polar plate consists of a central area (*c. a*) and a marginal area encircling the former (*m. a*) ("Polfeld" or "Mittelfeld" and "Randwulst" of previous writers; CHUN, '80, HERTWIG, '80). The central area is made up of a flat epithelium, while the marginal area is formed of a thicker one. Through the central area appears a number of circular muscle-fibres which functions as the sphincter of the sensory cavity. The peripheral part of the marginal

area is defined rather badly, the central area appearing to pass almost directly over into the ordinary epidermis surrounding the polar plate. The proximal part adjoining the sensory cavity, on the other hand, is defined very distinctly, and is covered with heavy ciliation especially at the median point of the free inner edge where exists a notch as a rule.

The prominences about the polar plates are kept quite erect, and the entrance into the sensory cavity is left wide open, as long as the animal rests calm (fig. 6). But, when this is irritated by giving some light stimulus, the free edges of the plates are suddenly brought together, and close up the entrance, under which condition, the median notch just mentioned becomes very prominent. If a little stronger stimulus be given, the entire aboral region is retracted below the level of the general surface of the body. The closure of the cavity is performed by the sphincter fibres mentioned above, while the retraction of the entire aboral region is worked out by collaboration of fibres abounding in the more peripheral parts. The lobation of the polar plates in *C. bocki* reminds one highly of the "sensory tentacles" described for *Ctenoplana* (KOROTNEFF, '86, WILLEY, '96) and also of the papilliform processes known in *Beroë* (CHUN, '80), both of which occurring in the same part of the plate.

The otolithic mass (fig. 6. *ot*) is situated in the centre of the sensory cavity and is seen doing the usual constant vibrating motion. It is generally spheroidal, but may be of a somewhat irregular shape. Frequently, there occur one or two supernumerary masses of small sizes besides the large normal one. The granules composing each mass (fig. 9) are globular, but may be of an irregular shape. Those of the latter shape are apparently formed by conglomeration of two or more globular ones.

From either transverse corner of the entrance into the sensory cavity, there arise two fine ciliary tracts (fig. 6, *cil. tr*) each of which passes along the interradial plane of the body. The tracts without doubt represent similar ciliary tracts ("Nerven", CHUN, '80), that range between the sensory capsule and the ribs in ordinary ctenophores. They can be traced up to the outer boundary of the unpigmented area, but no farther.

Under the polar plate shows through a pattern of a greenish hue and of a crescentic shape or of a shape somewhat resembling the letter W (fig. 6, *g. g*). This pattern is formed by an assemblage of peculiar fine granules found in deeper parts of the capsular wall. Similar granules are known in the same part of ordinary ctenophores (CHUN, '80).

In Pl. 4, fig. 8 is shown somewhat diagrammatically the structure of the aboral region of *C. bocki* in the retracted state, the figure representing the section of the region along the sagittal plane of the body. A prominent folding of tissues occurs below the general level of the epidermis above the sensory capsule. At the entrance into the capsule, one can recognize a thickening of the epidermis to be identified as the peripheral part of the marginal area of the polar plate. Below this part occurs a very thin ciliated epithelium, which constructs the central area of the plate (*c. a*); abundance of sphincter fibres (*sph*) are found in the parenchyme tissue directly adjoining this part. Next exists a thickening of the epithelium, which forms the proximal part of the marginal area of the polar plate.

The sensory capsule is approximately spherical in form, its wall is made up of slender ciliated cells. Owing to the topographical differences shown by these cells, one can distinguish some zones in the capsular wall:— Directly succeeding downwards the part constructing the proximal margin of the polar plate, is a zone carrying very long cilia (*cn*). The cilia appear to be cemented together by a material staining vividly with eosin. Without doubt, the cilia represent the cupule of the sensory capsule of ordinary ctenophores, although they are never found to fuse together so firmly as in those forms. The cells bearing them are roughly columnar in shape and the cytoplasm stains with eosin somewhat better than that of the cells in the neighbouring zones.

Below the zone mentioned above, the wall of the capsule is constructed for the greater part by very tall and slender cells carrying short cilia. The nuclei are situated in the wall in three to six strata. Near the bottom of the capsule, exists a zone of cells containing highly acidophilous granules (*g. g*). The granules are apparently the same that are observed to form the greenish pattern referred to before. In this same zone or perhaps below it occur cells which carry the cilia supporting the otolithic mass (*bal*). The cilia are distributed evenly on all sides of the capsular wall without fusing into "balancers" as in ordinary ctenophores. To each otolithic granule is attached a nucleus which comes from the mother cell of the granule.

As it is evident from the above description, the aboral sense-organ of *Coeloplana* may be said to be nearly identical in every point with that of ordinary ctenophores. But, it shows clearly the signs of degeneration as regards some features, as for instance, diffuse cilia instead of the balancers and also the rudimentary condition of the polar plates.

Tentacular Apparatus.

The tentacular apparatus of *Cocloplana* is largely of the same structure as that of the cydippid ctenophores. Two apparatuses make a pair and are placed in the transverse plane, one on either side of the sagittal axis of the body. The tentacle itself is an extremely contractile filamentous organ with numerous accessory branches arranged at regular intervals on it throughout its length. When fully extended, it may be more than twenty times as long as the diameter of the body in a moderately distended state and it can be withdrawn into a sheath formed by a caecal depression of the body surface. The proximal end of the tentacle is enlarged into a root-like structure called the tentacle-basis, and is attached to the wall of the sheath.

In all typical cydippid ctenophores (Pl. 2, fig. 3), the tentacle-sheath and the tentacle-basis lie nearly vertically, parallel with the main axis of the body, and the tentacle-sheath may be divided into two parts, one elongate vertically containing the tentacle-basis and the other set more or less oblique accomodating the tentacle-stem. These two parts of the tentacle-sheath are well represented in *Cocloplana* too (Pl. 2, fig. 4; Pl. 3, fig. 8), but they are both disposed horizontally, the part accomodating the stem directly on the roof of the part occupied by the basis; the entire sheath accordingly makes a sharp bent between those two parts. For the sake of description, I shall hereafter call these two parts of the tentacle-sheath one, the dorsal, and the other, the ventral compartment (*t. sh. d*; *t. sh. v*). More precise situation and configuration of the tentacle-sheath may be understood by Pl. 1, fig. 2.

The ventral compartment (Pl. 2, fig. 2; Pl. 3, figs. 1-8; *t. sh. v*) takes precisely the shape of the tentacle-basis which it encloses. In the dorsi-ventral view, the compartment is divided, though not very definitely, into three parts, viz. a relatively narrow median part lying in the transverse plane of the body and a pair of somewhat broader lateral parts placed on either side of the former. The dorsal compartment (*t. sh. d*) is flask-like in shape and provided with a conspicuous lateral outbulging on either side of its base. Moreover, it sends out towards the centre of the body a pair of small horn-like processes. The two compartments are communicated with each other near the proximal end by a relatively narrow median passage. With regard to the tentacle-sheath, ABBOTT maintains: "Lying normally below the main cavity of the sheath, but sometimes pushed to one side, is what may be called

the accessory sheath. The tentacle itself may be said to be anchored to the whole floor of this accessory sheath which spreads out into a broad flat cavity and is lined with formative tissue" ('07, p. 55). Evidently, the accessory sheath referred to is nothing but the ventral compartment of the sheath, therefore, not a characteristic structure of this animal, being found in all cydippid ctenophores too.

The tentacle-sheath is lined with a low epithelium of the ectodermal origin and is beset with cilia all over its surface. The cilia are rather short and stiff, especially those which are found in the distal parts of the dorsal compartment. The two kinds of gland cells occurring in the epidermis are also met with here, though much rarer than the ciliated cells. They are usually larger in size than the latter, bulging out above and below the level of the epithelium. According to ABBOTT ('07), the tentacle-sheath should be lined with endodermal cells in certain places, and the cells are said to proliferate by budding, giving rise to a kind of free cells of phagocytic function. It is highly probable that, the alleged endodermal cells are nothing else than the cells on the dorsal side of the tentacular canal, which are generally of enormous size and show a quantity of inclusions, besides, colloblasts are found among the inclusions rather commonly. It is not impossible that, the cells with such inclusions, especially those having colloblasts within, should be taken for phagocytes, although they are fundamentally different from them of course.

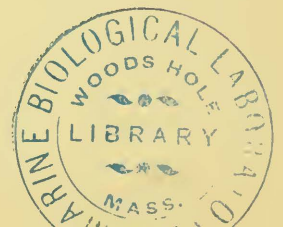
The tentacle-basis occupies the whole floor of the ventral compartment of the sheath and is situated quite horizontally. To bring about this peculiar disposition, the basis makes a turning of ninety degrees at a certain stage of development of the animal from the original vertical situation to the new horizontal one. The proximal end of the basis in this new situation is homologous with the original aboral end, and the distal end with the original oral end. Though peculiar is the disposition, the tentacle-basis does not show any deviation from that of cydippid ctenophores with respect to structure. It is made up of embryonal tissues in various developmental stages of the component parts of the tentacle. It consists of two distinct parts, one which gives rise to the muscular core of the tentacle-stem as well as of the accessory filaments (Pl. 2, figs. 2, 4; Pl. 3, figs. 3-6, 8; *t. r*) and the other, from which the epithelial parts of the same are derived (*b. ep*). I propose to call the former the tentacle-root and the latter the basis-epithelium.

In the total view, the entire tentacle-basis presents itself as a shield-shaped structure which consists of three distinct parts lying along

the transverse axis of the body, with two relatively broad parts on each side of the narrowest median part (Pl. 2, fig. 2). The median part ("Mittelstreifen", HERTWIG, '80, SAMASSA '92) is spindle-shaped in the dorsi-ventral view, it is made up of the tentacle-root and the part of the basis-epithelium overlying it. The lateral parts ("Seitenfeld", HERTWIG, '80; "Seitenstreifen", SAMASSA, '92) are oblong in shape and are formed by the part of the basis-epithelium which does not cover the tentacle-basis. The length of the three parts is nearly the same. The proximal end of the lateral parts is placed just outside of the transverse wall of the pharynx, while that of the median part attains somewhat nearer the centre of the body and is wedged in the median cleft of the pharyngeal wall to be described afterwards. The tentacle-stem is inserted at the end of the proximal one-third of the length of the median part of the tentacle-basis.

The basis-epithelium (Pl. 2, fig. 2; Pl. 3, figs. 5, 6, 8; *b. ep*) is, after all, that part of the epithelium of the tentacle-sheath which occupies the entire floor of the ventral compartment of the sheath. It differs from the epithelium of the other parts of the sheath in being considerably thicker, consisting, as it does, of very small cells superposed in more than forty cells deep. These cells all show a strong affinity for basic dyes, and the structure has a very conspicuous appearance in stained sections. The conspicuity is enhanced by the structure showing often some foldings (Pl. 3, fig. 6, *b. ep*). The differentiating process of the tissue of the basis-epithelium advances largely centripetally: the growing zone is situated in the marginal regions, and the tissue becomes more differentiated towards the central region, where it passes almost insensibly over into the epithelium of the tentacle-stem or into the colloblasts. In the marginal regions the basis-epithelium is very thin and is formed by extremely minute cells; it stains uniformly very intensely with haematoxylin. The epithelium becomes thicker towards the central region, and the individual cells grow larger and are better differentiated. The proximal and distal halves of the basis-epithelium differ from each other in their ultimate fates, the former developing into the epithelium of the tentacle-stem and the latter into colloblasts. Often there exist some isolated patches of young tissue among the older.

The tentacle-root (Pl. 2, figs. 2, 4; Pl. 3, figs. 3-6, 8; *t. r*) is a laterally compressed fan-shaped structure; it consists of embryonal muscle-fibres converging into the tentacle-stem. It is divided into two symmetrical halves by a kind of septal band of a gelatinous tissue situated in the



transverse plane. The formative zone of the accessory filaments is localized at the distal end of the tentacle-root (Pl. 3, fig. 8), while that of the tentacle-stem extends all through the remaining parts of the root. The rudiments of the muscle-fibre appear at first as a gelatinous mass stained uniformly (*m. f'*); the fibrous character becomes apparent only in a later stage with development (*m f*). The fibres show at first basophily, but acidophily afterwards.

As is indicated above, the accessory filaments (Pl. 3, figs. 6, 8: *a. f'*) develop from the distal end of the tentacle-root and are transferred gradually towards the stem with which they are connected at last (fig. 8). Each of them at first shows numerous nuclei in it, but no muscular characteristics whatever. Such primordial accessory filaments are found usually in crowd, so that there may appear as many as thirty of them in a single cross-section of the tentacle-root (Fig. 6, *a. f'*).

The tentacle-stem seems to present nothing peculiar than what is already known in cydippid ctenophores. It consists of a core of longitudinal muscle-fibres covered by an epithelium. The interspaces between the fibres are occupied by a gelatinous cementing matter called "Perimysin" by SAMASSA ('92). This contains some nuclei in it, whereas, the fibres do not show them altogether. The entire core is divided into two lateral halves throughout its length by a septal band of gelatinous tissue. This band is directly continuous with the gelatinous tissue that divides the tentacle-root into two lateral halves mentioned already.

The accessory filaments are attached to the stem on the ventral side, in the same plane as the band. Their structure conforms largely with ABBOTT'S description and figure of the same organ of *C. mitsukurii* ('07, Pl. 2, fig. 37). It is roughly cylindrical in form and consists of two kinds of tissues, one muscular and the other gelatinous, the former stains well, the latter only weakly, with acid dyes, and the latter alone contains nuclei in it. The distribution of the two kinds of tissues may be understood from Pl. 4, fig. 11 (longitudinal section) and fig. 10 (transverse section). A narrow slit-like space of the gelatinous tissue occupies the median plane, and on each side of it, occurs another space appearing crescentic in cross-section, outside the latter and close to, and parallel with, the lateral margin is found still another space which is as narrow as the median. The muscular tissue between those spaces is nearly the same in breadth everywhere. The accessory filament is identical in structure in the three species, no structure such as depicted in ABBOTT'S Pl. 10, fig. 38 having been met with.

All the accessory filaments are covered all over by colloblasts. These are apparently the same in structure as those of ordinary ctenophores. But as the descriptions on the structure of previous writers seem to be unsatisfactory, I shall deal with it in some length.

The colloblast or the adhesive cell (Pl. 5, fig. 12, g) consists of a bell-shaped main part which may be simply termed the head (*h*) and two accessory filamentous bodies, one spiral (*s. f*) and the other nearly straight (*c. f*), attached to the concave side of the head. The head is made up of a substance which stains fairly well with eosin. The convex surface is covered by refringent granules (*gr*) arranged in one layer, to which the sticky nature peculiar to the colloblast is probably to be attributed. Directly beneath this layer is found another of small spherules (*sphl*) arranged at fairly regular intervals from one another. They present somewhat higher eosinophily than the surrounding ground substance. A spheroidal body (*c. sph*) is situated nearly in the centre of the head. It takes up eosin as strongly as the spherules mentioned above. Some delicate fibrous tracts radiate from that body through the substance of the head. Besides, two filaments are connected with the body. One of them, the spiral filament (*s. f*), is of muscular nature, staining with eosin fairly well. The spiral makes seven or eight dextral turns around the other filament, which is to be called the central filament. This (*c. f*) is much finer than the spiral filament and passes almost directly through the axis of the coil of the latter. It is attached to the base of the spheroidal body in the head already described at the distal end, and to the external membraneous covering of the accessory tentacle at the proximal end. The spiral filament joins the central filament just at, or a little above this latter point of attachment. The central filament stains with haematoxylin very well, which character distinguishes it sharply from the spiral filament.

It is a rather remarkable fact that the existence of the central filament of the colloblast is not mentioned in the works of such authors, as CHUN ('80) and SCHNEIDER ('02). According to DELAGE and HÉROUARD ('01), its presence had been denied by VIGNON. HERTWING ('80), SAMASSA ('92) and ABBOTT ('07), however, have noticed the existence of the filament definitely. CHUN's figures show ('80, Pl. 18, figs. 6, 10 and 12) the spiral filament attached directly to the granular layer on the surface of the head, while HERTWING ('80) has pointed out the presence of a "Korn" at the centre of the latter, whence proceeds the spiral filament, referring undoubtedly to the spheroidal body described above. SAMASSA

('92), after calling attention to the difficulty of making out the minute condition of that part, has merely stated that, the central filament bends itself into the spiral at the spot. ABBOTT'S observation ('07) on the structure of the colloblast almost agrees with mine, but not on the nature of the spheroidal body. He seems to be of opinion that, the body is the cell-nucleus itself that has come from the mother cell. But this seems to be incorrect, since, beyond other facts, the body exhibits staining reaction entirely different from that of an ordinary cell-nucleus, being eosinophilous and not cyanophilous.

Next I may mention the development of the colloblast, although my observation on each successive stage is not very satisfactory. As already indicated, the colloblast develops in the distal parts of the basis-epithelium, where the epithelium is made up exclusively of the mother cells of the colloblast in various developmental stages. Each undifferentiated mother cell is polygonal in shape and provided with a disproportionately large nucleus situated in the centre (Pl. 4, fig. 12, a). The development is initiated by a change that consists in the differentiation of two kinds of granules out of the cytoplasm, one, very fine and eosinophilous, and the other, somewhat coarser, hardly stainable and appearing very refringent. The former assemble about the nucleus, which has become somewhat eccentric in situation, while the latter occupy the parts of the cell-body opposite to the nucleus (b). The segregation of the two kinds of granules becomes more and more apparent with development, meanwhile the nucleus has grown quite eccentric and located at the margin of the cell-body (c). Then the first trace of the spiral filament makes its appearance in the neighbourhood of the nucleus. It is like a cord turning spirally a few times (d); no doubt it is derived from the eosinophilous plasmic granules described above. The length of the filament increases with development at the expense of those granules, until finally, seven or eight spiral rings are formed. The refringent granules assemble on the surface of the cell and arrange themselves into the superficial layer. The main part of the cell-body changes into the head of the colloblast. The nucleus remains until a comparatively later period without showing any change whatever. At about the time when most of the rings of the spiral are formed, the nucleus begins to be elongated in the direction of the axis of the spiral. It is spindle-shaped for some time, but finally it is drawn out and becomes filamentous (f, g). Thus it is clear that, a colloblast develops from a single formative cell, the cytoplasm forming the head and the spiral filament, and the nucleus

becoming the central filament.

As regards the development of the colloblast, we have opinions of SAMASSA ('92), SCHNEIDER ('02) and ABBOTT ('07), which disagree much with one another. SAMASSA maintains that, a colloblast originates from two formative cells situated close to each other in the tentacle-basis, and one of them which is glandular, develops into the head of the colloblast, while the other which is a kind of interstitial cell, gives rise to the central and spiral filaments. The forming processes of those parts, however, are not given in detail. He states, for the concluding remark:—"Durch vorstehende Darstellung glaube ich erweisen zu haben, dass das man bisher als Greifzellen betrachtete, aus mindestens zwei Zellen zusammen gesetzt ist, von denen die eine den Drüsenantheil derselben, die andere den Central- und Spiralfaden bildet, welche Beide ja eigentlich nur einen einzigen Faden vorstellen" ('92, p. 102). SCHNEIDER is of opinion that, before the differentiation of the mother cell of the colloblast, the nucleus is multiplied by repeating division, until seven nuclei are formed in the same cell at last. One of these nuclei occupies the position at one end of the cell, where the cytoplasm has been in the mean time filled with yellowish refringent granules, SCHNEIDER calls this part of the cell the granular cell ("Körnerzelle"). The other part of the cell is split longitudinally into six portions named the fibrous cells ("Faserzellen"), in each of which one of the remaining six nuclei is enclosed. All the fibrous cells are elongated in the longitudinal direction. The granular cell is also divided longitudinally into six portions, and each of them is connected with a fibrous cell. Each portion of the granular cell develops into the head of the colloblast, and each fibrous cell into the spiral filament. Thus, according to SCHNEIDER's opinion, a single mother cell should give rise to six colloblasts.

ABBOTT's observation conforms nearly with mine as to the origins of the head and spiral filaments, but not on the development of the central filament as well as of the spheroidal body in the head. As to the central filament, he describes that the filament is "derived from the denser cytoplasm immediately surrounding the nucleus". And regarding the spheroidal body, he seems to be of the opinion that the body is derived from the nucleus of the mother cell, as it is previously remarked. However, it is certain that the spiral filament, as well as the spheroidal body, develops from the cytoplasm of the mother cell, and the central filament from the nucleus. The difference of staining reaction shows this most unmistakably, without mentioning other differences of minor

importance.

Gastro-vascular System.

The mouth is situated in the centre of the ventral surface of the body; it may however be more or less eccentric in situation in individuals in which the halves of the body divided by the sagittal plane are unequally developed. It presents itself as a small aperture of a roundish shape. It leads dorsally into the pharynx (Pls. 2 & 3; *ph'*) which is of a depressed form, pronouncedly wider than high, and not elongate in the vertical direction as in pelagic ctenophores. In the dorsi-ventral view, the pharynx is roughly quadrate-shaped, often somewhat elongated in the sagittal direction (Pl. 2, figs. 1, 2). But, in the horizontal sections, the pharynx is of a shape like the letter H with the transverse bar of H lying in the sagittal plane, the clefts in front and behind between the lateral bars of H being produced by the proximal ends of the tentacle-basis wedged therein. As viewed in vertical sections traversing parallel with the sagittal plane, the pharynx shows itself near the latter plane like a depressed U (Pl. 3, figs. 1, 2), but in places somewhat away from there, as a pair of isolated chambers (figs. 3, 4), the transverse bar of U being replaced by the proximal end of the tentacle-basis.

This peculiar condition of the pharynx, so different from the condition in ordinary ctenophores, is not to be considered as the result of mere reduction of its vertical axis. As is clearly shown by the development of the animal to be described later, the pharynx of the larva is at first perfectly the same as that of ordinary ctenophores; but, later it is sectioned into two parts, one situated dorsally and shorter in length and the other placed ventrally and of the greater length; the latter part spreads out into the body skirt, while the former persists as the pharynx of the adult animal. Hence, the pharynx of the adult is merely a part of the original larval pharynx. In relation with this peculiarity of the pharynx, there are several characteristics to be found with respect to the arrangement of the canal system.

The wall of the pharynx shows a large number of conspicuous folds disposed largely parallel with the sagittal plane of the body (Pl. 2, figs. 1, 4; Pl. 3, figs. 1-4, 8; *ph. f*). The folds are divided into four interradially placed subequal parts by two furrows that lie in the two periradial planes of the body.

As the development just mentioned already suggests, the epithelium

which lines the pharynx is of an essentially identical character with the ventral epidermis. It consists of ciliated cells and gland cells. But, excepting a small extent of the floor immediately within the mouth, where it is almost the same in appearance as the ventral epidermis, the epithelium of the pharynx is much taller and comprises much more numerous gland cells of very large size. Especially the folds exhibit quite numerous large gland cells, of which the granular cells appear very conspicuous, taking stains exceedingly well, the affinity of those cells for acid dyes much exceeds that of the same kind of cell in the epidermis. It seems that the chemical composition of the granules in those cells differs somewhat from that of the same in the epidermal granular cells. The folds are without doubt homologous with the so-called pharyngeal folds (Magenwülste) of ordinary ctenophores (cf. MORTENSEN, '12) (Pl. 2, fig. 3, *ph. f.*). This view is supported by agreement of the general macroscopical appearance, and also of the structure of the epithelium of the folds (cf. CHUN, '80, Pl. 8, fig. 15; Pl. 3, fig. 5).

In the pharyngeal cavity I have often met with exoskeletons of small amphipods or isopods, sometimes in small fragments and at other times in the complete state. Evidently, the soft parts had disappeared by the digestive function in the pharyngeal cavity, and in the function the secretion from the gland cells of the pharyngeal folds had played without doubt an important part.

At the bottom of the sagittal furrow on the pharyngeal roof, is a slit-like opening elongate in that plane, which leads dorsally into a short tube communicating with the infundibulum to be directly dealt with (Pl. 2, figs. 2, 4; Pl. 3, fig. 1; Pl. 4, figs. 8, 13; *oe*). This tube is compressed like the opening with the greater diameter in the sagittal plane, and is lined with an epithelium consisting largely of columnar ciliated cells with both kinds of the gland cells dispersed between them. The columnar cells are of an uniform size and shape in all places, and carry exceptionally strong cilia at their apices (Pl. 4, figs. 8, 13). This tube may be called "oesophagus" after MORTENSEN's terminology.

Along the median transverse plane of the wall of the oesophagus exist very large clear gland cells (*c. g.*), which make the wall project on either side strongly into the internal cavity of the oesophagus in the form of a broad ridge, giving the cross-section of the cavity a dumb-bell shape (fig. 13). The oesophagus frequently shows a few branch canals (fig. 8, *oe. br.*), which open into either the pharyngeal cavity or the infundibular cavity. Further, there may be found a canal which brings

the two cavities into communication along with the oesophagus. These branches and canal are lined with an epithelium which is identical with that of the oesophagus. Evidently, CHUN ('80) has recognized the oesophagus in the stomodaeum of ordinary ctenophores, contrary to MORTENSEN'S statement ('12). Thus, what CHUN has called "Trichterlippen" is to be identified apparently with the parts of the wall of the oesophagus that show the large clear gland cells described above and his "Trichterspalt" with the narrow passage between those parts.

The oesophagus communicates dorsally with the infundibulum (Pl. 2, figs. 2, 4; Pl. 3, fig. 1, Pl. 4, fig. 8; *i*), which forms the source of the whole endodermal parts of the gastro-vascular system. It is placed directly beneath the aboral sense-organ and is cup-like in shape, showing compression in neither direction. It is lined with a low ciliated epithelium, in which occur numerous nuclei arranged at very short and regular intervals (Pl. 4, fig. 8; *i*). The epithelium is very low on the roof of the cavity; it becomes gradually taller towards the bottom, where it goes into the oesophageal epithelium, the transition between the two kinds of epithelia being rather definite.

Directly from either sagittal side of the infundibulum, starts an excretory canal (Pl. 4, figs. 8, 14; *ex. c*), the part which can be identified with the infundibular canal of ordinary ctenophores (Pl. 2, fig. 3, *inf. c*) being absent. Each excretory canal proceeds to the dorsal direction and opens without branching to the exterior by the excretory pore situated in the sagittal plane just outside the sense-organ. ABBOTT ('07) maintains that, the excretory canals "arise in such a position that along the tentacular plane the lower one is to the right and the upper one to the left of that plane" (p. 53). But I found of the canals that both the starting point and the external opening lie right in the sagittal plane of the body. The excretory canal is lined with a low ciliated epithelium of the same character as that of the infundibulum for the greater part of its length. The epithelium thins strikingly close to the pore, even to an extent to become almost structureless and glassy in appearance.

In the surface view of living specimens (Pl. 4, fig. 6), the excretory canal shows through rather distinctly under the epidermis. The positions of the excretory pores are indicated by a peculiar assemblage of granular gland cells around a roundish or somewhat crescentic depression of the epidermis within the aboral unpigmented area referred to before.

The infundibulum sends off on either transverse side of its wall a

perradial canal (Pl. 2, figs. 2, 4; *per. c*), which forms the trunk of the entire canal-system of each half of the body. The canal is fairly broad but very short; it divides at once into three branches, one which proceeds in the perradial plane and two which lie on each side of it in the interradial plane. The former branch (Pl. 3, fig. 2, *t. c*), the tentacular canal, furcates into two secondary branches close to the proximal end of the tentacle-root which pass along the lateral sides of the latter. Each of the branch is expanded abruptly into a roomy canal at the proximal end of the basis-epithelium, and accompanies the whole extent of the latter (Pl. 2, figs. 2, 4, Pl. 3, figs. 3-8; *t. c*).

The two lateral branch canals of the perradial canal (Pl. 2, figs. 2, 4; Pl. 3, figs. 2-5; *s. ph. c*) run in the interradial direction, traversing obliquely the roof of the pharynx. On reaching just beyond the interradial corner of the latter, they bend sharply backwards and pass along the lateral margins of the pharynx towards the sagittal plane of the body and terminate shortly before reaching that plane. These canals without doubt represent the subpharyngeal meridional canals of ordinary ctenophores, and they may be termed the subpharyngeal canals.

From each furca of the tentacular canal, at about the position where it forms the lateral expansion mentioned before, there arises a canal on the dorsal side (Pl. 2, figs. 2, 4; Pl. 3, figs. 6, 7, *s. t. c*). Evidently, this canal is homologous with the subtentacular meridional canal of ordinary ctenophores, and it may be named the subtentacular canal. This canal runs along each side of the tentacle-sheath and terminates a short distance behind the external opening of the sheath.

Both the subpharyngeal and subtentacular canals give rise to several diverticula on the dorsal side which enter the dorsal tentacles. Further they send off numerous branches on the lateral sides, which undergo divisions and anastomoses and bring about the extensive canalar network in the peripheral parts of the body (Pl. 2, figs. 1, 2, 4; Pl. 3, fig. 2; *br. c*). The arrangement of the canalar network is subject to considerable individual variation, while the main parts of the canal system keep up constancy in that respect.

The endodermal epithelium may be divided into three kinds. The first kind is low and ciliated and consists of cells which are usually flat or cubical and more rarely somewhat cylindrical; further, it comprises so-called ciliated rosettes. This kind of epithelium apparently serves in making water in the canal circulate along through the canal system by means of the activity of the cilia. Further, it seems to absorb nutrition

towards the body parenchyme through the rosettes. The second kind is tall, non-ciliated and is made up of cells of large sizes which are more or less vacuolated and often amoeboid in character. No rosette occurs in this kind of epithelium. This epithelium performs intracellular digestion of food material and possibly excretory function too. For the sake of description, I shall call the first kind of epithelium the ciliated epithelium and the second the vacuolated epithelium. The ciliated epithelium constructs the ventral walls of the tentacular, subpharyngeal and subtentacular canals as well as both the dorsal and ventral walls of the peripheral branchlets. The vacuolated epithelium lines the lateral walls of the perradial, subpharyngeal and subtentacular canals. It also occupies the lateral sides of the canalar branchlets, where it forms a ridge-like tract on each side (Pl. 4, fig. 15; *v. c.*). The vacuolated epithelium develops to the utmost thickness on the dorsal side of the tentacular canal, where it consists of extremely bulky cells enclosing nuclei also of large size.

The third kind of epithelium, which may be called the "palisade" epithelium, because of its appearance somewhat reminding one of the palisade tissue of the plant leaf, is found on the dorsal side of the subpharyngeal and subtentacular canals (Pl. 5, fig. 11; *pal*). It presents a character practically between the above two kinds. It is fairly tall, slightly vacuolated and distinctly ciliated, but contains no rosette; it consists of tolerably large columnar cells closely juxtaposed. Since it is provided with both the cilia and the food-vacuoles, it can perform without doubt both of the functions of the two kinds of the epithelium previously mentioned.

The ciliated rosette, which occurs in the ciliated epithelium of the canal system, is of an identical structure with that of ordinary ctenophores (CHUN, '80, Pl. 16, figs. 37, 38; HERTWIG, '80, Pl. 21, fig. 8). It is composed of ciliated cells, small in size and pyramidal in form, arranged in two rings, superposed one upon another (Pl. 4, fig. 17). The inner ring of the two (*in. r.*) consists of cells usually eight in number arranged around a small central space. The cells carry very long and thick cilia which lie imbedded in the gelatinous parenchyme tissue. The tissue appears to be of more fluidal consistency in that particular part, being stained more weakly. The outer ring (*ou. r.*) is likewise made up of eight cells or so, and has usually a greater diameter than the inner ring, so that, the ring often shows its peripheral parts outside the margin of the inner ring in the front view of the rosette. The cilia borne by

the outer ring are rather short and stiff and project freely into the lumen of the canal. As CHUN ('80) has remarked, the cilia appear to be cemented together into a mass somewhat reminding one of a comb of the rib of ordinary ctenophores.

The rosette is found practically in any part of the ciliated endodermal epithelium of the canal-system, except possibly that of the epithelium of the infundibulum and of the perradial canal. Its situation is frequently marked by a funnel-shaped depression of the canal wall.

As to the function of the rosette, most of the previous writers have regarded the structure to be a passage through which the water in the canal flows into the body parenchyme. Judging from its appearance in general, but especially from the condition of the cilia, this is very likely to be the case.

As already mentioned, the vacuolated epithelium encloses food particles in the cell-body, of which pieces of striped muscles apparently of small crustaceans are the commonest. This fact indicates that, there takes place intracellular digestion in the endoderm, just as in ordinary ctenophores.

Besides food particles, the cells may contain an abundance of detrita, either organic or inorganic, which may be found to be enclosed in vacuoles. The part of the cell-body surrounding such a vacuole or vacuoles often comes out from the cell and forms a more or less distinct spheroidal body (Pl. 4, fig. 15, Pl. 5, fig. 4; *cor*). Such a body is eventually discharged or extruded, as it were, from the seat of their origin into the canal, to become the free corpuscles that float in, and move along with the water in the canal system. The corpuscles may be observed in various stages of extrusion on sections. On completion of this process, there are left in the matrix hollow spaces which nearly correspond in size with the liberated corpuscles. After repeated occurrence of the process, the matrix may present a much pitted or honey-combed appearance.

The corpuscles set free from the digestive epithelium are conveyed through the canal system evidently by the action of the cilia carried by the low epithelium. In living specimens, the circulation of the corpuscles offers a very remarkable spectacle under the microscope, as was noted by ABBOTT ('07). It presents an appearance somewhat reminding us of the circulation of blood-corpuscles through the blood-vessel. The direction of the current may differ within a short distance and may be reversed in one and the same place within quite a short duration of time. The

corpuscle (Pl. 4, fig. 15) varies a great deal in size and in the kind of inclusions. In Pl. 4, fig. 16 e-h are represented some of the corpuscles in natural state, while a-d shows them in fixed and stained condition. They are sometimes provided with a nucleus and rarely even with two nuclei (a-c), which have come without doubt from the matrix cells.

Besides the method of formation of the corpuscles just mentioned, there seems to be another by which larger bodies such as figured in fig. 16, i are produced. This latter method consists in the parts of the vacuolated epithelium loaded with foreign objects being simply constricted off from the matrix, as ABBOTT ('07) previously remarked. Although practically any vacuolated part of the epithelium may perform intracellular digestion, that of the dorsal wall of the tentacular canals appears to play the most important part of the function. The epithelium in that part has by far greater thickness than elsewhere and contains usually a very large quantity of foreign objects. Colloblasts may often be met with among the inclusions in that part; evidently, they have been caught in together with the food matter. The palisade epithelium on the dorsal side of the subpharyngeal and subtentacular canals also seems to digest food material intracellularly, as may be judged from the inclusions.

As regards the physiological significance of the process described above, it seems to be reasonable to regard the process to be a sort of excretory function. Anyway, it is certain that, by the production of the corpuscles, the indigestible parts of intracellularly ingested food are removed from those cells. At the same time, it is not impossible that, certain waste products of metabolism are ejected by means of the corpuscles which contain vacuoles without any solid inclusion whatever. Certain as the occurrence of the intracellular digestion in the animal, it seems probable that, that does not constitute the sole process of digestion, but this is effected in part also outside of the cells. The frequent occurrence of the remains of crustacean skeleton in the cavity of the canal system and especially in that of the pharynx as mentioned above, stands in favour of this view. It seems to me that, the process of the digestion begins in the pharyngeal cavity and is brought to a finish intracellularly in the vacuolated epithelium of the endodermal parts.

Before closing the accounts on the gastro-vascular system, I may point out some discrepancies existing between observations of previous writers and myself. According to ABBOTT ('07), there should be a pair of perradial canals which are given out from the infundibulum

in the sagittal plane. However, as far as my observation goes, such canals are never present, there being two perradial canals only, which start from the transverse sides of the infundibulum. He further maintains that, the meridional canals of ordinary ctenophores are entirely obliterated in *Coeloplana*. But there is no room for doubting that, the subpharyngeal and subtentacular canals do represent the meridional canals: those canals are lined with a tall palisade epithelium on the dorsal side and the gonads take their origin in that epithelium, precisely as it is the case with the meridional canals of the ordinary ctenophores. ABBOTT further denies the existence of cilia in the endodermal parts of the canal system. However, the ciliation is easily observed in any part of the low epithelium, provided the material be preserved tolerably well. The same fact is given in KREMPF'S work ('21). But it is rather noteworthy that, the palisade epithelium of the subpharyngeal and subtentacular canals shows distinct ciliation, since the epithelium of the meridional canals of ordinary ctenophores is devoid of cilia in that part.

KREMPF ('21) distinguishes two canal systems in *Coeloplana*, which he named "réseau méridien ou réseau gonadien" and "réseau pharyngeal" respectively. According to him, the former represents the meridional canals and their branches of ordinary ctenophores, and the latter the pharyngeal canals and their branches. But, so far as my observation has ascertained, canals which may be identified with the pharyngeal canals of ordinary ctenophores seem to be wanting in *Coeloplana*. The pharyngeal canal of ordinary ctenophores is sent out from the perradial canal at a point generally somewhat proximal to the branching of this canal into interradianal canals. Moreover, the pharyngeal canal shows a ridge-like tract along each sagittal side of its wall. In *Coeloplana*, however, canals with such distinguishing features can not be recognized altogether, and all the canalar network in the regions about the pharynx are the branches of the subpharyngeal canals.

Gonads.

Since both KOWALEVSKY and ABBOTT could not observe gonads in *Coeloplana*, the genital system of this interesting animal has remained unknown. Certain previous writers expressed their expectation à priori that, such an aberrant form would present a good many peculiarities when the condition of the gonads would be made out. And the fact is just as it had been expected, there are indeed several highly characteristic

features concerning gonads that have been revealed by the works of KREMPF and myself.

All the three species examined by me showed both the male and female gonads. In ABBOTT's species, *C. willeyi* and *C. mitsukurii*, most of the specimens obtained in July and August had male gonad in a mature or nearly mature condition, but, excepting a few individuals of large sizes, those collected during the winter or during the early spring months did not possess the male gonad, and in neither of those two species have I found any mature female gonad—this evidently shows that, the female gonad develops mainly in late summer or in early autumn the same as in *C. bocki* to be mentioned next. In this species, many of the specimens collected during summer and early autumn months had gonads of both sexes. Especially, individuals obtained between the middle of August and the end of September contained very large egg-cells almost without exception. The eggs seemed to be laid generally before the middle of October. Thus, in the beginning of October, 1919, I observed the species at Misaki, of which most of the individuals contained mature eggs and some of them were spawning. One and a half months later, in the latter part of November, when I examined the species again, however, I met with but rarely individuals containing eggs. In short, besides some negligible exceptions, the breeding season of *Coeloplana* may be said to extend from early summer to early autumn, the gonads developing in the main during summer months and the spawning taking place generally in late summer or in early autumn.

Coeloplana is hermaphroditic like all ordinary ctenophores. The genital elements develop in the dorsal wall of the eight canals representing the meridional canals of those forms, viz. the subpharyngeal and subtentacular canals (Pl. 2, figs. 2, 4). The eggs (*ov*) have their origin in continuous tracts throughout the length of those canals, the sperms (*te*), on the contrary, develop in a certain number of compact masses distinct from one another from the same canals. The relative position of the male and female cells in the same canal is similar to that found in ordinary ctenophores, the eggs situated on the perradial side and the sperms on the interradian side of the wall of the canal.

Testis.

The number of testis, i. e., each separate mass of sperms, occurring in one individual varies to some extent with different individuals. In the majority of the cases examined in all the three species, there were met

with two to five (rarely up to seven) testes along each subtentacular canal, while I could find only one or two testes along each subpharyngeal canal and that in rather rare cases in *C. bocki* (Pl. 2, figs. 1, 2, 4; *te*), more commonly, there occurs none altogether along this canal in that species; the two remaining species were always devoid of them along the same canal. In living specimens, the testes can be easily found even with the naked eye as small whitish spots situated serially along both sides of the tentacular sheath (Pl. 1, fig. 1; *te*). It happens but rarely, however, that all of the testes in the same canal develop simultaneously; more commonly we find that, while some testes contain fully developed spermatozoa in quantities, others in the same canal show the sexual cells still in the cellular state. The development of the testes arising in one and the same canal advances as a rule in centrifugal direction, the more peripherally situated testes being always in a less advanced stage of development than the more proximarily situated ones.

Each testis (Pl. 5, figs. 1, 2, 6) is spheroidal, pyriform or somewhat irregular in shape. It develops always in relation with those canals on their dorsal side, frequently at the end of a short stalk-like diverticulum arising on the interradial side of the canals. Each is made up for the most part of sexual cells interspersed with a few apparently non-sexual cells. The sexual cells form several compact masses which are marked off rather sharply from one another, much as in ordinary ctenophores. Each mass is separated by a membranous structure showing several nuclei of a flattened or a vesicular form.

In a half-mature testis such as figured in Pl. 5, fig. 4, various developmental stages of the sexual cell may be met with, the spermatozoa forming the apical part of the testis and the younger elements the basal. The male sexual cells of the earliest stage, the spermatogonia (*spg*), occur mainly in the basal parts of the testis. They are generally oblong in shape and are furnished with a spheroidal or ellipsoidal nucleus in the centre. The nucleus may measure 2-3 μ in diameter and encloses usually one or two nucleoli besides some chromatin granules. The testes of the earliest developmental stage are composed entirely of such cells. Successive developmental stages of the sexual cell up to the spermatozoon could not be followed out. Only a few stages most commonly met with are shown in Pl. 5, fig. 4. In the stage marked *spc*, the nucleus contains a single chromatin clump in the centre, leaving the peripheral parts quite clear—this apparently represents the synapsis stage. Next, in the stage indicated *spd*, the nucleus is pyriform and shows the

chromatin substance on the surface—this is probably the spermatid stage. The spermatozoon (*spz*, fig. 3) is filiform, with a very slender head tapering anteriorly a little and measuring some 7μ in length. The head of the spermatozoon of *Beroë*, as shown in CHUN's work ('80, Pl. 16, fig. 49), is nearly pyriform, it differs thus rather strikingly from that of the spermatozoon of *Coeloplana*.

Besides the sexual cells of various developmental stages described above, there are found in the testicular cavity cells that are apparently non-sexual in character (Pl. 5, figs. 2, 4, 8; *n.-s. c*). They are found among sexual cells and may be observed with utmost clearness when imbedded among the tails of spermatozoa. They resemble in appearance the spermatogonia fairly well, but may be distinguished by the greater size ($3-5\mu$ in diameter) and clearer appearance of the nucleus and also by the cytoplasm staining more strongly with eosin. Owing to the character mentioned last, the cells often stand out very conspicuously among the various elements in the testis. Of the three *Coeloplana* species, *C. willeyi* and *C. mitsukurii* seem to be provided with more numerous cells of this kind than *C. bocki*. The nature of those cells remains problematical to me, besides that, they perhaps perform some nutritive function for sexual cells. Such cells have not been described from any ctenophore so far.

The testis is covered by a membrane (Pl. 5, figs. 1, 2, 4, 8; *te. m*) which limits it from the surrounding parenchyme tissue. The membrane varies in thickness a great deal and often becomes so thin as to show an almost structureless appearance, although it never fails to reveal its nuclei to closer examination. Apically it continues into a tubular structure which opens to the dorsal surface of the body (figs. 1, 2, 8; *v. d*). This structure is made up of fairly tall ciliated cells arranged around a rather spacious lumen. In the cross-section of the tube, one can count about twenty such cells (fig. 8). The lumen is filled with a sperm mass frequently, and in one case have I observed a strand-like mass of sperms to lie just at the opening of the tube, partially outside of the opening and partially in the lumen of the tube. These observations seem to indicate that, the tube functions actually as the sperm-duct. At the opening of the tube, the epidermis often shows a slight depression (fig. 8).

In the testes of the earliest stage of development, the duct is represented by a short finger-shaped process from the apical part of the testis which terminates some distance from the dorsal surface of the body.

Moreover, both the duct and the covering membrane are formed by cells showing no definite feature to distinguish them from the spermatogonia. This fact apparently shows that both the duct and the membrane are derived from the spermatogonial cells.

In the testes that contain some spermatozoa, especially in those in which the greater part of the sexual cells have been transformed into spermatozoa, there are generally rather spacious vacant spaces to be found between the sperm masses and the testicular membrane, as well as between each sperm mass (figs. 1, 2, 4, 8). Of such spaces, the most spacious one is found in the apical part of the testis, at the base of the sperm-duct (*g. s*). This space was described by previous writers such as HERTWIG ('80) and GARBE ('01) under the name of "Genital-sinus". Judging from the fact that, such spaces are never present in the parts that consist entirely of spermatogonial cells, but occur invariably in the parts that contain spermatozoa, they seem to develop with the differentiation of the sperm-cells by the concomitant diminution of the volume of the cell masses.

From the above description it is evident that the male gonad of *Coeloplana* agrees very strikingly in several respects with that of *Ctenoplana* described by WILLEY ('96). The male gonad develops in both genera in certain separate masses more or less compact, instead of series of sexual cells as in ordinary ctenophores. Moreover, each testicular mass is provided with a certain number of sperm-ducts in both of the genera. Differences, however, may be found concerning some rather minor points:— While in *Ctenoplana* the number of testes is only four in each individual, in *Coeloplana* it is incompatibly larger; while the number of sperm-ducts belonging to each testis is from one to three in the former, it is always one in the latter. Anyway, such features of the testes, but especially the existence of the sperm-duct, are worthy of special notice, being unknown in any other ctenophore. MORTENSEN ('12) has entertained doubt on WILLEY'S observation recognizing sperm-ducts in *Ctenoplana*. Against this, WILLEY ('13) has contented and advocated his previous view. So far as can be judged from the observation in *Coeloplana*, WILLEY'S observation seems to have been correct in that respect, as suggested by KREMPF also ('21).

Ovary.

The ovary of *Coeloplana* develops as a continuous tract of egg-cells in the dorsal wall of the supharyngeal and subtentacular canals.

It presents no feature characteristic of the form in any respect. As shown in Pl. 5, fig. 7, each ovarial tract is made up of numerous developing egg-cells scattered with some glandular cells. Of the egg-cells, naturally of various sizes according to the stage of development, the large ones are situated, as a rule, close to the cavity of the canal and the smaller ones outside of the former in the order of sizes. The eggs which have arrived at their full development in the ovary, have a structure characteristic of the ctenophoran egg, consisting of two plasmic layers distinguishable from each other, one confined to a small extent of the superficial parts and granular in appearance, and the other occupying all the remaining parts and presenting an alveolar structure. The nucleus is imbedded somewhere in the outer layer and may measure some $20\ \mu$ in diameter. The small egg-cells are generally polygonal in form, apparently owing to mutual pressure. They contain a vesicular nucleus which is very large in size relatively to the size of the cell and has its chromatin substance often divided into some clumps of subequal sizes. The nucleolus is also large and spherical in shape.

The spaces among the egg-cells are occupied by the glandular cells, as also the space between the egg-cell mass and the ovarial membrane to be directly described. Of the glandular cells, one can distinguish two kinds, the granular and the clear, each resembling closely the two kinds of gland cells occurring in the epidermis dealt with above. The granular cells (*g. g.*), which are by far the commoner of the two, contain small secretory spherules staining very actively with eosin or iron-haematoxylin. The clear cells (*c. g.*) are scattered among the former, but they occur more commonly in the external parts of the ovary, quite close to the membrane. They take up haematoxylin fairly well.

The ovary is defined from the surrounding body parenchyme by a membrane appearing very similar to the testicular membrane (fig. 7, 11; *ov. m.*). The membrane may become extremely thin like the testicular membrane, in fact even to such an extent that it shows an almost structureless appearance, although revealing its flattened nuclei here and there by closer examination at any time.

At the outset of the development of the ovary, small egg-cells make their appearance in small clumps between the endodermal cells of the canal wall (Pl. 5, figs. 9, 11). They are at that stage very hard to distinguish from the spermatogonia, excepting for the difference in situation. The ovarial membrane seems to differentiate from some of the

egg-cells of such stage, but my observation is not sure enough to determine this.

The above description on the ovary is based upon observations in *C. bocki*. In the remaining two species, I could not find any mature egg, probably because of the season when the material of those species was secured. But, as far as could be ascertained from the available material, the two species showed no distinguishing feature with respect to the ovary; the largest nucleus of the ovarian eggs observed in those species was 12μ in diameter.

There remains to be described certain peculiar structures, which are to be looked upon as accessory parts of the ovary. These are deep invaginations from the dorsal surface of the body, which are arranged serially along all the subpharyngeal and subtentacular canals (Pl. 5, figs. 1, 6, 7, 9-11; *r. s*). Each of them is tubular in the external part and is expanded terminally into a globular ampulla-like or somewhat irregular-shaped swelling situated quite close to and often in direct contact with the ovarian membrane. The tubular part is sometimes approximately straight, but at other times somewhat curved. Further, it may be nearly perpendicular to the dorsal epidermis, but more frequently more or less oblique to it. This part is made up of ciliated cells of a pyramidal form with a large vesicular nucleus in the basal part of the cell (fig. 10; *r. s. t*). The number of the cells appearing in a cross-section of the tube is from six to ten. The internal lumen is rather spacious and roundish. The terminal vesicle is clothed with flat cells containing each a vesicular nucleus. The cytoplasm of the cells is sometimes tolerably compact and shows diffuse ciliation, but at other times it is vacuolated or attenuated and deprived of ciliation altogether. The former condition is common when the ovary which the structure accompanies is still immature and shows small egg-cells only, while the latter may be met with when the ovary contains some large egg-cells.

Sometimes, especially in the last-mentioned case, the invagination, especially the terminal expansion, contains quite a large quantity of spermatozoa (Pl. 5, figs. 1, 6, 7; *spz*). This observation makes it quite possible that the structure serves as a seminal receptacle. I shall call accordingly the structure by that name henceforth.

The number of seminal receptacles found along each of the subpharyngeal and subtentacular canals fluctuates within a wide limit with the size of the animal. In the majority of cases, however, it may be given as seven to thirteen to each subtentacular canal and four to

eight to each subpharyngeal canal, never exceeding sixteen to the former and ten to the latter. In living specimens, the seminal receptacles may be observed under a low-power lens as a series of minute whitish spots arranged nearly parallel with the series of the testes on its inner side (Pl. 2, fig. 1; *r. s*). In *C. bocki*, most of the specimens obtained during summer or autumn months were found to contain the sperm mass in the seminal receptacles. Pl. 5, fig. 6 illustrates a section of an individual of that species in which a nearly complete series of the receptacles occurring along a subtentacular canal have happened to appear, with all their terminal vesicles filled each with a sperm-mass. In *C. willeyi*, one very large specimen collected in February 1916 was found to contain a sperm mass in most of the seminal receptacles. In *C. mitsukurii*, I have come across no individual showing the organ in such a state.

As to the origin of the spermatozoa in the organ, it is without doubt that they have come from the dorsal side of the body by descending through the tubular part. But it remains to be shown whether the spermatozoa have originated from another individual, though this is very likely to be the case. It is also problematical how and where the spermatozoa in the organ meet the eggs, but probably they make their way through the tissues intervening and reach and fertilize the eggs nearly at the time when the eggs fall into the cavity of the canal. The tissues, in fact, appear to be very diffuse and they seem to give no great hinderance against the movement of the spermatozoa towards the eggs.

The question as to which germinal layer of the ctenophore gives rise to sexual cells was discussed much among previous workers. Aside from the writers of older days, CHUN and HERTWIG expressed both in 1880 opinions entirely conflicting with each other, the former author taking the view of the endodermal origin of the sexual cells and the latter that of the ectodermal origin. Subsequently, the former ('92) undertook a renewed research on the same subject and arrived at a conclusion practically the same as his previous one. This conclusion CHUN's was refuted by SAMASSA ('92), who expressed his opinion in agreement with HERTWIG, and in reply to him, CHUN, for the third time ('98), insisted on his former opinion. GARBE, a little later ('01), undertook the same study and came to a conclusion largely in conformity with CHUN's. In addition to the opinions given above, another assuming the mesodermal origin of sexual cells was introduced by SCHNEIDER

('04). This author has asserted that, the sexual cells take their origin in the mesodermal gelatinous tissue and migrate into the endoderm, where they undergo development and maturation. MORTENSEN, more recently ('12), based upon his study in *Tjalfiella*, expressed his opinion in favour of the endoderm hypothesis.

Now, my observation in *Coeloplana* has ascertained that, the sexual cells of either sex make their appearance in the basal part of the endoderm of the canals representing the meridional canals of ordinary ctenophores. However, the observation falls short of proving whether or not the migration of the cells such as assumed by SCHNEIDER does take place. But so much it may be said as certain that, if the migration occurs, it would be in some very early stage of the development of the cells, when these are still very small and extremely hard, if not altogether impossible, to recognize from the other kinds of cells in the body parenchyme. Anyway, it is certain that, contrary to HERTWIG'S view, the sexual cells pass most of their lives in the endoderm. That view HERTWIG'S is based upon his observations on a cydippid, *Callianira*, which has some flask-like invaginations along each meridional canal, at the base of peculiar wing-shaped processes of the aboral pole of the body. He has given the invaginations the name of "Genitalsäckchen", upon the assumption that the cells lining their terminal part would undergo multiplication and give rise to gonads. This hypothesis was supported further by the existence of certain cell strands that stretch between the epidermis and the enveloping membrane of the gonads. Each of these strands, called by him "Verbindungsstang", should be transformed from the neck portion of the Genitalsäckchen by complete obliteration of the internal lumen, except in the terminal part where it persists as the genital sinus. Against this assumption HERTWIG'S, CHUN ('92) has objected, in the first place, that, the invaginations occur in no ctenophore other than *Callianira*, and even in this form are absent from the oral parts of the meridional canals whence also develop gonads; in the second place that, the invaginations show no variation with respect to their situation and number between quite young and fairly old individuals; in the third place that, the neck portion never undergoes such a change as assumed by HERTWIG, moreover, they differ greatly in their histological features from the ovary; and lastly, even if the development of the ovary could be explained in this way, there remains to be answered the question on the origin of the testis. These objections are, in my opinion, all of great importance, and this is especially so as

to the nature of the invaginations. Indeed, HERTWIG himself seems to be rather skeptical on this latter point and he has acknowledged the possibility of attributing to those structures some unknown sensory function ('80). Now, the seminal receptacles of *Coeloplana* described above recall much of the structures under discussion. Both are flask-like invaginations from the dorsal epidermis which are situated along each meridional canal in approximate numbers, the receptacles four to thirteen, the 'Säckchen' six to seven. Discrepancy may be found only in the character of the cells that line the blind end of the invaginations, these cells being flattened in the receptacles and cylindrical in the Säckchen. In view of the facts given above, we are very likely to be justified in drawing a homology between the two kinds of invaginations, and if so, the observation that the invagination functions as the seminal receptacle in *Coeloplana* appears to throw some light on the question on the function of that structure in *Callianira*.

I have also often met with a structure that resembles closely what has been described by HERTWIG from the cydippids under the name of 'Verbindungsstrang'. That is a tract of cells stretching between the epidermis and the ovarian membrane, and shows sometimes a tubular structure (Pl. 5, fig. 7, *c. st*), but appears at other times as a solid strand of cells (fig. 5; *c. st*). Further, it is not uncommon that, it terminates freely in the body parenchyme without reaching the epidermis, which fact shows clearly that the tract develops from the ovary and not from the epidermis. Apparently the tract has nothing to do with the origin of the sexual cells nor with seminal receptacles. Perhaps, it is morphologically homologous with the sperm-duct, but it is certain that the tract does not serve as an oviduct, as the eggs always fall into the lumen of the canal and are laid through the mouth aperture.

Lastly, the space found in the testicular cavity, 'Genitalsinus' of previous writers, arises evidently in correlation with the development of spermatozoa in that cavity, and it is never found in the testes which have developed no spermatozoa as yet. According to CHUN ('92), the space communicates with the cavity of the canal in certain cydippids, but I could not find such a feature in the present form.

KREMPF ('20, '21) holds an opinion entirely at variance with me concerning the nature of the invaginations that are found along the ovarian tracts. Indeed, one of the greatest discrepancies between the results of his work and mine may be said to lie in this point. Whereas I have attributed to the invaginations the function of sperm-receptacles,

he regarded them to be testes and called them "follicules testiculaires". He has distinguished them from ordinary testes in their smaller sizes and has considered the latter to be composed of two or three of the former, giving them the name of "testicules composés". Certainly, the invaginations in question show a close resemblance to the testes in their general appearance and in the contents they enclose. Nevertheless, the fact that they are not the testes, but function most probably as sperm-receptacles may be clear from the following features they show:— First, the invaginations are situated right above the ovarian tracts, i. e. on the perradial side of the wall of the subpharyngeal and subtentacular canals, while the testes are found on the interradian side of the same canals— Pl. 2, fig. 1 illustrates most unmistakably the relative situation of the invaginations and the testes; they are arranged in two parallel series clearly distinct from each other (Text-fig. 11 of KREMPF'S work, '21 seems to represent a young ovary and not a testis, contrary to his explanation). Second, the cavity of those invaginations is frequently quite empty everywhere. Such empty invaginations are found generally in specimens in which both the ovaries and the testes are still immature, and in such invaginations the terminal vesicle shows, as a rule, a clear and definite outline. In specimens with the gonads showing mature eggs and sperms, on the other hand, the invaginations contain a sperm mass almost without exception, and the wall of the terminal vesicle is often vacuolated or attenuated, showing distinct signs of degeneration. The third and most convincing fact is that, the contents of the invaginations are invariably mature sperms and any immature male element is never met with in them.

Body Parenchyme.

The body of *Coeloplana* is much less bulky than that of pelagic ctenophores and contains but a small quantity of the gelatinous tissue. It is however traversed richly by muscle-fibres and pigment cells, so that it looks very different from the same tissue of those ctenophores. The muscle-fibres form nowhere what may be called the bundle; nevertheless, assemblages of fibres running in the same direction are quite common. The mouth, to begin with, is surrounded by the fibres that serve as sphincters. When the animal is dead, the fibres relax and open the mouth widely, so as to expose the pharyngeal folds. The otolithic capsule is also provided with powerful sphincter fibres mentioned already.

Around the pharynx, the oesophagus, as well as the infundibulum, one can find some fibres proceeding in the main dorsi-ventrally, besides some circular ones intersecting with them (Pl. 3, fig. 1). A fairly large assemblage of fibres starts from each sagittal side of the infundibulum (fig. 2, *m. f.*); this divides immediately into two secondary groups, which proceed along the perradial canal and farther along the furca of the tentacular canal, each on the ventro-lateral side of the former canal and on the ventral side of the latter. The fibres become less prominent towards the peripheral parts of the body gradually merging into the surrounding tissues. Relatively thick fibres abound in the peripheral parts of the body ventrally to the canal branchlets. They run mostly in the radial direction and show profuse branchings especially in the parts directly internal to the margin of the body. These are without doubt the fibres that play the most important part in the animal's crawling movements. The tentacle-sheath is surrounded by two sets of fibres, one longitudinal and the other circular, intersecting rather irregularly with each other. The individual fibres show no difference whatever in structure from those of ordinary ctenophores; some of the fibres present the characteristic terminal branchings as mentioned above.

The pigment cells are distributed all through the body parenchyme in the parts directly under the dorsal epidermis. They are all very irregular in form, presenting a somewhat dendritic appearance; they contain a nucleus in the central part of the cell-body (Pl. 5, fig. 13). The pigment is deposited in the cell-body in minute spherules, which show differences in coloration according to the general shade of the dorsal surface of the body. Besides, there occur, in all individuals, pigment cells made up of yellowish spherules. Mingled with such ordinary pigment cells and nearly in equal frequency with them, are found pigment cells of a peculiar kind (fig. 12). They are generally more irregular in form than the former, and appear milky by reflected and yellowish by transmitted light. The spherules contained in the cell are of rather variable size, though always finer than those of the former kind. The nucleus is placed always in the central parts of the cell.

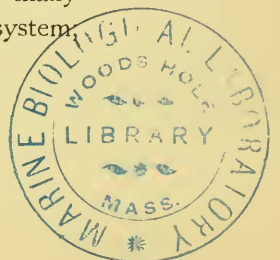
There are further peculiar cell-assemblages scattered in the body parenchyme which are made up each of a few cells arranged mostly longitudinally (fig. 14). The plasm stains strongly with eosin; the nucleus is relatively very large and provided with a distinct nucleolus. MORTENSEN ('12) has described similar cell groups from *Tjalfiella*, and

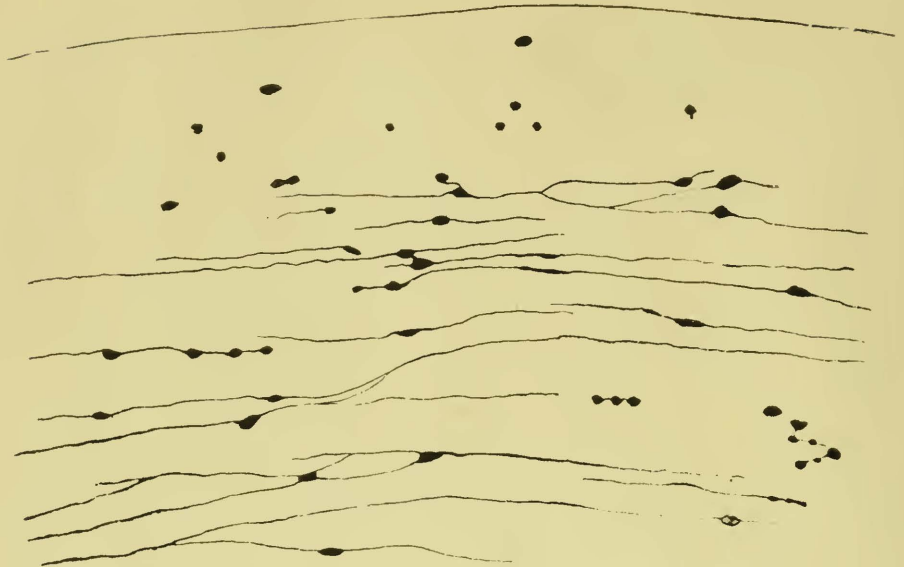
he regarded them to be a developmental stage of the muscle-fibres.

Besides the elements mentioned above, the body parenchyme contains a remarkable body (Pl. 4, fig. 10; *co*). It occurs in all parts of the parenchyme, but especially in abundance in the ventral part of the peripheral region of the body. It is generally oval, spheroidal or sausage-shaped, and consists of granules which resemble very much, but are somewhat coarser than, the granules occurring in the gland cells of the epidermis, and present equally strong affinity for eosin. Several flattened nuclei are found among the granules and on the surface of the body, indicating that it is made up of so many cells of a glandular nature. The body shows no organic connection with any other tissue. The nature of the body remains quite unknown to me. ABBOTT ('07) has assumed that it may be a kind of parasitic organism. But, since it reveals no other organization than that stated above, and further it is distributed fairly regularly through the parenchyme, I am more inclined to regard it to be a kind of reserve material.

There remains to be described the nervous system. Concerning the nervous system of the Ctenophora in general, very little is known as yet. The results of the investigations of previous workers remain not only very incomplete but also conflicting with one another. Apart, for the present, from the old works such as EIMER's, we have thus far in this field works by CHUN ('80), HERTWIG ('80), SAMASSA ('92) and BETHE ('95), which may be outlined as follows:— CHUN, to begin with, has regarded the aboral sense-organ and the ciliated grooves that connect the organ to each rib to represent the nervous system, and has termed the former "Centralnervensystem", and the latter "Nerven"; he has denied the existence of ordinary nervous system in the Ctenophora. HERTWIG, on the contrary, has maintained the presence of two kinds of nerve-plexuses, one in the subepithelial and the other in the mesodermal region of the body. Against this opinion of HERTWIG, SAMASSA has stated that, the ctenophores have no special nervous system. BETHE, somewhat later, reexamined HERTWIG's preparations and accepted this author's opinion; he further demonstrated by the methylene-blue vital staining method, the existence of a nervous plexus in the subepithelial region in a certain ctenophore.

I could find nothing about the nervous system by examination of ordinary sectioned preparations, and I employed the methylene-blue vital staining method. Thus I could obtain, after many unfruitful trials, some figures very likely to be of the nervous system.





Text-figure 1. Nerve-plexus in marginal region of body, the transverse line on the upper end shows the margin of body. $\times 600$.

the above text-figure is an example. Perhaps it may be acknowledged that the figure shows a close resemblance to that in BETHE's work ('95). The staining method is briefly as follows:— The animal was submerged in sea-water which had been coloured deep blue by that stain; after some thirty minutes the animal was taken out of the water and laid upon a slide with one drop of that water and exposed in the air for about half or one hour; it was then covered with a slip and examined with the microscope. Few of the animals died during the manipulation. When the staining was satisfactory, there came out an element stained deep blue which appeared like the figure. It occurs directly beneath the ventral epidermis in the regions close to the external margin of the body. It consists of cells with extremely fine but very long fibrous processes. The cell-body may be spheroidal, spindle-shaped, etc. and of somewhat variable sizes, though always much smaller than the gland cells in the epidermis which stain somewhat with the same dye. It stains uniformly and very deeply, rendering the examination of the nucleus almost impossible. The processes given out from the cell are from two to four. They are extremely fine throughout their length; but since they take the stain as strongly as the cell-body, they are not very difficult to make out. They run largely parallel with

the margin of the body, often taking a more or less undulating course. Branching and varicose appearance are not uncommon. The fibres are readily distinguished from the muscle-fibres prevailing in the same regions by being extremely fine.

According to ABBOTT ('07), fairly remarkable nerve-ganglia should be found close to the aboral sense-organ in the interradian regions. However, I could not succeed in finding them in spite of several special attempts. Sometimes I used the wasser-blau-eosin method, which the author recommends very highly, but I could make out nothing like ganglia in those regions. Accordingly, I am inclined to entertain doubt as to the presence of such ganglia as pointed out by him. Certainly, he has given clear figures of the alleged ganglia; further, he has called attention to KOROTNEFF's statements ('86) which show an allied structure in the same parts in *Ctenoplana*. Nevertheless, I can not help regarding the alleged ganglia in either case to be muscle-fibres in reality, before some clear evidence for their nervous nature would be presented. The same parts in *Coeloplana* are traversed by muscle-fibres very richly and the groups of the fibres give in sections figures somewhat resembling ganglia; they stain with methyle-blue very strongly.

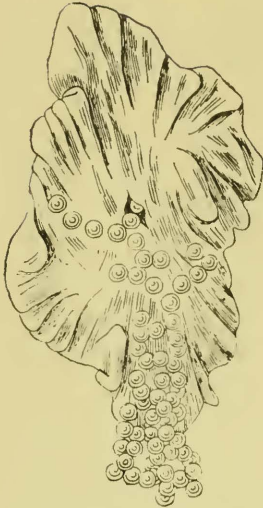
Development.

The development of *Coeloplana bocki* was described briefly in my previous paper ('20, a). In the following, somewhat fuller accounts will be given. KREMPF ('20, c, '21) also has given description of the development of *Coeloplana gonoctena* which he studied in Annam. As he has pointed out, the results of our studies are in almost full agreement.

In many individuals of *C. bocki*, secured during summer or autumn months of 1918 and 1919, I came across egg-clusters overlain by them (Text-fig. 2). They contained cleaving eggs or cydippid-like embryos of various developmental stages. Further, I could rear up the eggs and the embryos to some advanced stages in the aquarium and fill up most of the gaps existing between the stages obtained. So that, the development of the animal could be followed up to a tolerably satisfactory measure.

Egg.

The eggs, so far as observations in the aquarium have ascertained,



Text-figure 2. *Coeloplana bocki* KOMAI. An individual laying eggs, seen from the ventral side. $\times 8$.

may be laid practically at any time of the day. I found them laid sometimes in the early morning, at other times in the daytime and at still other time at mid-night. The eggs do not become pelagic as in the ordinary ctenophores; they are kept under the body of the mother animal, where they undergo development and reach the stage in which the larva is completely formed. The number of eggs carried by an individual is generally from ten to fifty, but may be as large as two hundred. They are all agglutinated together by gelatinous strings of an extremely sticky nature. All eggs in the same cluster are in nearly the same stage of development.

Unsegmented eggs (Pl. 6, fig. 1) show essentially the same structure as those of pelagic forms. A distinct membrane (*c. m*) envelops each egg. The space between the membrane and the egg-body is relatively narrower than in eggs of those forms, so that the egg-body may almost be said to be in direct contact with the membrane, which fact being far from the case with the eggs of the pelagic forms. The space appears to be filled with a thin gelatinous substance. The non-pelagic characteristic of the eggs is apparently due to the scantiness of the gelatinous substance in that space.

The size of the egg varies slightly. The entire egg surrounded by the membrane measures in an average diameter about 0.3 mm. and the egg-proper 0.25 mm. As in ordinary ctenophores, the egg-body consists of the superficial membrane (fig. 3, *s. m*), the ectoplasm (fig. 1, 3; *ec. pl*) and the endoplasm (*en. pl*). The superficial membrane is extremely thin and devoid of granulations. The ectoplasm is much thicker and occupies the peripheral parts of the egg-body. It has the same thickness all around the egg, and presents a granular appearance. The endoplasm occupies by far the greater part of the egg-body and shows a coarse alveolar structure. The alveoles are rather small as compared with those of the eggs of pelagic forms. Two polar bodies (*p*) are frequently seen lying on the surface of the egg-body. They are either spherical or more or less flattened. More rarely, there occur three bodies lying side by side, apparently resulting from the division of the

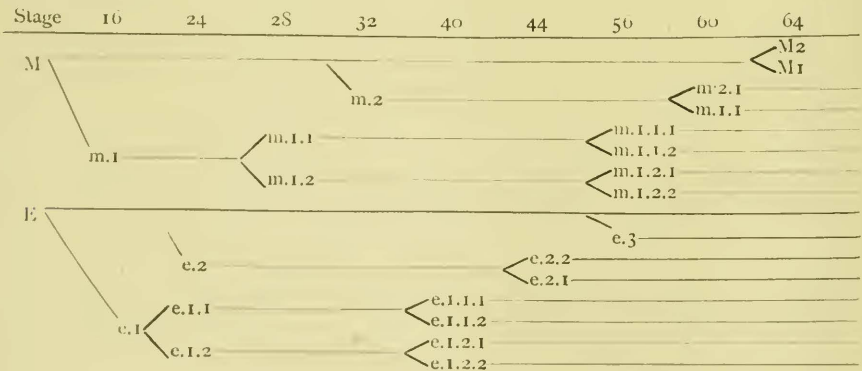
first polar body. In addition, there is to be seen occasionally a low prominence somewhere on the surface of the egg-body, but generally in the neighbourhood of the polar bodies (*ent. c*); this apparently represents the entrance-cone of the spermatozoon.

Segmentation.

The segmentation of the egg advances essentially in the same way as in ordinary ctenophores, known to us through ZIEGLER's work on *Beroë* ('98) and YATSU's on *Beroë* and *Callianira* ('11). The first cleavage (fig. 2) is meridional. The cleavage furrow appears at the vegetative pole in the neighbourhood of the polar bodies and advances towards the opposite animal pole. About the cleavage head (fig. 3), one can recognize a clear radial arrangement of the ectoplasmic granules and some delicate fibrous bodies projecting from the surface of the egg. The second cleavage plane (fig. 5) is also meridional, but perpendicular to the first; it divides each cell into two equal daughter cells (fig. 6). As in ordinary ctenophores, the first cleavage plane corresponds with the pharyngeal or sagittal, and the second with the tentacular or transverse plane of the future larval as well as adult body. The next or third cleavage plane is "diagonal", as in the eggs of ordinary ctenophores (fig. 7). It traverses each cell obliquely, beginning at a point between the vegetative pole and the equator of the egg-body on the outer side and ending between the animal pole and the equator on the inner side; it cuts each cell into two daughter cells of somewhat different size, a larger cell placed nearer the vegetative pole and a smaller nearer the animal pole. The four smaller cells are situated in two groups each consisting of two cells situated in close contact with each other, one on either side of the second cleavage plane (fig. 9). As is well-known, such an arrangement of the blastomeres in the eight-cell stage is characteristic of the cleavage in the Ctenophora. For the sake of description, I shall name after YATSU the four larger cells of this stage M (middle-cells) and the four smaller cells E (end-cells). In the fourth cleavage, each of the eight cells gives rise to a very small cell at the animal pole and thus the 16-cell stage is attained (fig. 10). This stage consists of eight large cells (macromeres) and eight very small cells (micromeres), of which the former are situated nearer the vegetative pole and the latter nearer the animal pole, so that we may call those two poles the macromere and micromere pole respectively. Of the eight

micromeres, those produced by E are somewhat smaller in size than the same budded off from M. The succeeding divisions result in the formation of micromeres alone, the number of macromeres remaining eight for a comparatively long period. The accompanying table gives the order of the cleavage up to the 64-cell stage.

Of the micromeres in the 16-cell stage, *e. 1*, i. e., the cells produced by E, divided each into two daughter cells of somewhat different size, of which that situated nearer the median plane (*e. 1. 1*) is somewhat larger than the other placed away from it (*e. 1. 2*). At about the same time, but a little later, a second micromere (*e. 2*) is budded off from E (fig. 11); this micromere is nearly as large as *e. 1. 2*. We have now the 24-cell stage before us. This stage soon turns into the 28-cell stage, through an equal division of *m. 1* by a vertical furrow (fig. 12). Directly succeeding this, *m. 2* is given off close to *m. 1. 2* (32-cell stage). Then a fairly long pause of cleavage sets in, and after that *e. 1. 1* and *e. 1. 2* are divided, the former unequally and the latter equally (*e. 1. 1. 1* > *e. 1. 1. 2*; *e. 1. 2. 1* = *e. 1. 2. 2*) (40-cell stage) (fig. 13). Soon later, *e. 2* undergoes equal division by a vertical furrow (44-cell stage), and then comes an interval of cleavage again. After the interval, *m. 1. 1* and *m. 1. 2* cleave unequally (*m. 1. 1. 1* > *m. 1. 1. 2*; *m. 1. 2. 1* > *m. 1. 2. 2*), and nearly simultaneously, *e. 3* is given off. This is a large cell which measures about one half of E in diameter (56-cell stage). Next, *m. 2* divides equally by a vertical furrow (60-cell stage) (fig. 14). Then, the divisions of the macromeres set in. In these divisions, the cleavage furrow advances in the direction the reverse of that of the first three divisions already described, the cleavage beginning at the animal pole and ending at the vegetative. Of the macromeres, M divides prior to E, giving the 64-cell stage.



As will be clear from the foregoing description, as well as from the accompanying table, the divisions of the micromeres in the sub-pharyngeal octants, i. e., the divisions of the cells arising from M, generally come somewhat later than those of the corresponding micromeres in the subtentacular octants, i. e., the divisions of the cells produced by E—this tendency is also known in the cleavages of the egg of ordinary ctenophores. In the eggs under my examination, it took roughly eight hours for unsegmented eggs to develop to the 64-cell stage; one cleavage required from three to five minutes to accomplish.

For some time after the stage described last, micromeres keep on multiplying by division of the previously existing micromeres, and also by new buddings from macromeres. Meanwhile, E cleaves into two, and the number of macromeres becomes sixteen. Then, the epibolic gastrulation begins to take place.

Gastrulation.

In the stage at the close of the segmentation stage just prior to gastrulation, the macromeres are arranged in a bowl-shaped group, at the margin of which on the concave side, there exist assemblages of micromeres, while on the opposite side, the macromeres are exposed. Then some "mesodermal cells" of METSCHNIKOFF ('85) (fig. 15, *mes*) are budded off from the macromeres on the convex side of the group. Unfortunately I could ascertain nothing regarding the fate of those cells. In the mean time, the micromeres are multiplying rapidly and gradually spreading over the macromeres. While this change is going on about the micromeres, the concavity of the macromere group diminishes, and the gap between the micromeres on the micromere pole enlarges (fig. 16). Fig. 17 represents a stage during the process seen from the micromere pole, where a moderately large elliptical gap exists between micromeres, showing macromeres within. At the macromere pole too, there is another but somewhat smaller opening. The two openings of the two poles communicate with each other through a fairly wide passage existing between the macromeres and elongate in the transverse direction. Both of the openings are closed up by multiplying micromeres with the advancement of the gastrulation. The questions which pole is closed first, and which pole becomes the oral pole, were discussed much among previous writers on the development of the Ctenophora (cf. CHUN, '80). My observation in the the present form has shown clearly that, it is

the macromere pole that is closed first and develops the stomodaeal invagination, just as it was given by CHUN ('80) for the development of *Beroë*.

Towards the end of the gastrulation, the shape of the entire egg, which has been somewhat flattened up to this time, again becomes globular (figs. 18-21). For some time after the closure of the opening of the macromere pole, there remains still a large aperture at the micromere pole which leads into a roomy axial space (figs. 18, 19). This space diminishes in width gradually, the change beginning near the macromere pole and advancing towards the micromere pole, so that at a period during the change, the space may show a funnel-shape (fig. 20). Meanwhile, the layer of micromeres on the surface of egg, or the ectoderm as it may be called now, has given rise to a thickening at the macromere pole (fig. 21, *stm*), which represents the first trace of the stomodaeal invagination. As development still goes on, the opening at the micromere pole is also closed, and at the same time the axial space is reduced into a narrow longitudinal slit throughout the length, except in a small part at the middle where it persists as a moderately broad cavity (figs. 22, 23). Shortly after the closure of the opening of the micromere pole, there appear the first traces of the aboral sense-organ, tentacles and ribs nearly simultaneously, all as ectodermal thickenings. The aboral sense-organ develops from the micromere pole, while the tentacles and ribs make their appearance on the lateral sides nearer the micromere than the macromere pole.

The aboral sense-organ (figs. 25, 26; *s*) arises on that pole as an ectodermal thickening made up of columnar cells. It sinks gradually below the general surface of the body and forms a globular capsule. The formation of the otoliths takes place somewhat later than the appearance of the comb-plates in ribs. The first traces of the ribs are discernible at a fairly early period (fig. 22, *r*), in fact even somewhat prior to the closure of the opening of the micromere pole, as four streaks of a peculiar kind of ectodermal cells of a small size and granular appearance radiating from that pole and traversing the surface of the gastrula. The formation of the stomodaeum as a distinct invagination takes place somewhat later than the appearance of the rudiments of tentacles and ribs, although the ectodermal thickening which is destined to develop into it arises directly after the closure of the opening of the macromere pole.

As development still goes on, the ectodermal thickenings of the

tentacular rudiments become more and more prominent, and raised upon the surface of the gastrula on each side into a narrow longitudinal ridge-like elevation (figs. 22 & 23). The ribs develop comb-plates, of which there appear at first six or seven in each rib nearly at the same time. The cilia of the comb-plates are very fine and short as yet and are not easy to observe. The stomodaeum shows itself now as an invagination having a distinct internal cavity.

The thickenings of the rudiments of the tentacles gradually disappear from the surface of the body, by sinking down below the level of the surface (figs. 24, 25). Among the endodermal cells, appears a space communicating with the broadest part of the axial cavity mentioned above and shaped H in the dorsi-ventral view, with the transverse bar of H situated in the pharyngeal plane and the two lateral bars parallel with the tentacular plane, each of the apical and basal ends of the latter bars lying at the centre of each body quarter formed by the intersection of those two planes.

Meanwhile, the stomodaeal invagination elongates up to almost the middle point of the vertical axis (figs. 26 & 28). The broadest part of the axial cavity of the endoderm is carried upwards, together with the ascending apex of the invagination, to a level somewhat nearer the aboral than the oral pole. Subsequently, the cavity is widened into the lumen of the infundibulum, while its branches become the endodermal sacs of the embryo.

The gastrula now has become a typical cydippid larva. At first, the surface of the body of the embryo appears uneven, the outline of each ectodermal cell being shown quite distinctly; soon, however, it becomes smooth all over the surface. The combs begin to beat, at first each in its own rhythm, but afterwards in unison, so that the embryo commences to rotate in the egg-membrane.

Cydippid Larva.

Pl. 7, figs. 1-3 represent an unhatched cydippid larva of a very early stage. The shape of the body is spheroidal narrowing gently towards the oral pole and with its pharyngeal and tentacular axes nearly equal and slightly longer than the vertical axis. At the aboral end of the last mentioned axis, lies the sense-organ (*s*) and at the opposite end, the mouth (*m*), besides a pair of tentacular rudiments (*t*) and eight ribs (*c*) both located in the aboral half of the body. The

condition of the sense-organ is nearly the same as depicted in Pl. 7, fig. 20 of CHUN's monograph or in Pl. 2, fig. 3 of MORTENSEN'S paper ('12). When viewed from above, the organ has a rhomboidal outline with the longer diameter in the sagittal plane of the larva. The part at the ends of the diameter represents the rudiments of the polar plates. They are defined from the more centrally situated parts very vaguely as yet; in some later stages, however, they come to be marked off quite clearly from the latter. The otoliths (*ot*) lie as aggregates of four or five granules, one at each end of the shorter diameter. The sense-organ still lacks the ciliary covering. The ribs are arranged in four close pairs, each row comprising six or seven comb-plates with very short cilia. The rudiments of tentacles appear on the surface each as an elongate oval area with both the aboral and oral ends elongate into short processes. The entire area may be distinguished into a central and a peripheral part, of which the former is depressed slightly below the general surface of the body, while the latter is raised a little above it. In the side view of the larva on the tentacular plane (fig. 1), the inner margin of the tentacles describes an arc which stretches from beneath the sense-organ to the oral end of the oval area on the surface.

The mouth is nearly round and small as yet. The pharynx (*ph*) which the mouth leads into presents also a roundish outline in the optical cross-section. The internal end of the pharynx is situated nearly midway between the oral and aboral poles of the body, where it bears a short prominence indicative of the oesophagus (*oe*). The endoderm consists of four pouches situated interradially, the boundaries of which show through clearly in the oral view of the larva as two straight lines intersecting cruciately. The larva rotates very actively within the egg-membrane by means of the cilia of the ribs.

Some of the larvae of this stage were fixed with FLEMMING'S solution, imbedded in paraffin and sectioned. The shortage of available material as well as the difficulty of imbedding prevented me from obtaining good sections. Nevertheless, figs. 8-12, which represent some of the serial sections made approximately transverse, though somewhat oblique, to the vertical axis, will give an idea of the structure of the larva in this stage. The epidermis is rather thin and very simple, showing as yet no gland cells whatever. Each comb-plate is made up of three or four longitudinal rows of columnar cells, four or five times as tall as the neighbouring epidermal cells, with the plasm appearing somewhat

clearer than that of the latter cells and the nucleus large and located in the basal part of the cell.

The aboral sense-organ (*s*) is spherical in form and consists of fairly tall columnar cells. The tentacular apparatuses are nearly the same as those of the adult in every respect, save for that, the long and contractile stem of the latter is represented by a very short and inconspicuous prominence (*t. s*). Each tentacular apparatus is enclosed within a pouch-like depression, the rudimentary tentacle-sheath (*t. sh*). The inside wall of the sheath is thickened into the tentacle-basis which consists of small cells arranged in strata four to six cells deep (*b, ep*). The tentacle-basis is continued into the tentacle-root along the transverse plane of the body, which presents itself as a conspicuous crest-like prominence directed towards the centre of the body and showing a muscular characteristic. Towards the lateral sides of the sheath, the tentacle-basis diminishes in thickness gradually and gives place to a thin epithelium of an appearance perfectly identical with the ordinary epidermis of the larva.

The pharynx (*ph*) is lined with tall cylindrical cells, as also the oesophagus (*oe*) into which it communicates. The latter opens upwards into the endodermal cavity representing the infundibulum (*i*). Unfortunately, the histological condition of the endodermal parts of this stage could not be studied clearly.

As development advances, the body of the larva comes to present a distinct lateral compression, growing broader in the transverse direction than in the sagittal (fig. 5). The sense-organ (figs. 5-7; *s*) acquires the ciliary covering. The cilia of the comb-plates grow much longer and make the larva rotate more actively than before. In each tentacular apparatus (*t*), the stem makes its appearance on the surface of the body, at first as a tubercle-like prominence with some rudimentary colloblasts scattered here and there on its surface. The mouth is widened considerably along the transverse axis of the body. Both the lower and upper halves of the pharynx show distinct lateral compression, but in directions perpendicular to each other, the former elongate in the tentacular direction, and the latter in the pharyngeal.

The lateral compression of the body already noted becomes more prominent with development. At the same time, the region about the tentacular apparatus is brought upwards to the same level as the sense-organ (Pl. I, fig. 5). Moreover, there appears a slight longitudinal depression along each pair of the ribs, so that the body looks in the

oral or aboral view as depicted in Pl. 1, figs. 6 & 7. In the sense-organ appear a few otoliths in the central part besides those existing in the marginal parts mentioned before. The area representing the polar plate (*p. p*) is elevated into a transverse ridge on each side of the sense-organ. A few new comb-plates are added to each rib; the cilia of each plate have grown somewhat longer. Yellowish pigment spots make their appearance in the part surrounding the pharynx and in the parts about the tentacular apparatuses; moreover, pigment spots looking whitish by reflected light and dusky by transmitted are formed in the latter parts.

As the development advances further, the lateral compression of the body grows still more remarkable, in fact to such an extent that the sagittal axis measures about $\frac{2}{3}$ as long as the transverse axis. At the same time, the parts neighbouring the mouth come to be demarcated rather sharply off from the rest and the parts surrounding the aperture of the tentacle-sheath are brought somewhat above the level of the aboral sense-organ.

In consequence of these changes, the body comes to be roughly heart-shaped with a subtruncate oral end when viewed on the transverse plane, and nearly pyriform when looked at on the sagittal plane. The longitudinal depressions along the ribs grow deeper. The number of comb-plates increases and at the same time the cilia grow much longer. The movement of the larva in the egg-membrane, however, becomes less active than before, on account of the want of space therein preventing the free movement of the long cilia. In the larva of this stage (figs. 8-10), one can see in the sense-organ some ten otolithic granules making an aggregate at its centre, and over the organ a highly vaulted covering formed already. The comb-plates are about ten in each rib. The tentacles have been greatly elongated and are of a club-like shape, though as yet somewhat shorter than the height of the body even when fully extended. They are now thickly beset with colloblasts on the surface. The mouth aperture has widened a great deal along the tentacular axis, while the internal half of the pharynx has done so along the pharyngeal axis. The oesophagus likewise presents a clear lateral compression, in the same direction as that half of the pharynx, and its oral end is more or less produced into the cavity of the pharynx. Pigment spots are now found in quantities in the parts adjoining the mouth, sensory capsule and tentacular apparatuses. The existence of the pigment in the superficial parts of the body renders the examination

of the internal structure fairly difficult, yet one can clearly witness that the endoderm is still very simple and consists of four sac-like pouches as it was in the previous stage.

As the development of the larva still advances (figs. 11, 12), the pigment spots increase very much in all the superficial parts of the body. Besides yellowish ones, there appear brownish spots, particularly in quantities in regions around the mouth, so that the egg now becomes visible as a yellowish-brown spot even with a naked eye. Meanwhile, the parts neighbouring the tentacular apparatus have grown very prominent and marked off fairly sharply from other parts. The tentacles have been elongated considerably, so as to be somewhat longer than the height of the body. They are now provided with four or five branches. The tentacle-sheath has grown somewhat deeper, and the gape of the mouth fairly wider than before. The upper and lower halves of the pharynx are demarcated sharply off from each other by the appearance of a constriction between them.

The larva of such a stage has already undergone its full development in the egg and is ready to hatch out. Such a larva is frequently observed in stretching movements in the egg-membrane and in pressing the mouth region against the membrane as if it attempts to free itself. Eventually, the membrane ruptures at a place, whence escapes the larva, directing the mouth forwards, as does the larva of ordinary ctenophores also (Pl. 7, fig. 21).

A number of larvae of this stage were fixed with Flemming's strong solution, imbedded in paraffin and sectioned. Several series of tolerably good sections were thus obtained, of which some are represented in Pl. 7, figs. 13-19, Pl. 3, figs. 9-11.

The epidermis shows already the definitive feature, consisting, as it does, mainly of the two kinds of the gland cells described already. It exhibits some topographical differences in thickness; as a general rule, it is thicker in the oral, than in the aboral parts of the body. The thinnest part of the epidermis exists outside of the tentacle-sheath, where it is only $4\ \mu$ and about $\frac{1}{3}$ as thick as the thickest part near the mouth aperture. The aboral sense-organ (Pl. 3, fig. 9; Pl. 7, figs. 13, 15, s) shows a structure similar to that of the adult animal. It is a subspherical capsular organ made up of tall columnar ciliated cells; the nuclei are arranged in the wall in three to five layers, except in parts at the bottom, where they form but one or two layers in the lower half of the thickness of the wall, leaving the upper half quite free of them. A few otolithic

granules are found in the parts forming the margin of the area just referred to, showing that here exist the matrix cells of the granules. The cilia supporting the otolithic mass are still very fine. On either sagittal side of the sense-organ, is found a rather tall crest-like process, which is ciliated all over its inner side—this part represents the polar plate without doubt. Probably, the process is divided into a few lobe-like portions in some later stage as we have seen in the adult animal. The tentacular apparatuses are disposed nearly vertically, instead of horizontally as they are in the adult, although they diverge somewhat from each other at their oral ends. They present a structure nearly the same as in the youngest cydippid larva described above. The tentacle-stem is inserted at the end of one-third of the length of the tentacle-root from the aboral end (Pl. 7, fig. 13; *t. st*). It is very much longer than it was in the earliest stage of the larva mentioned above. The core of the stem shows already the muscular feature clearly; its growing point exists near the oral end of the tentacle-root. A few accessory filaments are attached to the tentacle-root at the parts directly below the point of insertion of the tentacle-stem and above the middle point of the length of the tentacle-root. The filaments are covered by the rudiments of colloblasts all over. The mouth shows itself as a slit-like aperture elongate in the transverse direction. The stomodaeum is divided into three parts, viz. the external and the internal halves of the pharynx and the oesophagus. Of these, the external half of the pharynx is most spacious, it is flattened, like the mouth aperture, in the transverse plane, the diameter of the cavity measured along the transverse axis being about four or five times the length of the diameter in the sagittal direction. The internal half of the pharynx shows a lateral compression too, but in the direction perpendicular to the former, its diameter in the sagittal direction being about twice the length of the diameter in the transverse direction. Lastly, the oesophagus is flattened in the same plane as the internal half of the pharynx; its oral part is produced into the lumen of the latter for a short distance, so as to be telescoped into that.

The configuration of the stomodaeum may be understood more clearly by a collaboration of cross-sections. In Pl. 7, fig. 19 is shown a section from a level very near the oral end of the body. It exhibits the cross-section of the external half of the pharynx which is compressed in the way described above. Next fig. 18 has been taken from a section passing through the boundary of the external and internal halves

of the pharynx; the cavities of the two halves make together a cruciate form. Finally, fig. 17 represents a section of a more aboreal region; the stomodaeal wall shows itself in this figure as a set of rings of different sizes placed one inside of another. Of the three rings in all, both of the two outer rings are the wall of the internal half of the pharynx folded upon itself, while the third and innermost ring is the oesophageal wall.

The stomodaeum is clothed with an epithelium which consists of ciliated cells and gland cells. Of the gland cells, both kinds, viz., the granular and the clear, may be met with in nearly the same number. The ciliated cell is developed much better in the oesophageal wall than in the pharyngeal, whereas, the gland cell is by far commoner in the latter than in the former. The wall of the pharynx measures about $15\ \mu$ in the thickest part near the mouth aperture.

The oesophagus communicates dorsally into the infundibulum by a rather small roundish aperture. The infundibulum (Pl. 3, fig. 9, Pl. 7, figs. 13, 16; *i*) is a relatively spacious chamber of a cup-like shape, situated directly beneath the aboral sense-organ and between the paired tentacular apparatuses. It is nearly as wide in the transverse as in the sagittal direction, and is divided laterally, though not very sharply, into two halves placed one on each side of the transverse plane, by the internal end of the tentacle-root produced for some distance into the cavity (Pl. 7, fig. 16; *i*). The infundibulum is lined on all sides with endodermal cells, of which the cells clothing the roof are fairly low, as compared with those lining other parts. The cells may be vacuolated and contain food particles.

The lateral halves of the infundibulum give rise each to an excretory canal which ascends along the sagittal side of the sense-organ and opens to the exterior right at the outside of the crest-like prominence described above (Pl. 3, fig. 9, Pl. 7, fig. 15; *ex. c*). This canal unlike that of ordinary ctenophores is not divided before the opening. It is lined with the direct continuation of the epithelium of the infundibular wall. From each half of the infundibulum, towards the oral direction, two canals of a relatively broad calibre are given out; they descend through the parenchyme tissue that occupies the interradian parts of the body, and terminate blindly at the level directly above the oral aperture. The canals keep a close attachment to the tentacle-bases throughout their length, with their external wall closely attached to the internal margin of the latter. There the canalar wall is made up

of very tall and vacuolated cells, as also the wall on the opposite side adjacent to the pharynx; on the other sides, the canal is lined with a much lower epithelium. It is no doubt that, the canals just referred to have developed from the endodermal pouches of previous stages. It is also certain that, they develop into the subtentacular pouches to be described in the next stage. Attention may be also called to the presence of a pair of outbulgings at the middle parts of the sagittal wall of the infundibulum (Pl. 7, fig. 16; *s. s. p*). They are very short and only indicated, yet, it is very probable that, they are the rudiments of the subsagittal pouches to be seen in the next stage. The epithelium shows there sparse but distinct ciliation. The parenchyme of the body consists of gelatinous tissue for the greater part, with some isolated cells scattered about, and also with small fibrous bodies apparently to be identified as the rudiments of muscles; the latter are found rather abundantly around the mouth. The parts about the tentacle-sheath contain some pigment-cells.

Metamorphosis.

Now returning to the larva liberated from the egg (Pl. 2, figs. 13, 14); it swims about very actively by means of combs, and while so doing, it moves the parts about the tentacle-apparatus vigorously inwards and outwards, which movement gives the tentacles hanging from the aperture of the tentacle-sheath at the top of that part a violent swinging motion. The swimming movement of the larva is highly characteristic. Instead of the gentle and steady locomotion by means of the regular and harmonious beatings of comb-plates of ordinary ctenophores, the larva has a quite sudden and jerky method of locomotion reminding one somewhat of that of copepods. This is evidently due to the disproportionate length of the cilia of the combs for the small size of the larva, the cilia performing sweeping movements and bringing about the peculiar jerky locomotion of the larva. The length of the time during which the larva performs such movement varies somewhat. I found in some cases the larva remain in that state more than one day, while, a larva that came under my examination one day in the early part of September of 1918, passed the stage in only four or five hours. Sooner or later, the larva takes to swimming much less frequently than before but remains most of the time at the bottom. Then, it begins to adhere there by means of the extended surface of the external half of the pharynx and somewhat

later even to have a gliding movement, using the extended pharyngeal surface as the sole (fig. 14). The appearance of the larva performing such locomotion recalls distinctly that of *Lampetia* in similar attitude, taking of course no account of the great difference in size in the two forms. It is usually the case with the larva in this stage that after a short time of crawling, it recommences swimming about by means of comb-plates, but again, before very long, sinks to the bottom to return to crawling, thus performing the two modes of locomotion practically alternately. The structure of the larva at this stage differs in no way from that of the time of the liberation, except some slight changes undergone by certain organs or tissues such as:— all kinds of pigment spots have increased considerably in all parts of the body, rendering the examination of internal structure almost impossible, especially spots coloured brownish are found in quantities in the regions adjoining the mouth, the tentacular apparatuses and the sense-organ: the spots looking opaque by transmitted light that have been scattered here and there without order up to this time, now are distributed evenly throughout the surface of the body: the gape of the mouth has become much wider than before. The oral part of the body is capable of great change in shape by means of muscle-fibres developed therein.

In the next four or five hours, most of the cilia of the comb-plates become either bent or broken off in the middle or even fall off, showing clearly that the degenerating change of those swimming apparatuses has already set in, so that the larva becomes entirely incapable of swimming, although the remaining cilia still continue to beat as before. The tentacles grow longer and develop new accessory filaments, while the sole of the extended pharynx spreads out very widely all around. Sooner or later, the cilia fall off entirely; the sole becomes enlarged extensively in all directions, and is flattened out in an almost film-like manner (fig. 15). The larval body in this state consists of two distinct parts, a broad and thin basal expansion and a hump-like elevation in the centre of it, of which the former has been transformed from the part of the body around the external half of the pharynx and the latter from the parts above it. Unfortunately I could observe a single specimen to undergo metamorphosis and the specimen died when the condition just described was attained, but it is easy to imagine that by gradual depression of the elevation just mentioned, the entire body would assume the habitus of the adult.

Of the individuals that have completely transformed into the adult

shape and that were taken from the alcyonacean host, the smallest and youngest observed was the one only 1 mm. in the diameter (Pl. 7, fig. 22). This specimen showed some features standing between the last larval stage and the adult. In the dorsiventral view, the pharynx (ph') exhibits a quadrate shape somewhat elongate in the sagittal direction, and the oesophagus (oe) is fusiform in the optical section, both parts therefore approaching the definitive state very closely. Moreover, the tentacular apparatuses (t) show no feature to distinguish the specimen from the adult, except for the shortness and simpleness of the stem, and the sense-organ (s) is nearly the same as that of the adult. The most notable point in the internal structure of this specimen is the condition of the gastro-vascular system: the system consists of eight broad and subequal pouches arranged radially around a central cavity representing the infundibulum and a canal system occurring in the peripheral part of the body. Of the eight pouches, four are placed in relation with the tentacle-basis on each side of the transverse plane and may be called the subtransverse pouches ($s. t. p$), while the remaining four are situated on each side of the sagittal plane and may be called the subsagittal pouches ($s. s. p$). It is without doubt that, the subtransverse pouches have developed from the four canals described in the larva previous to metamorphosis, while the subsagittal pouches have arisen from the four outbulgings that were then very short and only indicated. It is no less certain that, subsequently, each of the former pouches will give rise to the tentacular and subtentacular canals, while each of the latter will develop into the subpharyngeal canal. The peripheral canal system ($br. c$) is relatively broad and shows only sparse branchings and anastomoses. The relation of those canals with the central pouches could not be studied clearly, yet, it is certain that, they are communicated with the latter somewhere in their course.

The central part of the body which contains the pouches are situated on somewhat higher level than the peripheral parts which show branching canals, indicating without doubt that, the former has been transformed from the central elevation of the metamorphosing larva.

It is interesting to note that, the specimen under description exhibits a singular resemblance in structure with the young stage of *Gastrodes parasiticum* KOROTNEFF to be described in the second part of this paper. This is especially so in the condition of the gastro-vascular system, which consists of eight pouches subequal in size and arranged radially around the infundibulum, four in relation with the tentacular

apparatuses and four on each side of the sagittal plane, just as in that form. This fact seems to stand in favour of the opinion of the present author on the systematic position of *Gastrodes*, that the form should be assigned to the Platyctenea.

Systematic position.

Since its first discovery made by KOWALEVSKY in 1880, *Coeloplana* has often been regarded as a form which occupies a very peculiar systematic position. This is because the animal possesses several features common with flatworms on one hand, while showing many other characteristics standing for its affinity to ctenophores on the other. In fact, this peculiarity has not failed to attract the discoverer's attention, notwithstanding that the form was then represented by an unique specimen. The Russian zoologist pointed out so ably that:— "As to the systematic position of *Coeloplana** we know too little to decide it at present; especially do I feel it necessary to examine an individual that has attained maturity. Nevertheless, so far as I could ascertain, it may be pointed out, among other facts, that the animal shows affinity to the Turbellaria on one hand and to the Ctenophora on the other. It approaches the Turbellaria in its general habitus and life habit, whereas, such features as, the situation of the mouth and otocyst at the centre of the body with the latter above the former, the existence of two diverticula projecting from the intestinal canal and terminating on the sides of the otocyst, the presence of tentacles and their sheath, and further, the division of the intestinal cavity into four primary parts, show the relationship of the animal with the Turbellaria" (Translated from Russian with Professor A. OKA's kind aid).

Two years after this discovery, LANG (1882) published a brief remark on the systematic position of *Coeloplana* apropos of the description on the structure of *Gunda* and the argument on the relationship of the Plathelminthes with the Coelenterata and Hirudinea. Of his great work on the Neapolitan Polyclada published still two years later (1884), the same author devoted its concluding chapters to his well-known theory on the affinity of the Turbellaria with the Ctenophora, and he has attempted to derive the former class from the latter by taking *Coeloplana* as an intermediate form between the two. He has described in detail

* originally spelt "*Cocleplana*".

how an ancestral ctenophore could be transformed into a flatworm, by passing through a transitional stage which is so nicely represented by *Coeloplana*. The following quotation from the work will serve in making clear his view on the question:— "Fassen wir die Resultate unserer Vergleichung der *Coeloplana* mit den Ctenophoren und Polycladen zusammen, so können wir sagen: Die Achsenverhältnisse von *Coeloplana* sind diejenigen der Ctenophoren und zugleich die nämlichen, wie sie bei den Polycladen entsprechend den Befunden der Ontogenie und vergleichenden Anatomie ursprünglich waren. Wenn wir der secundären Verschiebung des aboralen Poles an ein nunmehr als vorderes zu bezeichnendes Körperende gebührend Rechnung tragen, so ist die Lage der Sinnesorgane (incl. Tentakeln) und der Aufbau des Gastrovascularapparates bei den drei Typen identisch. Das Mangel(?) eines von Ectoderm herstammenden Vorraums des Gastrovascularapparates entfernt *Coeloplana* ebensoweit von Ctenophoren als von den Polycladen. Die übrige Gastrovascularapparat gleicht im ganzen mehr dem der Polycladen, die Tentakeln mehr denen der Ctenophoren. Von den Ctenophoren hat *Coeloplana* die aboral Gehörkapsel, von Polycladen die plattgedrückte Körpergestalt, das continuirliche Wimperkleid, das Fehlen der Rippen.

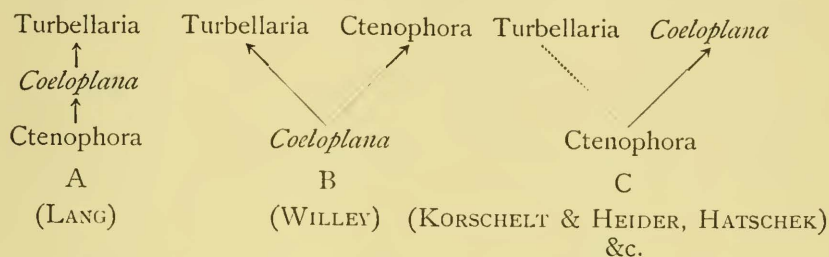
"So weit es bei unserer gänzlichen Unbekanntschaft mit wichtigen Organsystemen erlaubt ist, die systematische Stellung von *Coeloplana* zu beurtheilen, so ergiebt sich nach dem Gesagten die Ansichten KOWALEVSKY'S, dass *Coeloplana* eine Zwischenform zwischen Polycladen und Coelenteraten, spec. Ctenophoren sei, als richtig und, wie ein Vergleich mit den anderen Gruppen des Thierreichs sofort zeigen würde, nach dem gegenwärtigen Stande unserer Kenntnisse als die einzig mögliche". ('84, p. 649).

Two years after the publication of LANG'S work, KOROTNEFF discovered *Ctenoplana*, and in the work dealing with it, he expressed his opinion on the systematic position of the two genera, *Coeloplana* and *Ctenoplana*:— "Kurz gefasst, kann man mit Rechte sagen, dass die *Ctenoplana* mit der *Coeloplana* zwei Übergangsformen sind, welche an verschiedenen Seiten der Scheidenlinie zwischen den Ctenophoren und Planarien stehen: die *Ctenoplana* neigt sich mehr den Ctenophoren, die *Coeloplana* den Planarien zu, obschon die beiden Formen zu derselben Zeit nahe verwandt sind" ('86; p. 251).

The theory of LANG'S on the affinity between the Ctenophora and the Turbellaria, which may be shown somewhat as in the accompanying

diagram A, was supported by many other writers and the view that *Coeloplana* represents the intermediate stage between the two classes was accepted fairly widely. Nevertheless, there were several authors who expressed their opinions at variance with LANG concerning the origin of the Turbellaria and also on the systematic position of *Coeloplana*. Among such authors we can distinguish:

(1). One who regarded *Coeloplana* to be an ancestral form, from which both the Ctenophora and the Turbellaria have been derived WILLEY ('96), (B).



(2). Those who considered *Coeloplana* as a specialized ctenophore. KORSCHOLT & HEIDER ('90), HATSCHKE ('91), BOURNE ('00), DELAGE & HÉROUARD ('01), SCHNEIDER ('02) and WILLEY (a later work, '13), (C). Many of these authors denied at the same time the existence of a phyletic relationship between *Coeloplana* and the Turbellaria such as is assumed by LANG and his followers.

As to WILLEY's opinion given first, I feel it unnecessary to dwell upon it now, since it has been discarded afterwards by the author himself, and also we have elaborate discussions of that in ABBOTT's ('07) and MORTENSEN's ('12) works.

Next, of the opinions of the writers named last, they are largely in accordance with one another and differ only in minor points. I shall give some instances of the opinions below:—

KORSCHOLT & HEIDER ('90), to begin with, stated:— "Man hat in den merkwürdigen Formen: *Coeloplana Metschnikowii* und *Ctenoplana Kowalevskii* directe Zwischenformen zwischen Ctenophoren und Turbellarien zu erkennen geglaubt. Uns scheinen dieselben jedoch keine weiteren Eigenthümlichkeiten darzubieten, als sich aus dem typischen Ctenophorenbau durch Anpassung an die kriechende Lebensweise ungezwungen erklären lassen. Die Uebereinstimmung mit den Turbellarien würde sodann auf blosser Analogie beruhen. Eine solche Erklärung erscheint zulässig, da auch unter den echten Rippenquallen einigen Formen das

Vermögen zukommt, sich mittelst der sohlenförmig verbreiterten Mundränder an feste Flächen anzusaugen und an denselben zu kriechen (*Lampetia*), so dass hier der Ausgangspunkt für eine Entwicklung nach dieser Richtung gegeben ist" ('90, p. 101).

HATSCHKE ('91) has asserted:— "Wir müssen zunächst bemerken, dass, *Coeloplana* und *Ctenoplana* wahrscheinlich nicht mit der aboralen Fläche kriechen, sondern mit dem ausgebreiteten Schlunde, wie dies auch andere Ctenophoren gelegentlich thun. *Ctenoplana* ist sogar noch eine eigentlich pelagische Form. Wir haben es hier wohl mit aberranten Ctenophoren-Formen aber nicht mit Uebergangsformen zu den Polycladen zu thun" ('91, p. 319, foot-note).

Next, DELAGE & HÉROUARD are of opinion that:— "Mais les ressemblance de *Ctenoplana* et de *Coeloplana* avec les Turbellariés semblent surtout adaptives et sont probablement secondaires: ce seraient, comme le dit HATSCHKE dans son traité de zoologie, des Cténaires aberrants ou plutôt ayant subi une réduction, puis la disparition des caractères cténaroides qui sont en rapport avec la vie pélagique (forme globuleuse, palettes), et ayant pris de plus en plus ceux qui sont en rapport avec la locomotion rampante (aplatissement, sole plantaire ciliée) et qui les rapprochent des Planaires uniquement parce que celles-ci sont aussi des animaux rampants. Déjà chez un Cténaire vrai, *Lampetia*, on trouve un commencement d'adaptation à la vie côtière, l'animal pouvant ramper et se fixer par la bouche comme avec une ventouse. On s'accorde à dire que ces caractères adaptifs n'ont pas de valeur phylogénétique, en sorte qu'il ne reste guère en faveur des affinités planariennes des Cténaires que les caractères embryogénique, reconnus par SELENKA" ('01, p. 761).

Thus, it is evident that, most, if not all, of the authors who expressed their opinions at variance with LANG on the question of the affinity of the two classes, regarded *Coeloplana* to be a specialized ctenophore which creeps with the inner surface of the extended pharynx used as a sole and that its striking resemblance with the Turbellaria only affords us a fine instance of the phenomenon of converging evolution.

More recently, MORTENSEN ('12), apropos of the discovery of *Tjalfella*, took up the question of the affinity of the two classes anew and arrived at a conclusion practically the same as LANG's. He closes his long train of discussion with the following words:— "Having thus discussed the different points of the SELENKA-LANG's theory to which objections have been raised as well as those which are affected by the facts brought to light by the more recent reseaches on

Ctenoplana and *Coeloplana* and especially, those here recorded on *Tjalfiella*, we may state as the main result that all the new facts are decidedly in favour of the theory, which now seems thus strengthened that serious objections can scarcely be raised against it any more. . . . A necessary conclusion from the close affinity between Ctenophores and Polyclads would seem to be, that the Ctenophores ought to be classified with the Platyhelmsia instead of with the Coelenterates, their affinities with the latter being, indeed, rather problematical, or, in any case, much less conspicuous than those with the Polyclads" ('12, p. 58).

But regarding the problem on the homology of the ventral surfaces of *Coeloplana*, *Ctenoplana*, *Tjalfiella* and polyclads, he seems to be of an opinion differing not only from all the previously named authors but also from LANG. Thus he gives:— "While LANG appears to think the flat shape of the polyclads the result of a simple shortening of the main axis, the edge of the Planarian body thus corresponding to the equatorial zone of the Ctenophoran body, HATSCHKE (Lehrbuch der Zoologie, p. 319) points out that *Coeloplana* and *Ctenoplana* 'wahrscheinlich nicht mit der aboralen Fläche kriechen, sondern mit dem ausgebreiteten Schlunde, wie dies auch andere Ctenophoren gelegentlich thun'. Likewise K. C. SCHNEIDER regards the flat oral side of *Coeloplana* and *Ctenoplana* as homologous with the lower part of the pharynx of other Ctenophores, the well known *Lampetia pancerina* CHUN, which even uses the inverted pharynx for creeping, being taken as the proof of the homology.— The morphology of *Tjalfiella* and *Ctenoplana* decidedly gives no support for this theory. It is the transverse furrow which becomes the flat underside, in the middle of which is the opening of the pharynx. In *Lampetia* there is no trace of a transverse furrow, the eversion of the sagittally compressed pharynx being morphologically quite a different thing, though it may physiologically serve the same purpose, viz. to form a flat surface adapted to perform creeping movements" (the same, p. 56).

Now, after finishing the review of the opinions hence put forward concerning the systematic position of *Coeloplana*, let us consider how the facts given in the foregoing pages may throw light on the same problem. First of all, I may give the undeniable conclusion drawn from the study on the structure and development of this animal that, the evidence is indubitably in favour of the view that, *first, Coeloplana is nothing but an extremely specialized ctenophore, adapted to the creeping mode of life, instead of to the pelagic habit, and second, the flatness and*

dorsiventrality of its body has been produced by the out-spreading of the lower part of the pharynx. In short, all the evidence supports the opinions of the authors ranked in (2) given in p. 63. As the basis of this assertion, I may bring forward the statement first that, the general structure of the body, showing clear biradial symmetry with the sense-organ and the mouth-aperture occupying the central position and the tentacular apparatus situated on each side of it, is perfectly in accordance with that of all ctenophores. Further, both the aboral sense-organ and the tentacular apparatus are almost perfectly identical with those of cydippid ctenophores. Even the arrangement of the gastro-vascular system and of the genital system, which appears at first sight highly characteristic of the present form, reveals itself on closer examination to be a mere deviation of rather minor importance from the condition prevailing in ordinary ctenophores. To mention more minute histological features, the ectoderm and endoderm are practically of the same structure as those of ordinary ctenophores, especially the existence of colloblasts and ciliated rosettes, both in the typical forms, as well as the branching of muscle-fibres at the ends, serves as a strong argument in favour of *Coeloplana's* being a genuine ctenophore. But the facts regarding development are still more convincing. As shown above, *Coeloplana* begins its development from an egg of the same structure as that of ordinary ctenophores and, after passing through the segmentation and gastrulation stages, both showing no deviation whatever from those in ordinary forms, develops into a typical cydippid larva; subsequently, the stomodaeum of the larva is sectioned into an internal and an external half, of which the latter is spread out into a broad and flat ventral sole, while the former becomes the pharynx of the adult. The fact that, the ventral surface of *Coeloplana* has been developed in this way can as well be seen from some anatomical features that the animal shows. As already mentioned, the tentacular apparatus of this animal agrees in all structural features with that of cydippid ctenophores, but it is characterized by its horizontal disposition, and this fact may be accounted for only by assuming the occurrence of such a change as mentioned just above. Similar argument may be made as to the situation and arrangement of the gastro-vascular system. Further, the ventral epidermis presents a character very different from the dorsal, but much in conformity with the pharyngeal epithelium.

ABBOTT ('07) has asserted, with full justice that:— "The weight of morphological evidence bears out the conclusion that *Coeloplana* is a

very highly specialized ctenophore, derived from the cydippida" (p. 62). But, I can not agree with his argument upon the homology of the canal-systems of *Coeloplana* and cydippid. He started that argument from a conception that the flatness of the body of *Coeloplana* had been derived merely from the reduction of the principal axis of the cydippid. It was accordingly but natural for him to have arrived at some conclusions, evidently erroneous, as for instance that, "The Cydippid meridional canals have disappeared in *Coeloplana*". (p. 65).

As already mentioned, MORTENSEN seems to be in an opinion, on the homology of the creeping surface of platyctenids, somewhat different from KORSCHOLT & HEIDER, HATSCHKE, and others. He has given, in the description of the development of *Tjalfiella*, that, a peculiar "transverse furrow" appears on the ventral side of the body of the cydippid-like larva, which furrow divides the ventral part of the larva into a pair of lobes and by the out-folding of the lobes the flat sole of the adult is formed. The alleged transverse furrow, however, seems to be nothing else than the oral aperture of the larva which has become elongated in the transverse direction. This fact will be readily seen, if one examines the origin and fate of that furrow in MORTENSEN's descriptions and compares that with the same of the oral aperture of *Coeloplana* given in the foregoing pages. Further, the fact that, the inner surface of the furrow is lined with an epithelium of the same character as that of the upper part of the pharynx, affords another evidence of that furrow being nothing but the oral aperture.

KREMPF ('20, c, '21) also regards the ventral aperture of the larva of *Coeloplana* not to be the mouth, nor the cavity which the aperture leads into to represent the pharynx. This argument he has based mainly upon the fact that the aperture and cavity are much wider in the transverse direction than in the sagittal. But such condition of the aperture and cavity obtains only in the relatively advanced stage of development, both of them being almost equally wide in every direction in the earlier stages; consequently it is futile to lay much stress upon such a condition of the aperture and cavity. The development of the animal described above shows plainly that the parts mentioned are to be identified with the mouth-aperture and pharynx of ordinary ctenophores. Further evidence for my opinion on the homology of the ventral surface is given already.

It may then be taken as granted that, *Coeloplana* is a highly specialized ctenophore adapted to creeping life instead of floating, and



also that, its flatness and dorsiventrality has resulted from the out-spreading of the external part of the pharynx. But there should remain the question to be answered on the affinity of the form to the Turbellaria, that is, whether *Coeloplana* does represent an intermediate stage in the evolution of the Turbellaria from the Ctenophora, or whether its resemblance with the former group is nothing more than an instance of the phenomenon of converging evolution. Before entering upon this question, I shall enumerate the following points regarding which *Coeloplana* is departed from the ordinary Ctenophora and approaches the Turbellaria:

- (1) the creeping mode of life,
- (2) the flatness and dorsiventrality of body,
- (3) the absence of comb-plates,
- (4) the presence of pigment,
- (5) the presence of an extensive ramifying gastro-vascular canal-system,
- (6) the presence of powerful muscular system,
- (7) the division of male gonad into some compact sperm masses.
- (8) the presence of a duct to each sperm mass,
- (9) the presence of seminal receptacles.

It can not be denied that, on account of the presence of these features, the resemblance of *Coeloplana* to the Turbellaria is very striking. Nevertheless, it would be hasty to conclude from this fact alone that *Coeloplana* stands phylogenetically between the Ctenophora and the Turbellaria, because, all of the above features, in my opinion, can as well be regarded simply to have arisen in relation with the peculiar creeping habit of the animal, thus, taken together with the similar characteristics of the Turbellaria, affording only a fine instance of the phenomenon of converging evolution. Indeed, each of those features can be accounted for equally well by assuming either of those two hypotheses, and this shows that it is difficult to settle this question by the anatomical data alone. So, naturally, our attention is directed to the facts about development. It is probable that, should *Coeloplana* be really a form standing phylogenetically between the Ctenophora and the Turbellaria, its development would show some deviation from that of the Ctenophora in general and approach as much to the development of the Turbellaria. However, as a matter of fact, the development of *Coeloplana* is identical with that of ordinary ctenophores in every detail, except for that peculiarity in the condition of the oral aperture and

pharynx which appears in the advanced stage of the larva and which leads to the production of the flattened shape of the adult. And, what seems to be the most important, is that, this way of the production of the flatness and dorsiventrality of the body of *Coeloplana* is entirely different from that which brings about the same feature of the body of the Turbellaria — while in the former, that results from the out-opening of the lower part of the pharynx, in the latter, according to LANG ('84), it is due to the bending of the principal axis of the larval body towards the anterior direction and by the concomitant growth of the body in the plane perpendicular to the original vertical axis. Thus, the facts about development apparently point to the conclusion that, the close resemblance of *Coeloplana* to turbellarians in several structural features has developed mainly by the converging evolution of the two forms and can not be taken as evidence of the former standing phylogenetically close to the latter. Besides this fact, if the Turbellaria has developed from the Ctenophora, it seems to be improbable that the former has arisen from a highly specialized form of the latter; it is by far more natural to assume that the Turbellaria has developed from an ancestral and less specialized form of the Ctenophora. But, it must be admitted as well that, in spite of the fact mentioned above, the actual existence of such a form as *Coeloplana* among the Ctenophora affords a strong suggestion as to how an ancestral ctenophore might have changed into a turbellarian, as it has been pointed out by KORSCHULT & HEIDER ('90) and BOURNE ('00).

Summary.

(1). *Coeloplana* is represented in the waters of Misaki by three distinct species, namely, *C. willeyi* ABBOTT, *C. mitsukurii* ABBOTT and *C. bocki* KOMAI, of which the anatomy was studied in all the three, and the development in the last-named species.

(2). The epidermis is the same in structure as in ordinary ctenophores, consisting of gland cells and interstitial cells; of the gland cells, two kinds, the clear and the granular, may be distinguished. In the epidermis of the ventral side, the interstitial cells are replaced by ciliated cells.

(3). The aboral sense-organ is nearly identical with that of ordinary ctenophores; in *C. bocki*, the margin of polar plates is divided into some lobes.

(4). The tentacular apparatus also shows no difference from the condition in cydippid ctenophores, excepting that, the tentacle-basis is disposed horizontally instead of vertically, and also that, the shape of the tentacle-sheath has undergone a peculiar modification.

(5). The colloblast is the same in structure as that of ordinary ctenophores; it consists of a head and two filamentous bodies, one spiral and the other straight, attached to the head.

(6). In the stomodaeum, the oesophagus is differentiated distinctly from the pharynx; the pharynx is provided with numerous folds on the roof, which are homologous with the pharyngeal folds of ordinary ctenophores.

(7). The main part of the canal-system is arranged in nearly the same way as in ordinary ctenophores; the infundibulum sends out on each transverse side a perradial canal, from which proceed two side-branches representing the subpharyngeal meridional canals; the perradial canal runs straight into the tentacular canal which is furcated into two branches that accompany the lateral halves of the tentacle-basis; from each of the branches of the tentacular canal, starts a canal that represents the subtentacular meridional canal.

(8). The endoderm consists of two kinds of epithelium, viz. the tall and vacuolated epithelium that performs intracellular digestion of food material and the low and ciliated epithelium that serves in circulating water through the canal-system. The dorsal wall of the canals that represent the meridional canals is lined with a peculiar kind of epithelium which shows a feature intermediate of the above two kinds. The vacuolated epithelium swallows various matters that enter the canal; the refuse matter after digestion is rejected together with small amount of the surrounding plasm in the form of a corpuscle that circulates through the canal-system.

(9). *Cocloplana* is hermaphroditic; gonads develop in the dorsal wall of the eight canals that represent the meridional canals of ordinary ctenophores.

(10). The female gonad arises along the entire length of each of those canals in a continuous linear tract of egg-cells, exactly as in ordinary ctenophores. Besides the egg-cells, the ovary contains two kinds of glandular cells, one appearing granular and the other clear, of which the former is by far the commoner than the latter.

(11). Along and close above each ovarial tract, is found a series of deep invaginations of the dorsal epidermis each of which is tube-like

in the external part and is expanded terminally into an ampulla-like swelling. The invaginations often contain a sperm mass, so that it is evident that they serve as sperm-receptacles.

(12). The male gonad develops as some separate compact masses of sperm-cells along the canals mentioned above. Each sperm-cell mass or testis is provided with a duct that opens on the dorsal surface of the body, and serves in leading the spermatozoa outside.

(13). In the body parenchyme, muscle-fibres are developed much better than in ordinary ctenophores; besides, there occurs a peculiar element of unknown nature that resembles somewhat in appearance the granular gland cell of the epidermis. Moreover, there is a system of very delicate fibrous bodies which is probably the nervous system.

(14). The newly laid egg shows a remarkable resemblance with that of ordinary ctenophores, but for the much smaller quantity of the gelatinous substance outside of the egg-body. It consists of an ectoplasm presenting a granular appearance and an endoplasm with an alveolar structure. The egg develops under the body of the mother animal without becoming pelagic.

(15). The segmentation of the egg was observed up to the 64-cell stage; it advanced almost precisely as in the eggs of ordinary ctenophores.

(16). The epibolic gastrulation is accomplished similarly as in the eggs of ordinary ctenophores. In the gastrula persists an opening at the animal or micromere pole for some time after the closure of another opening at the opposite vegetative or macromere pole.

(17). The gastrula develops into a typical cydippid-like embryo which is furnished at one pole of the subspherical body with a round mouth-opening and at the opposite pole with a sense-organ, besides a pair of tentacular apparatuses and eight comb-plate rows situated laterally.

(18). As development advances, the body of the embryo comes to show a strong lateral compression, growing much wider in the tentacular direction; at the same time, the pharynx is divided into two portions, of which the external portion becomes widened in the tentacular direction, and the internal in the sagittal direction.

(19). For some time after hatching, the larva swims about actively in water by means of comb-plates, but gradually comes to remain at the bottom, where it begins to crawl on the surface of the everted external portion of the pharynx.

(20). Finally, the larva gives up swimming, the cilia of comb-plates falling off, and the basal sole of the larval body becomes widely

spread out to assume the state of the adult individual.

(21). After the larval body has completed its metamorphosis, there arrives a stage in which the main part of the canal-system consists of eight pouches arranged around a central space much as in a certain young stage of *Gastrodes parasiticum*.

(22). All the facts given above, both anatomical and embryological, show clearly that, first, *Coeloplana* is nothing more than a highly specialized ctenophore adapted to the creeping mode of life, and, second, the flatness and dorsiventrality of the body of this animal has been brought about not by the simple reduction of the main axis, but by the out-spreading of the external half of the pharynx of the original cydippid-like form.

(22). The striking resemblance between *Coeloplana* and the Turbellaria is apparently no more than an instance of the phenomenon of convergence and can not be looked upon as an evidence of a close consanguinity of the former with the latter.

GASTRODES PARASITICUM KOROTNEFF.

Historical Remarks.

Gastrodes parasiticum KOROTNEFF is a peculiar coelenterate living parasitic in the body of *Salpa*. It was described first by KOROTNEFF in 1888; the generic name was given with reference to the structure of the body which resembles that of a gastrula. As to the systematic position of the animal, the author stated that, "Wenn wir aber die Verwandtschaft der *Cunocantha* mit dem *Gastrodes* konstatiren, sind wir eo ipso gezwungen, den *Gastrodes* als die Larvenform einer *Cunina* zubetrachten" ('88, p. 657). This opinion was discarded afterwards ('91) by the same author when he had undertaken a renewed study of the animal. He arrived at the conclusion that, "Im Grossen und Ganzen habe ich konstatiren können, dass es sich um eine entoparasitische Aktinie handelt, die sich wegen ihrer Lebensweise sehr vereinfacht und zugleich modificirt hat, indem sie sich einem Scyphostoma bedeutend nähert" (p.614). Against this, however, HEIDER ('93), another worker on the same animal, expressed his opinion that, "Der zweistrahlig radiäre Typus, welcher dem Baue von *Gastrodes* zu Grunde liegt, legt die Vermuthung nahe, dass es sich hier um eine parasitäre Ctenophore oder um den parasitären Jugendzustand einer Ctenophore handelt" (p. 117).

Recently, the present author has ascertained that the animal is a ctenophore unmistakably, and moreover that it is a form most probably referable to the peculiar group *Platyctenida* ('20, b).

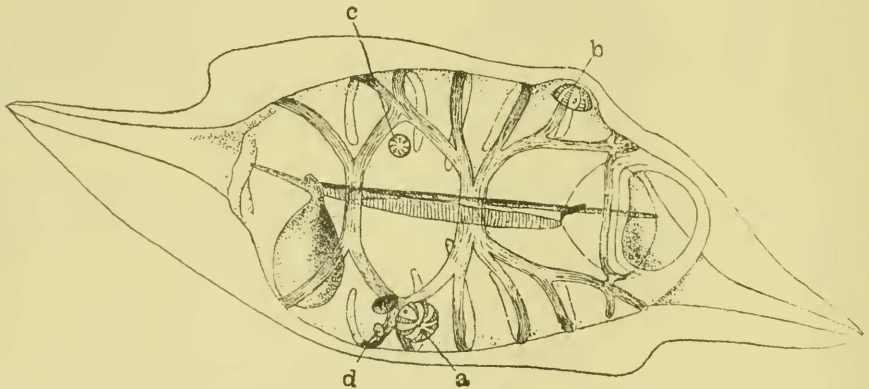
Material and Methods.

The material were all secured from *Salpa fusiformis* CUVIER, which is the commonest *Salpa* in the neighbourhood of Misaki. More than twenty individuals of the parasite were collected during the first five days of April 1919 and observed alive. Many of them were fixed and examined in sections as well. In addition, more than one hundred examples were obtained from specimens of *Salpa* which had been collected in the same locality by Mr. AOKI a few years before and preserved in formalin. In fresh examples much of the internal structures may be observed from outside. In fixing the material, acetic sublimate solution (saturated aqueous solution of corrosive sublimate 100 parts

+glacial acetic acid 3 parts) was used with preference. The specimens preserved in formalin also were found to retain much of the original condition fairly satisfactorily, and they were observed as total preparations stained with borax-carminc or cut into sections. Sections were always prepared with paraffin method, and stained with DELAFIELD'S haematoxylin and eosin. To find out individuals of small sizes in the body of *Salpa*, I found it helpful to stain the entire host body with borax-carminc, extract sufficiently, clarify with clove-oil, and examine with low-power microscope. Even very small specimens were detected without difficulty by this method.

External Features.

The parasite is a small transparent and colourless organism. The body is round and disc-like, about equally broad in all directions, distinctly convex on the dorsal side and more or less concave on the ventral. It is generally more convex on the dorsal side than concave



Text-figure 3. *Salpa fusiformis* CUVIER, harbouring four individuals of *Gastrodes parasiticum* KOROTNEFF in various developmental stages a-d. $\times 3$.

on the ventral, so that the body is thickest in the central part and thinnest in the marginal. It varies in size rather greatly, fluctuating from 0.15 to 3 mm. in diameter, with the height measuring nearly one quarter of the breadth. Small individuals show slight concavity on the ventral side and are very approximately disc-like; large ones, on the contrary, are generally rather highly vaulted and may even appear hemispherical in form (Pl. 8, fig. 1). The animal is imbedded always

in the mantle of the host body (In my preliminary paper, 1920, b, I have given erroneously as if the parasite were found in the test of *Salpa*). The parasite is situated with its ventral side commonly directed towards the centre of the body of the host, but sometimes away from that. As pointed out by HEIDER ('93), it may be found practically anywhere in the mantle, and there is no tendency that it inhabits more commonly in the neighbourhood of the nucleus of the host, contrary to the remark of KOROTNEFF ('88). It may occur, as a matter of fact, in parts far from the nucleus; even the processes in front and behind of the body of *Salpa* are often infected by the parasite. The frequency of the occurrence of the parasite fluctuates within a fairly wide extent. In a swarm of *Salpa* which I met with one day of 1-4, April 1919, only four individuals of *Salpa* out of more than one thousand were inhabited each by one *Gastrodes*, while, on another day of the same period, I could secure fifteen or sixteen specimens of the parasite out of about one thousand individuals of *Salpa*. And, judging from the examination of the specimens of *Salpa* presented by Mr. AOKI, it seems that, the frequency of the occurrence of the parasite may amount much higher — say, even up to 25 percent of the number of the individuals of the host. Generally, only a single individual is found in the same host, but, not very uncommonly more than one; in the case shown in the text-figure, the host harbours four individuals of the parasite. It is usual in such cases as mentioned last, that the parasites represent very different stages of development.

When it is liberated from the body of the host, the parasite assumes as a rule somewhat more strongly vaulted appearance (fig. 1). It can alter its external shape only a little, it may become slightly broader in some direction than other; it has, however, only a limited capacity of changing its shape and has no power of locomotion whatever.

Structurally, the animal shows fairly great individual variation with difference of its size. In most individuals occur, at the mid-dorsal point of the body, the sense-organ (figs. 1 & 2, *s*) and on the lateral sides a pair of tentacular apparatuses (*t*). Besides, there may be found in large specimens eight ribs (*c*), which radiate from the sense-organ and run towards the margin of the body.

In the large individuals such as represented in fig. 1, which measure about 3 mm. in diameter, the structure conforms largely with that of ordinary cydippid ctenophores. The aboral sense-organ (*s*)

shows a distinct otolithic mass in the centre of its cavity. The ribs (*c*) begin directly outside the sense-organ and terminate at the level about the end of two-third the distance from the aboral pole to the margin of the body. Each rib consists of about twenty comb-plates made up of relatively long cilia, whose beating movements can be observed from the surface of the body of the host. From each interradial corner of the entrance into the sense-organ, arises a ciliary tract ("Nerv", CHUN, '80) (fig. 2, *cil*, *tr*), which soon divides into two branches and advances to the aboral end of each rib.

The tentacular apparatus is located on the lateral sides of the body at a position nearly midway between the aboral pole and the margin of the body. It is nearly the same in structure as in cydippid ctenophores, except for the differences that the tentacle-stem (fig. 8, *t. st*) is represented by a very short stump-like process having no branches altogether, and that the tentacle-sheath is quite shallow as compared with that of those ctenophores. Along and under each rib, shows through a meridional canal (*m. c*), which is rather broad especially near its oral blind end, where it may exhibit slight lateral expansions—this tendency is especially marked in subtentacular meridional canals. The spaces between the meridional canals are traversed by some fibres, apparently muscular in nature. Beyond the oral end of the tentacular apparatus, may be observed a pharyngeal canal (*ph. c*) having a narrower calibre than the meridional canals.

The ventral surface of the body shows conspicuous foldings (fig. 11); the folds are arranged mostly parallel to the margin of the body. At the centre of the surface, exists an opening elongate in the direction perpendicular to the axis of the tentacles. The entire ventral surface is covered with cilia, the ciliation is particularly heavy in the parts surrounding the opening.

In individuals somewhat smaller in size (about 1.5 mm. in diameter; fig. 2), the otolithic granules (*ot*) are situated at the ends of the tentacular axis of the sensory cavity. The comb-plates (*c*) are about fifteen in number in each rib, and they bear very short cilia. In the tentacular apparatus (*t*), the stem has not been differentiated as yet. The meridional canals (*m. c*) are more roomy than in the larger individual and appear as broad sacs.

In examples still smaller (1 mm. in diameter; fig. 3), the aboral sense-organ can hardly be observed from outside, although discernible in sections as a distinct thickening of the epidermis (fig. 15, *s*), and the

ribs are not represented altogether; the condition of the tentacular apparatus (*t*), however, shows no difference from that in the preceding stage.

Next in the individuals of the stage represented in fig. 4, the diameter of the body measures some 0.5 mm.; the gastro-vascular system is in the form of a connected pair of cavities, each of which is laterally divided into four peripheral pouches representing the meridional canals (*m. c*). The opening on the ventral surface is scarcely compressed; the tentacular apparatus (*t*) is indicated merely by a thickening of epidermis appearing sickle-shaped in the dorsi-ventral view. This represents the stage that has been described and figured by KOROTNEFF and HEIDER, both of whom had apparently observed no examples of more advanced stages.

In individuals still smaller in size (0.2–0.3 mm. in diameter; figs. 5, 6), the rudiments of the tentacular apparatus (*t*) are defined only indistinctly, the gastro-vascular cavity exhibits an appearance of a single roomy central cavity, which may be divided peripherally into four subequal parts in relatively large examples (fig. 5). In figs. 7–10 the views of the animals stained with borax-carminé are represented. The individual shown in fig. 7 is in about the same developmental stage as the specimen in fig. 6, and the gastro-vascular cavity is roundish in form, although its outline is not represented clearly in the figure. No rudiments of the tentacular apparatus can be recognized as yet. Fig. 16 illustrates a vertical median section of this stage.

In stages still earlier than the above the external form differs considerably from that of the older stages. Thus, in the stage represented in fig. 8 the body is much less flattened than in the preceding stages and is approximately hemispherical and somewhat concave on the ventral side. Next in fig. 9 the body is subcylindrical, much higher than broad, bluntly pointed at one end and slightly concave at the other; the breadth of the body measures about 0.08 mm, and the height about 0.12 mm. Unfortunately, I could obtain no sections of such early stages, but so far as could be witnessed by superficial observations, the animal had developed no opening at the centre of the ventral surface as yet. The last mentioned stage seems to be nearly the earliest one that can be observed in the mantle of the host. But I was fortunate enough to secure a younger individual (fig. 10) killed apparently while trying to bore into the body of the host, with one half of its cylindrical body imbedded in the test of the host, and the other half lying freely

outside the latter. I could also prepare longitudinal sections of this individual (Pl. 9, fig. 9). This is a typical planula both in the external and in the internal features; the body is covered with flagella all over the external surface and is filled within by large endodermal cells.

Anatomical and Histological Features.

It will be convenient, in giving description of the anatomical and histological features of the animal, to give facts about large individuals as examples; but most of the accounts given may be considered to apply to smaller individuals as well, unless otherwise be stated specially.

Epidermis.

The epidermis of the dorsal side of the body is very simple as compared with the same of ordinary ctenophores. It consists entirely of ordinary epithelial cells and comprises no glandular elements altogether. It shows some topographical differences in thickness, being thickest in parts forming ribs (25-30 μ) and thinnest in regions between them (4-6 μ). The dorsal epidermis is constructed mostly with a few, one or two, cell layers throughout, irrespective of the thickness, so that the individual cells are tall and cylindrical where the epidermis is relatively thick, and low and flattened where this is relatively thin.

The cells forming comb-plates (Pl. 9, fig. 2) are cone-shaped with the apex turning outside and carrying the cilia of the comb. Each comb-plate consists of an assemblage of such cells, with seven or eight cells in each vertical row, and three or four in each transverse row. The two consecutive plates in the same rib are separated from each other by seven or eight ordinary epidermal cells. The epidermis of the ventral side shows distinct ciliation all over. It is somewhat thicker than the dorsal epidermis almost everywhere, measuring usually 20-25 μ .

Aboral Sense-organ.

The aboral sense-organ (Pl. 9, fig. 1) is constructed similarly as in ordinary ctenophores. It is globular in shape. Its wall consists of slender ciliated cells, and shows nuclei in the whole thickness in three or four strata, except at the bottom part where the nuclei are not found in the superficial half of the thickness. An otolithic mass (*ot*) is situated

in the centre of the capsular cavity in examples of large sizes. It is globular in form and is made up of spherical granules, to each of which is attached the nucleus of its matrix cell. The mass is supported by some "balancers" (*bal*) which are made up of peculiar long cilia borne by cells situated close to the bottom part of the wall just referred to. The entrance into the cavity of the sense-organ is beset with long cilia, which construct together a covering over the capsule (*cu*). The existence of polar plates could not be made out with certainty, although it is possible that, the parts of the epidermis directly outside the capsule which contain nuclei in 2 or 3 strata would represent them. In individuals of smaller sizes the aboral sense-organ may be represented by a simple thickening of the dorsal epidermis, where neither otolithic granule nor any ciliary covering has been formed as yet (Pl. 8, fig. 15, *s*).

Tentacular Apparatus.

The tentacular apparatus consists of the tentacle-sheath, tentacle-basis and tentacle-stem, all of which are developed much in the same way as in ordinary ctenophores. The tentacle-stem (Pl. 8, fig. 1, Pl. 9, figs. 3 & 4; *t. st*) is quite short and simple and has no branches altogether; otherwise it agrees perfectly with that of ordinary ctenophores. It is composed of a muscular core and an epithelial covering (fig. 4). Several nuclei (*n*) of relatively large sizes are found in the core; evidently, they belong to the tissue cementing muscle-fibres together. Some of the cells of the epithelium contain a vesicular nucleus and numerous refringent granules (*col*)—these cells are the primordia of the colloblast. The tentacle-sheath (fig. 3, *t. sh*) is much shallower than that of ordinary ctenophores; indeed, it can hardly be called sheath. Its inside wall is thickened into a pad-like structure, the tentacle-basis (Pl. 8, fig. 1, Pl. 9, fig. 3; *t. b*), which contains quite numerous nuclei superposed in several layers. In very small individuals the tentacular apparatus is entirely lacking.

Gastro-vascular System.

The opening at the centre of the ventral surface of the body leads dorsally into a tubular passage (Pl. 8, figs. 3-7, 11, 13, 15, 16; *oe*). This passage is elongate in the transverse direction in large examples

(figs. 3, 13), while it gives a roundish cross-section in smaller ones (figs. 4-7). It is lined with the epithelium of the ectodermal origin, which is identical in appearance with the ventral epidermis except the ciliation being somewhat heavier. This passage represents, without doubt, the oesophagus, a part of the stomodaeum which is recognizable in all ctenophores but developed especially well in platyctenids (cf. MORTENSEN, '12; present paper, p. 25 *et seq.*). As mentioned above, very young individuals lack the oesophageal opening.

The oesophagus opens dorsally into the infundibulum (Pl. 8, fig. 11; *i*), which lies directly under the aboral sense-organ. The infundibulum is a relatively spacious chamber of a depressed shape, slightly wider in the sagittal, than in the transverse direction. It is clothed all around with a very low epithelium, which shows clear ciliation in the bottom part. Perhaps the cilia exist in the epithelium of the roof too, but I could not observe them in that region. The epithelium lining the roof of the infundibulum is somewhat vacuolated.

The infundibulum represents the source of the entire canal-system of the body, which is arranged much in the same way as in ordinary cydippid ctenophores. From each transverse side of the infundibulum, there starts a perradial canal which runs obliquely oralwards and communicates with the meridional, tentacular and pharyngeal canals, just as in those ctenophores. All of these canals are rather broad relatively to their short length.

The meridional canals (Pl. 8, figs. 1-4, 11-14; *m. c*) are very broad throughout their length especially in individuals of small sizes. The pharyngeal canals (figs. 1, 2, 13, 14; *ph. c*) are found only in large individuals; they run along the transverse wall of the pharynx and terminate nearly at the same level as the oral ends of the meridional canals. The part of the body harbouring the pharyngeal canal is often raised up on the ventral side of the body (fig. 14). The canal has always a narrower calibre than the meridional canals. The tentacular canals (fig. 14, *t. c*) are very short but have the same structure as those of the cydippids. The infundibulum further sends out an excretory canal (fig. 12, *ex. c*) from each sagittal side of its wall. This canal proceeds to the dorsal direction and opens to the exterior just outside the sense-organ (fig. 11, *ex. p*). The canal furcates into two branches shortly previous to the opening, of which one branch opens to the exterior, while the other terminates blindly in the surrounding tissue, just as it is in ordinary ctenophores. In small individuals the gastro-

vascular system is more or less simplified, as mentioned already.

Of the epithelium constructing the wall of the gastro-vascular system, one can distinguish two sorts, which may be called the ciliated and the vacuolated epithelium respectively. The former (Pl. 9, fig. 6; *en*) is low and resembles somewhat the ventral epidermis. It shows vesicular nuclei at rather regular intervals. But I could not find ciliated rosettes in that epithelium nor in any other part of the body. The latter kind of epithelium, on the other hand, is more or less thickened and contains vacuoles and food material. Of the food material, the one depicted in Pl. 9, fig. 2, *f* is most commonly met with. It is an aggregate of granular bodies which take acid dyes weakly and contain a small and highly basophilous nucleus. This is surely what KOROTNEFF ('91) has called 'Plasmahäufen'. Evidently they are nothing more than the blood-corpuscles of *Salpa* taken into the cells. The detritus matter or undigested part of food material is expelled into the lumen of the canal together with a small amount of the surrounding cytoplasm and forms corpuscles that rotate along with water through the canal-system, just in the same way as ABBOTT has described in *Coeloplana* ('02, '07). In living individuals the rotation of such corpuscles offers a striking spectacle just as in *Coeloplana*. Pl. 9, fig. 5 shows one of such corpuscles just about to be formed and another already formed and lying in the canal lumen. The corpuscles often contain a nucleus which sometimes exhibits clear signs of degeneration.

The distribution of the two kinds of epithelium in the canal-system resembles much that in ordinary ctenophores. In the meridional and tentacular canals, the external side is lined by the vacuolated epithelium, whereas the internal side is clothed with the ciliated (Pl. 8, figs. 11-14). In the tentacular canal, the wall on the external side is thickened very much and contains quite a large quantity of food material. The wall of the pharyngeal canal is made up of the vacuolated epithelium on the lateral sides and of the ciliated one on the external and internal sides (fig. 13, *ph. c*). The excretory canals are lined with the ciliated epithelium of the same character as that of the infundibular wall.

Gonad.

It is a rather striking fact that all of the individuals of *Gastrodes* examined, notwithstanding their small sizes, contained very large egg-cells. But, in spite of this fact, none of the individuals showed

sperm-cells. Moreover, the situation of the egg-cells is very unusual: they develop in the ventral epidermis, instead of in the wall of the meridional canals as in ordinary ctenophores. They are found dispersed between the ordinary epidermal cells (Pl. 8, figs. 11, 14, 16, Pl. 9, figs. 6 & 7; *ov*), developing no structure to be termed ovary. The egg-cells may occur practically anywhere in the ventral epidermis, as well as in the oral half of the oesophageal wall. But, as a general rule, large egg-cells are found nearer the margin of the body and small egg-cells in the central region. Especially, the cells of the largest sizes occur in parts a little internal to the margin of the body, where they form a nearly complete circle (Pl. 8, fig. 7). Smallest egg-cells, to be unmistakably recognized as such, are found in the central part of the body; they are situated between the basal parts of the epidermal cells (Pl. 9, figs. 6 & 7). Moreover, since nearly complete gradations may be found between such cells and ordinary epidermal cells, we seem to be justified to decide that the egg-cells develop from the ectoderm. Perhaps the cells arrive there by migration from other places, as it has been maintained by SCHNEIDER ('04) in *Beroë*, yet, I could observe nothing of this kind. Anyway, if the migration of germ-cells takes place in *Gastrodes*, it seems to occur in a very early stage of the animal, when the germinal layers are not differentiated well as yet.

The developing egg-cells send out a stalk-like plasmic process to the margin of the epidermis (fig. 6), where its terminal end often assumes a funnel-shape, apparently to facilitate absorption of nutriment directly from the body of the host. Large egg-cells are accordingly pyriform; the nucleus is found in the broad basal part which is imbedded within the parenchyme tissue under the epidermis. The length of such egg-cells surpasses much the thickness of the latter. Some large egg-cells present a somewhat amoeboid appearance (fig. 7). The largest egg-cells observed measured about $60\ \mu$ in length, $40\ \mu$ in breadth, the nucleus and the nucleolus about $30\ \mu$ and $10\ \mu$ in diameter respectively. In the egg-cells of such sizes, one can discriminate in cytoplasm the differentiation of the central and superficial layers, of which the former is eosinophilous and may show a granular appearance, while the latter is cyanophilous and exhibits fine longitudinal striations especially in the parts constituting the stalk-like process mentioned above. The nucleus contains a large nucleolus, besides some rod-shaped chromatin granules distributed here and there in the nuclear cavity. The nucleus is mostly spheroidal in shape, but may be provided with a short process directed towards the

free margin of the epidermis. This condition of the egg-cells recalls much of that of the egg-cells of actiniae described and figured by HERTWIGS ('79). The authors give that the eggs in those forms arise in the basal part of the mesenterial epithelium and become imbedded in the mesogloea, but they keep connection with the surface of the epithelium by means of a stalk-like process sent out from the egg-body, so that the entire egg assumes a pyriform; further, the process shows longitudinal striations. Thus the resemblance of the egg-cells in the two forms is very close.

Eggs showing an alveolar structure as in ordinary ctenophores were not met with, in spite of the fact that the nucleus may be nearly as large as that of mature eggs of ordinary ctenophores given by previous writers. Thus, while the diameter of the nucleus of the egg in the present form measures about $30\ \mu$, according to CHUN ('80), it measures in: *Beroë* $40\ \mu$, *Cestus* $35\ \mu$, *Euchlora* $28\ \mu$, *Eucharis* $26\ \mu$, and *Lampetia* $13\ \mu$ respectively. I have also observed in the egg of *Coeloplana* the diameter of the nucleus measured $20\ \mu$ on the average.

Small individuals contain as a rule small egg-cells, and large ones larger cells besides small. Thus the diameters of the nuclei of the largest egg-cells contained by individuals of various sizes have measured:

Diameter of body (mm.).	Diameters of egg-nuclei (μ),
0.15.....	7, 7, 7.5, 7.5.
0.25.....	8, 8, 8, 7.5.
0.3.....	14, 11, 11.
0.35.....	12, 11, 15.
0.5.....	22, 19, 16.
1.2.....	22, 22, 24, 24.
1.4.....	26, 24, 24, 24.
2.4.....	27, 30, 28, 30.
2.5.....	28, 32, 30, 31.

The egg-cells may be recognized in any stage mentioned above, in fact even in the earliest developmental stage of the animal, when the body is cylindrical as yet (Pl. 8, fig. 9; *ov*). In the planula-stage too, I was able to make out some cells apparently sexual. They lie dispersed among the endodermal cells and may be distinguished from the latter by the features that the cytoplasm appears much more compact and the nucleus is somewhat larger in size.

When the eggs are laid remains unknown, but probably soon after the liberation of the parasite from the body of the host. Sometimes

I have met with some egg-cells of very large sizes lying outside of the ventral epidermis (fig. 14), and others just about to be liberated through it. Perhaps this shows nothing more than an artefact, yet it apparently forecasts the fact that the eggs are laid outside through the ventral epidermis. Moreover, many egg-cells may be found in the epidermis of the parts between the meridional canals, and it is almost impossible to imagine the falling of those cells into the lumen of the canals. In any case, the occurrence of the egg-cells in the ectoderm is quite unique in the Ctenophora—evidently, this feature has developed in relation with the characteristic mode of life of *Gastrodes*. But, it is not very striking that, such small individuals, less than 3 mm. in body diameter, show very large egg-cells, since in certain ctenophores a peculiar mode of reproduction called dissogony is known to occur, where minute individuals can develop eggs and sperms precociously (CHUN, '92). Both KOROTNEFF ('88, '91) and HEIDER ('93) have observed egg-cells in *Gastrodes* and recognized their situation in the ectoderm.

In spite of the fact that the egg-cells were found in all individuals, no sperm-cells, neither mature nor of any developing stage, could be met with. This observation makes it possible that, the parasite propagates parthenogenetically, which opinion seems to be taken also by KOROTNEFF ('88). This author, however, gives in his later work ('91) that, he observed sperms in the endoderm of one small specimen. But, judging from his figure and description of the alleged sperms, they seem to be nothing more than blood-corpuscles of *Salpa* taken up by the endodermal cells. My examinations of a series of specimens of various sizes have revealed no figure suggesting of the existence of sperms whatever.

Body Parenchyme.

The body parenchyme contains but small quantity of cellular elements. Relatively numerous isolated cells showing some plasmic processes are found under both the dorsal and the ventral epidermis. The area between ribs is traversed by fibres running horizontally (Pl. 8, fig. 1). The fibres are muscular in nature without doubt; they show branchings as in ordinary ctenophores (Pl. 9, fig. 8).

Developmental Cycle.

HEIDER (1893) assumes that, the entrance of *Gastrodes* into the

body of *Salpa* should occur in a very young stage of the latter, when the cellulose mantle is but slightly developed. The observation of the planula stage noted above, as well as of the very young stages of the parasite, however, shows that the infection may take place in the advanced stage of the host. And, judging from the various sizes of the examples of the parasite which may be found in one and the same individual of the host, it is very likely that, the infection may occur at various stages of the host.

As to the change in the structure of the parasite after the entrance into the body of the host, we may infer from the material at hand as follows:— The planula which has bored into the body of the host will make its way through the test and arrive at the mantle layer. Then it will cast off the cilia, and the end of its cylindrical body directed inwards will become concave and the body will grow gradually broader than high, to assume finally a hemispherical shape. The parasite will undergo development by taking nutriments from the host. The gastro-vascular system, tentacular apparatus, aboral sense-organ and ribs will develop meanwhile, and the stage shown in Pl. 8, fig. 1 will be attained in time. This represents, without doubt, the most advanced parasitic stage of the animal. Very likely, the parasite will leave sooner or later the host and become free. The eggs will be laid not very long after the liberation. They will pass through the segmentation stage as usual. But we have reason to assume that, the segmentation is somewhat different from that which prevails in ordinary ctenophores and more or less approximates the condition known in other coelenterates. The structure of the ovarian egg, as well as the existence of the planula stage, suggests this very much. At any rate, the egg will develop into a planula which enters into the body of *Salpa*. These apparently represent the ordinary developmental cycle of the animal. As to the fate of the individual after the spawning, it is not impossible that, it undergoes further development, and finally metamorphoses into an animal looking quite different from the parasitic stage, although we have no data at present to assure this.

Systematic Position.

Regarding the systematic position of *Gastrodes*, there can be no doubt whatever, that it belongs to the Ctenophora, as HEIDER ('93) has already pointed out. But to which order of the class should it be

assigned to? To answer this, it is evidently necessary to elucidate the change undergone by the animal after the liberation from the body of the host. Nevertheless, the observation on the parasitic stage decides that, the animal bears close relationship to the Platyctenea on one hand and to the Cydippida on the other. Above all, the fact that the ventral surface of the body is lined all over with the ciliated epithelium, as also that profuse foldings are developed in the central parts of that surface, shows clearly that the ventral surface of *Gastrodes* is morphologically homologous with that of platyctenids. Then, the surface may be regarded to have arisen by the out-turning of the pharynx, and this is the feature that characterizes most the group Platyctenea. Besides, the flatness and dorsiventrality of the body of the animal, as well as the arrangement of the parts of the body, especially that of the canal-system, can be accounted for only by assuming such a change as mentioned above having affected the body of *Gastrodes*.

Clear as the affinity of *Gastrodes* to the Platyctenea in these respects, it can not be denied that in other respects the resemblance is rather slight. The animal has no bright coloration, nor any branching canal system, and it is provided with pharyngeal canals which lack all platyctenids thus far known. Furthermore, it shows a great deviation from those forms in the condition of the gonad. But, it should be mentioned as well that, the habitat of *Gastrodes* in the body of *Salpa* apparently makes it necessary for the parasite to retain the original colourless and transparent condition. The difference in the condition of gonads differentiates the form from all the members of the other orders of the Ctenophora as widely as from those of the Platyctenida. Towards the Cydippida, the form approaches especially in the conditions of the canal-system—for instance, the meridinal canals are simple and the pharyngeal canals are developed. In short, so far as can be judged from the condition of the parasitic stage, *Gastrodes* shows undeniable relationship to the Platyctenea on one hand and to the Cydippida on the other. But, the fact that the form shares with the former order the most characteristic feature of the structure of the body, viz. the out-spreading of the pharynx into the ventral body surface, apparently makes the form to be grouped into the order Platyctenea.

The presence of a planula stage in this form, however, is unique in the entire group of the Ctenophora,* and may be said to differentiate

* CHUN ('80) has given that he observed very delicate cilia covering the surface of the body of a certain larval stage of *Eucharis*; perhaps, this stage represents the planula stage.

it sharply, not only from other members of the Platyctenea, but also from those of all the remaining orders. Further, it may be pointed out that, the occurrence of that stage in *Gastrodes* is an evidence for the affinity of the two sub-divisions of the Coelenterata, Cnidaria and Ctenophora, notwithstanding that certain authors are often inclined to ignore the affinity and put greater emphasis on the relationship of the Ctenophora with the Turbellaria. The planula of the present form, as previously mentioned, represents a solid mass of endoderm covered by a skin of ectoderm. In this respect, and also in other structural features, it resembles much the same stage of the Hydrozoa. This fact stands possibly for the close relationship of the Ctenophora and the Hydrozoa.

The effect of the parasite to the host seems to be rather trifling, and all the host showed normal development of the embryo, although a contrary observation may be found in HEIDER'S work ('93).

Summary.

(1). *Gastrodes parasticum* KOROTNEFF is a parasitic ctenophore found in the mantle of *Salpa*.

(2). It shows some differences between individuals of different sizes in its external and internal features. Largest individuals measure about 3 mm. and smallest about 0.1 mm. in the diameter of the body.

(3). The structure of large individuals is essentially the same as that of a cydippid. It is provided with an aboral sense-organ, eight rows of comb-plates and a pair of tentacular apparatuses, each of the same structure as that of a cydippid. The arrangement of the gastro-vascular system is also the same as in that form.

(4). Small individuals may be without the sense-organ, comb-plates and tentacular apparatuses, moreover, the gastro-vascular system is more or less simplified, as shown in Pl. 8, figs. 3-8.

(5). The most notable point concerning structure is that the pharynx has been opened out to give the animal a flattened shape and distinct dorsiventrality, the original external surface of the cydippid-like body becoming the dorsal surface of the animal and the original inner surface of the pharynx the ventral surface of it.

(6). In the smallest individuals the shape of the body is cylindrical, much as in cydippid ctenophores, and this stage is preceded by a distinct planula stage showing ciliation on the whole external surface of the body. The animal penetrates into the body of the host in this

stage and becomes a parasite.

(7). The egg-cells are found in the ventral epidermis, i. e. in the original pharyngeal epithelium, they show a structure very different from that of the eggs of ordinary ctenophores, having no alveolar layer in the centre.

(8). *Gastrodes* shows relationship to the Platyctenea on one hand and to the Cydippida on the other, but the distinct dorsiventrality of the body which has resulted from the out-opening^{*} of the pharynx apparently makes the form to be grouped into the former order.

(9). The existence of a planula stage in *Gastrodes* affords an evidence of the close relationship of the Ctenophora to the Cnidaria. Moreover, the resemblance of the planula with that of the Hydrozoa suggests a consanguinity between the Ctenophora and the Hydrozoa.

INTERRELATIONSHIP OF THE MEMBERS OF THE ORDER
PLATYCTENEA; AFFINITY OF PLATYCTENEA
TO OTHER ORDERS OF CTENOPHORA.

The order Platyctenea has been erected by BOURNE in 1900 to receive the genera *Coeloplana* and *Ctenoplana*. At present it should include *Tjalffiella* in addition and most probably *Gastrodes* too. As to the first three genera, a detailed comparative study was undertaken by MORTENSEN, and the reader is referred to his work in 1912. Nevertheless, the following brief general review of the order would not be superfluous. Of the four genera, *Coeloplana* and *Tjalffiella* are devoid of comb-plates in the adult stage, while *Ctenoplana* and *Gastrodes* retain them. In the tentacular apparatus, the tentacle-basis is much like that of cydippids in all of the four, except that it is disposed more or less horizontally instead of vertically. The secondary branches of the tentacle are present in *Coeloplana* and *Ctenoplana*; in *Gastrodes* the tentacle is represented by a short stump-like process. In the condition of the endodermal parts of the gastro-vascular system, the following distinctions may be met with:— In *Coeloplana*, eight canals representing the meridional canals of ordinary ctenophores can be distinguished. In *Ctenoplana*, on the other hand, the main part of the system appears to consist of four interradially situated sac-like pouches—such a condition is found in the larval stages of all ctenophores, so that *Ctenoplana* may be said to retain the condition of that stage in the adult. In *Tjalffiella*, each of the meridional canals is reduced into a short stalk-like diverticulum from the perradial canal. Finally, in *Gastrodes*, the gastro-vascular canals are arranged in large examples much in the same way as in ordinary ctenophores, whereas, in small ones, they are represented by a connected pair of cavities and each of the cavities, in a certain particular stage, is laterally divided into four broad pouches, showing thus a striking resemblance with the condition in a certain developmental stage of *Coeloplana*.

To all the four genera is common the feature that, the larval pharynx is divided into two parts, of which the external part is spread out and forms the ventral side of the animal. This peculiarity of the pharynx constitutes, in my opinion, a feature which is the most characteristic of the members of the Platyctenea, leading, as it does, to the flatness and dorsiventrality of the body, which is to be looked upon as the most important distinctive character of the group. Further, the

features that pharynx is thrown into numerous folds, that the oesophagus is differentiated well, as also that the infundibular canal is obliterated, are recognizable in various degrees in all the members of the group. Besides, except in *Gastrodes*, excretory canals show no branching and pharyngeal canals are wanting.

In *Coeloplana*, eggs develop in a linear tract from each of the eight canals that represent the meridional canals of ordinary ctenophores, while sperms arise in a certain number of separate masses along the same canals. In *Ctenoplana*, eggs have not yet been found, but sperms are known to develop in compact masses much as in *Coeloplana*, and of the masses, there occurs but one to each canalar pouch, there being in all four masses in each individual. In *Tjalfiella*, both eggs and sperms develop on the wall of the aforesaid eight diverticula of the perradial canals, the sperms on the interr radial, and the eggs on the perradial side of each diverticulum. In *Coeleplana* and *Ctenoplana*, the sperm-masses are provided with ducts for the passage of the sperms to the outside. In *Gastrodes*, the sperms have not been observed as yet, the eggs are found scattered in the ventral epidermis. In *Tjalfiella* and *Coeloplana*, the larval stage is perfectly like a cydippid and provided with comb-plates.

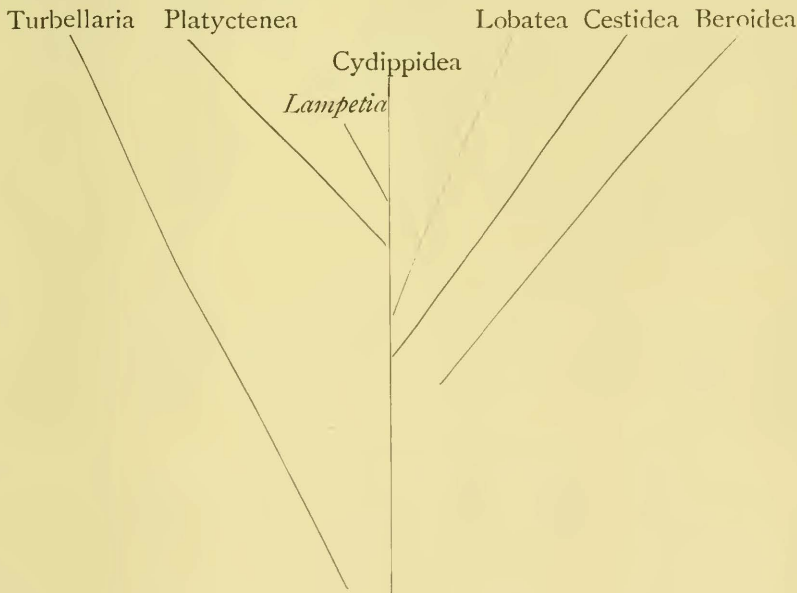
In view of such points uniting the four genera together or distinguishing them from one another as mentioned above, it seems to be reasonable to arrange the genera under a common group and erect it as a separate order under the class Ctenophora, as it has been done by previous authors. And we may give the diagnosis of the order Platyctenea somewhat as follows:—

“Creeping, sessile or parasitic Ctenophora. Body flattened, presenting distinct dorsiventrality as the result of the out-spreading of the external part of the pharynx. Comb-plates may be wanting in adult. Colourless or brightly coloured. Gastro-vascular canals generally branching. Tentacles of cydippid type, sometimes rudimentary”.

Regarding the relationship of the Platyctenea to other orders of the Ctenophora, it is without doubt that there is a direct and close consanguinity between the order and the Cydippidea. This is especially clearly shown in the development of *Coeloplana* and *Tjalfiella*. Further, the compression of the body, with the transverse axis longer than the sagittal, is a feature common to the two orders and differentiates them from the remaining. Similar fact may be said with respect to the tentacular apparatus; it is only those two orders that are provided with

ordinary pinnate tentacles, in the remaining orders the tentacles may be entirely lacking (Beroidea), or replaced by the peculiarly modified "secondary" tentacles (Lobatea & Cestidea). Finally, the out-spreading of the pharynx is nicely foreshadowed by a cydippid, *Lampetia*, as it has been pointed out by previous writers. With the Lobatea, the Platyctenea is evidently more remotely related than it might appear at first sight, since it differs rather strikingly from that order in the relative length of the sagittal and transverse axes of the body, in the conditions of the tentacular apparatus, of the canal system, but especially of the pharynx. The "lobes" characteristic of the Lobatea should be looked upon as the outgrowth from the oral parts of the body and can not be homologized with the parts that have given rise to the body-skirt characteristic of the Platyctenea. While in the formation of the lobes the pharynx is not concerned at all, the skirt of the Platyctenea develops by the out-opening of the pharynx; the former arise from the parts below the level of the oral aperture but the latter from the parts above it.

Then, the diagram illustrating the mutual relationship of all the orders of the Ctenophora as well as the origin of the Turbellaria may be somewhat as shown below:



DIAGNOSIS OF ALL KNOWN SPECIES OF PLATYCTENEA.

Order Platyctenea, BOURNE ('00).

Family Gastrodididae nov.

Genus *Gastrodes*. KOROTNEFF ('88)

Parasitic in *Salpa*; disc-like, but more or less concave on ventral side; colourless; comb-plates present only in large individuals; meridional canals broad especially in small individuals, showing little sign of branching; tentacles rudimentary; eggs scattered in ventral epidermis, sperms unknown. 1 species:

Gastrodes parasiticum KOROTNEFF ('88).

Size: up to 3 mm. Locality: Nizza, Misaki.

Family Ctenoplanidae WILLEY ('96).

Genus *Ctenoplana* WILLEY ('96).

Both swimming and creeping; body more or less cap-like, brightly coloured; comb-plates present; tentacles with numerous branches; meridional canals represented by four interradially situated broad pouches, with richly anastomosing branch canals. Sperms developing in compact masses provided with sperm-ducts, eggs unknown. 3 species:

Ctenoplana korvaleskii KOROTNEFF ('88).*

Colour crimson; body in swimming attitude shaped like a truncate pyramid; median dorsal surface concave; free margin of skirt frilled. Size: 6 mm. Locality: West coast of Sumatra.

C. rosacca WILLEY ('96).

Colour crimson; body in swimming attitude of a quadrilateral form; median dorsal surface convex; free margin of skirt plain. May be a variety of preceding species. Size: 6 mm. Locality: Eastern Archipelago of New Guinea.

C. korotneffi WILLY ('96).

Colour green; body in swimming attitude roof-shaped; median dorsal surface upraised with two upright end-knobs; free margin of skirt slightly frilled. Size: 6 mm. Locality: Eastern Archipelago of New Guinea.

Family Tjalfiellidae nov.**

Genus *Tjalfiella* MORTENSEN ('10).

Sessile, body laterally compressed, elongate in transverse direction;

* Specific diagnosis taken from WILLEY (96, p. 336).

** MORTENSEN has referred *Tjalfiella* into Ctenoplanidae, but the difference between *Tjalfiella* and *Ctenoplana* is surely quite sufficient for creating a distinct family for each of them.

comb-plates absent in adult; tentacles without branches; pharyngeal cavity with an accessory opening on each transverse end of body upon the summit of a chimney-like vertical elevation; meridional canals reduced into short diverticula from perradial canals; branching canals present, but rather sparse, showing no anastomoses; gonads arising on lateral walls of the above diverticula; viviparous, eggs developing into cydippid-like embryos in brood-cavities at the lateral parts of body. One species:

Tjalffilla tristoma MORTENSEN ('10).

Size: 20 × 5 mm. (in large specimens). Locality: West coast of Greenland, found attached to *Umbellula*.

Family Coeloplanidae WILLEY ('96).

Genus *Coeloplana* KOWALEVSKY ('80).

Creeping; body flat, shape extremely changable; brightly coloured; comb-plates absent in adult; tentacles with numerous branches; meridional canals well developed, branching canals showing rich anastomoses; sperms developing in some compact separate masses, eggs in a continuous linear tract, from each canal representing meridional canal; sperm-mass with a duct opening to dorsal surface of body; larva cydippid-like. 5 species:

Coeloplana metschnikovii KOWALEVSKY ('80).

Colour greyish; without "dorsal tentacles" (?).

Size: 6 × 4 mm. Locality: Red Sea near Tor.

C. willeyi ABBOTT ('01).

Colour variable, may be purplish, reddish or rosy, scattered with yellowish-white spots on the margin of body and at the bases of dorsal tentacles. Size: 20-60 mm. (in extended state). Locality: Misaki.

C. mitsukurii ABBOTT ('01).

Colour less variable than the former or the next species, generally light yellowish-brown, without yellowish-white spots. Size: nearly the same as above. Locality: Misaki.

C. bocki KOMAI ('20).

Colour variable as much as in *C. willeyi*, or even more, always forming a dozen or more streaks parallel to tentacular axis, yellowish-brown spots absent. Locality: Misaki, found attached to *Dendronephthya* sp. Size: ca. 15 mm. (in extended state).

C. gonoctena KREMPF ('20).

Colour milky-white, scattered with brown spots. Size: 10-30 mm. in length, 5-10 mm. in breadth. Locality: Coast of Annam, found attached to *Alcyonium kremphi* HICKSON.

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EXPLANATION OF PLATES 1-9.

Abbreviations.

a.f	Accessory filament of tentacle.
a.f'	Developmental stage of the same.
bal	Balancer of otolithic mass.
br. c	Branching canal-system.
c.	Comb-plate.
c.a	Central area of polar plate.
c.c	Ciliated cell.
c.f	Central filament.
c.g	Clear gland cell.
c.g'	Senescent stage of the same.
cil	Cilia.
cil.tr	Ciliated tract.
col	Colloblast.
cor	Excretory corpuscle in gastro-vascular canal.
c.sph	Central spheroidal body of colloblast.
c.st	Cell-strand.
cu	Ciliary covering of aboral sense organ.
d.t	Dorsal tentacle.
E	Macromeres of subtentacular octants (end-cells).
e1-3	Micromeres budded off from end cell.
ec	Ectoderm.
ec.pl	Ectoplasm.
e.m	Egg-membrane.
en	Endoderm.
en.pl	Endoplasm.
en.s	Endodermal sac
ent.c	Entrance-cone.
eo	Eosinophilous body in parenchyme tissue.
ex.c	Excretory canal.
ex.p	Excretory pore.
f	Food-matter.
fl	Flagella.
g.g	Granular gland cell.
gr	Granular layer.
g.s	Genital sinus.
h	Head of colloblast.
i	Infundibulum.
i.c	Interstitial cell.
inf.c	Infundibular canal.
in.r	Inner ring of ciliated rosette.
M	Macromeres of subpharyngeal octants (middle cells).
m	Mouth.
m'	Mouth of adult.
m1-3	Micromeres budded of from middle-cell.
m.a	Marginal area of polar plate.

mac	Macromere.
m.c.	Meridional canal.
m.f.	Muscle-fibres.
m.f'	Developmental stage of the same.
mic	Micromere.
n	Nucleus.
n.s.c.	Non-sexual cell in testis.
oc	Oesophagus.
oc.br	Branch canal of oesophagus.
ot	Otoliths.
ou.r	Outer ring of ciliated rosette.
ov	Egg-cell.
ov.m	Ovarial membrane.
ovy	Ovary.
p	Polar bodies.
pal	Palisade epithelium.
per.c	Perradial canal.
ph	Pharynx.
ph'	Inner section of pharynx (i. e. pharynx of adult).
ph''	Outer section of pharynx (i. e. part to form sole).
ph.c	Pharyngeal canal.
ph.f	Pharyngeal folds.
pg	Pigment.
p.p	Polar plate.
r.s	Seminal receptacle.
r.s.t	Tubular part of seminal receptacle.
s	Aboral sense-organ.
s.f	Spiral filament.
s.m.	Superficial membrane.
spc.	Spermatocytes.
spd	Spermatids.
spg.	Spermatogonia.
sph.	Sphincter.
s.ph.c.	Subpharyngeal canal.
sphl	Eosinophil spherule in colloblast.
spz	Spermatozoa.
s.s.p	Subsagittal pouch.
stm.	Stomodaeal invagination.
s.t.c	Subtentacular canal.
s.t.p	Subtentacular pouch.
t	Tentacle.
t.b	Tentacle-basis.
t.c	Tentacular canal.
te	Testis.
te'	Testis developed along subpharyngeal canal.
te.m	Testicular membrane.
t.r	Tentacle-root.
t.st.	Tentacle stem.

t.sh	Tentacle-sheath.
t.sh.d	Dorsal compartment of tentacle-sheath.
t.sh.v	Ventral compartment of tentacle-sheath.
ve	Vacuolated epithelium of endodermal wall.
v.d.	Sperm-duct.
v.ep	Ventral epidermis.

Plate 1.

All figures are sketches in living state

- Fig. 1. A branch of a stock of *Dendronephthya* sp., with several *Coeloplanac* (*C. bocki*) on its surface; $\times 1$.
2. *Coeloplana willeyi* ABBOTT in extended state; $\times 2$
3. *Coeloplana mitsukurii* ABBOTT in extended state and with one of the tentacles fully drawn out; $\times 2$.
4. *Coeloplana bocki* KOMAI in extended state and with both tentacles about to be pushed out; $\times 3$
- Figs. 5-15. *C. bocki*; $\times 170$.
- 5-7. Larva of the stage in which pigment spots have appeared for the first time, *i. e.*, stage somewhat more advanced than in Pl. 7, Figs. 1-3:
- Fig. 5. View on transverse plane.
6. Aboral view.
7. Oral view.
- Figs. 8-10. Larva of somewhat more advanced stage;
- Fig. 8. Aboral view.
9. View on transverse plane.
10. View on sagittal plane.
- Figs. 11-12. Larva of still more advanced stage;
- Fig. 11. View on transverse plane.
12. View on sagittal plane.
- Figs. 13-14. Larva directly after hatching out;
- Fig. 13. View on transverse plane; a posture during swimming.
14. Aboral View; larva creeping on the expanded sole of inner surface of pharynx.
15. A larva during metamorphosis, adhering to the substratum by the thinly spread-out sole; the main body laid back and seen on the transverse plane.

Plate 2.

- Fig. 1. *Coeloplana bocki* KOMAI in fully extended state, drawn with the aid of ABBE's drawing apparatus; $\times 10$.
2. The same, diagrammatic figure showing the structure of body; in the upper half, the gastro-vascular system and gonads, and in the lower half, the tentacular apparatus is shown.
3. Diagrammatic figure showing the structure of Cydippid ctenophore.
4. The same showing the structure of *Coeloplana* viewed on transverse plane.

Plate 3.

Figs. 1-7, 9-11. *C. bocki*; Fig. 8. *C. willeyi*.

Figs. 1-7. Sections of body of adult parallel with the sagittal plane; the planes of sections are shown in Pl. 1, Fig. 2 (A-A: Fig. 1, B-B: Fig. 2, C-C: Fig. 3, D-D: Fig. 4, E-E: Fig. 5, F-F: Fig. 6, G-G: Fig. 7); $\times 60$

Fig. 8. Submedian transverse section of body of adult; only the median part of the left half are shown; $\times 60$.

Figs. 9-11. Sections of larva of the stage directly after hatching, parallel with the sagittal plane; the planes of sections are shown in Pl. 7, Fig. 20 (A-A: Fig. 9, B-B: Fig. 10, C-C: Fig. 11); $\times 300$.

Plate 4.

Figs. 1, 2, 17. *C. mitsukurii*; Figs. 3-9, 16 e-i. *C. bocki*; Figs. 10-15, 16 a-d. *C. willeyi*.

Fig. 1. Dorsal epidermis; $\times 1000$.

2. Ventral epidermis; $\times 1000$.

3. The same; $\times 1000$.

4. Dorsal epidermis; surface view of a fresh material; $\times 420$.

5. Ventral epidermis; surface view of a fresh material; $\times 420$.

6. Aboral region of a specimen observed alive, view from surface, with the entrance into the sensory cavity opened; $\times 170$.

7. Parts adjoining polar plates of a specimen observed alive, side view, with the aboral lobate prominences kept erect; $\times 170$.

8. Semi-diagrammatic figure showing the sagittal section of central part of body adjoining aboral sense-organ; $\times 300$.

9. Otolithic granules; $\times 700$.

10. Cross-section of the core of accessory filament; $\times 550$.

11. Median longitudinal section of the same; $\times 550$.

12. Successive developmental stages of colloblast; $\times 1400$.

13. Cross-section of oesophagus; $\times 150$.

14. Horizontal section of the region adjoining polar plates and excretory canals; $\times 150$.

15. Section of the region including a branch of anastomosing canal-system; $\times 400$.

16. Corpuscles in gastro-vascular canal; a.d. fixed and stained material; $\times 900$; g-i. fresh material; $\times 420$.

17. Ciliated rosette; $\times 1400$.

Plate 5.

Figs. 1, 4, 6, 7, 12. *C. bocki*; Figs. 2, 5, 9-11, 13, 14. *C. willeyi*; Figs. 3, 8. *C. mitsukurii*.

Fig. 1. Testis and ovary, $\times 150$.

2. Testis and very immature ovary; $\times 150$.

3. Spermatozoa; $\times 1600$.

4. A part of testis, showing sperm-cells in various developmental stages; $\times 600$.
5. Very young testis; $\times 500$.
6. Section including a series of sperm-receptacles; $\times 160$.
7. Ovary containing egg-cells in various developmental stages and seminal receptacle containing spermatozoa; $\times 360$.
8. Apical region of testis with sperm-duct; $\times 400$.
9. Very young ovary with cellular strand connecting epidermis and ovarian membrane; $\times 500$.
10. Seminal receptacle, showing cross-section of tubular part; $\times 550$.
11. Young ovary with seminal receptacle; $\times 400$.
12. Peculiar kind of pigment-cells in fresh state; $\times 420$.
13. Ordinary pigment-cells in fixed and stained state; $\times 1,400$.
14. So called rudiments of muscle-fibres; $\times 1,400$.

Plate 6.

All *C. bocki*. sketches in living state; $\times 170$, Fig. 4. $\times 300$.

- Fig. 1. Unsegmented egg.
2. First cleavage.
3. Cleavage-head, showing spinning of plasm in superficial layer and radial arrangement of granules in ectoplasm.
4. 2-cell stage.
5. 2-cell stage about to become 4-cell stage; view from vegetative pole.
6. 4-cell stage.
7. 4-cell stage about to become 8-cell stage; side-view with animal pole above.
- In all the following figures showing side-view of eggs in segmentation and gastrulation stages, animal pole (micromere pole) is above and vegetative pole (macromere pole) below.
8. 8-cell stage; side-view.
9. the same; view from animal pole.
10. 16-cell stage about to become 20-cell stage.
11. 24-cell stage about to become 28-cell stage.
12. 28-cell stage; view from micromere (animal) pole.
13. 32-cell stage about to become 40-cell stage.
14. 56-cell stage about to become 60-cell stage.
15. A stage during gastrulation, view from macromere (vegetative) pole; some "mesodermal" cells budded off from macromeres; also note the number of macromeres is 16.
16. A stage during gastrulation nearly the same as, or somewhat more advanced than, in the foregoing figure; view oblique from micromere pole.
17. A stage during gastrulation, somewhat more advanced than in the preceding figure; view from micromere pole.
18. Optical section of a stage directly after the closure of macromere pole; view on transverse plane.
19. The same egg; optical section, view from micromere pole; quadrate pore at the centre is the opening on micromere pole, round pore of dotted line, the optical section of axial space.
20. A stage somewhat more advanced than in the preceding figure, with an opening on micromere pole; side view.

Fig. 21. Optical section of a stage somewhat more advanced than in the preceding figure.

22. A stage directly after the closure of the micromere pole.

23. Optical section of egg of about the same stage as in Fig. 22.

24. A stage somewhat more advanced than in the preceding figure; view on tentacular plane.

25. The same; view on sagittal plane.

Figs. 26-28. A stage more advanced than the preceding figure; Note the stomodaéal invagination much advanced than in the preceding stage;

26. View on tentacular plane.

27. Aboral view, showing the H-shaped endodermal space.

28. View on sagittal plane.

Plate 7.

All *C. bocki*; Figs. 1-6, sketches in living state, $\times 170$; Figs. 7-19, $\times 300$.

Figs. 1-3. Young cydippid larva;

Fig. 1. View on tentacular plane.

2. Aboral view.

3. View on sagittal plane.

Figs. 4-6. Larva of somewhat more advanced stage;

Fig. 4. View on tentacular plane.

5. Aboral view.

6. View on sagittal plane.

Figs. 7-11. Successive horizontal, but a little oblique sections of larva in a stage nearly the same as in Figs. 1-3; planes of sections are shown in Fig. 12, (A-A: Fig. 7, B-B: Fig. 8, C-C: Fig. 9, D-D: Fig. 10, E-E: Fig. 11).

Fig. 13. Section in transverse plane of larva directly after hatching out.

Figs. 14-19. Successive horizontal sections of larva in the same stage as in Fig. 13; planes of sections are shown in Fig. 20, (D-D: Fig. 14, E-E: Fig. 15, F-F: Fig. 16, G-G: Fig. 17, H-H: Fig. 18, I-I: Fig. 19).

Fig. 21. Larva hatching out; $\times 65$.

22. A stage after completion of metamorphosis; the main parts of endoderm are composed of eight radially-situated subequal pouches.

Plate 8.

Gastrodes parasiticum; Figs. 1-3, $\times 50$; Figs. 4-6, $\times 90$; Figs. 7-10, $\times 180$.

Fig. 1. One of the largest and oldest individuals observed; sketch in living state.

2. Somewhat younger individual than above, with body-diameter measuring about 1.5 mm; sketch in living state. The meridional canals are roomy and sac-like. The tentacle-stem has not developed as yet.

3. Individual with body-diameter measuring about 1 mm; sketch in living state. The ribs have not developed as yet.

4. Individual with body-diameter measuring about 0.5 mm; sketch in living state. The gastro-vascular system is in a form of a connected pair of cavities each of which is laterally divided into four peripheral pouches.

5. Individual with body-diameter measuring about 0.3 mm; sketch from material in formalin. The gastro-vascular cavity is in a form of a single roomy chamber divided peripherally into four subequal pouches.
 6. Stage a little earlier than above; sketch from material in formalin and through the test of host. The gastro-vascular cavity is of a simple roundish form. Notice the assemblage of blood-corpuscles of host around the parasite.
 7. Stage about the same as above; sketch from stained material. Notice egg-cells arranged in a complete circle.
 8. Stage in which the body is nearly hemispherical; sketch from stained material.
 9. Youngest stage observable in the body of *Salpa*. Egg-cells are still recognizable, *ov.*
 10. Planula-stage killed while boring the test of the host, with upper half of body lying freely outside and lower half imbedded in the test; sketch from stained material. Notice that the entire surface of body is covered with flagella.
 11. Median vertical section of the most advanced stage; $\times 90$. The section-plane is slightly oblique to the sagittal plane of body. Notice the profuse foldings on the ventral surface.
- Figs. 12-14. Three sections from a series of horizontal sections of the most advanced stage; $\times 100$. Throughout the figures the section-plane is slightly oblique to the horizontal plane and the right half is from a level a little below the left half.
15. Median vertical section of about the stage in fig. 3; $\times 160$. The section-plane is a little oblique to the transverse plane of body.
 16. Median vertical section of about the stage in figs. 6 and 7; $\times 240$.

Plate 9.

Gastrodes parasiticum.

- Fig. 1. Median vertical section of aboral sense-organ; $\times 360$.
2. Longitudinal section through a rib; $\times 500$. This figure also shows a part of vacuolated epithelium of meridional canal underlying the rib. Notice the aggregates of blood-corpuscles of host taken as food-matter.
 3. Tentacular apparatus of the most advanced stage. Horizontal section; $\times 150$.
 4. Tentacle-stem. Longitudinal section; $\times 900$.
 5. A part of canal wall showing the formation of excretory corpuscle; $\times 600$.
 6. A part of ventral epidermis harbouring several egg-cells of various developmental stages; $\times 900$.
 7. Egg-cell amoeboid in appearance; $\times 900$.
 8. Muscle-fibres showing branchings; $\times 500$.
 9. Median longitudinal section of planula; $\times 300$.

FIG. 1



FIG. 2



FIG. 3



FIG. 4

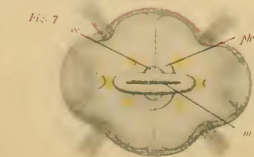


FIG. 7

FIG. 5

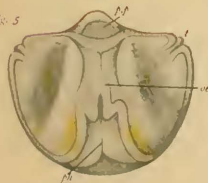


FIG. 6

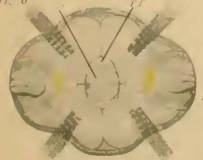


FIG. 9



FIG. 11



FIG. 14



FIG. 13

FIG. 15



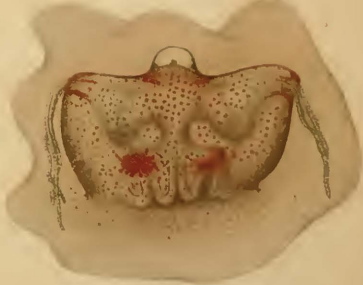
FIG. 10



FIG. 12



FIG. 8



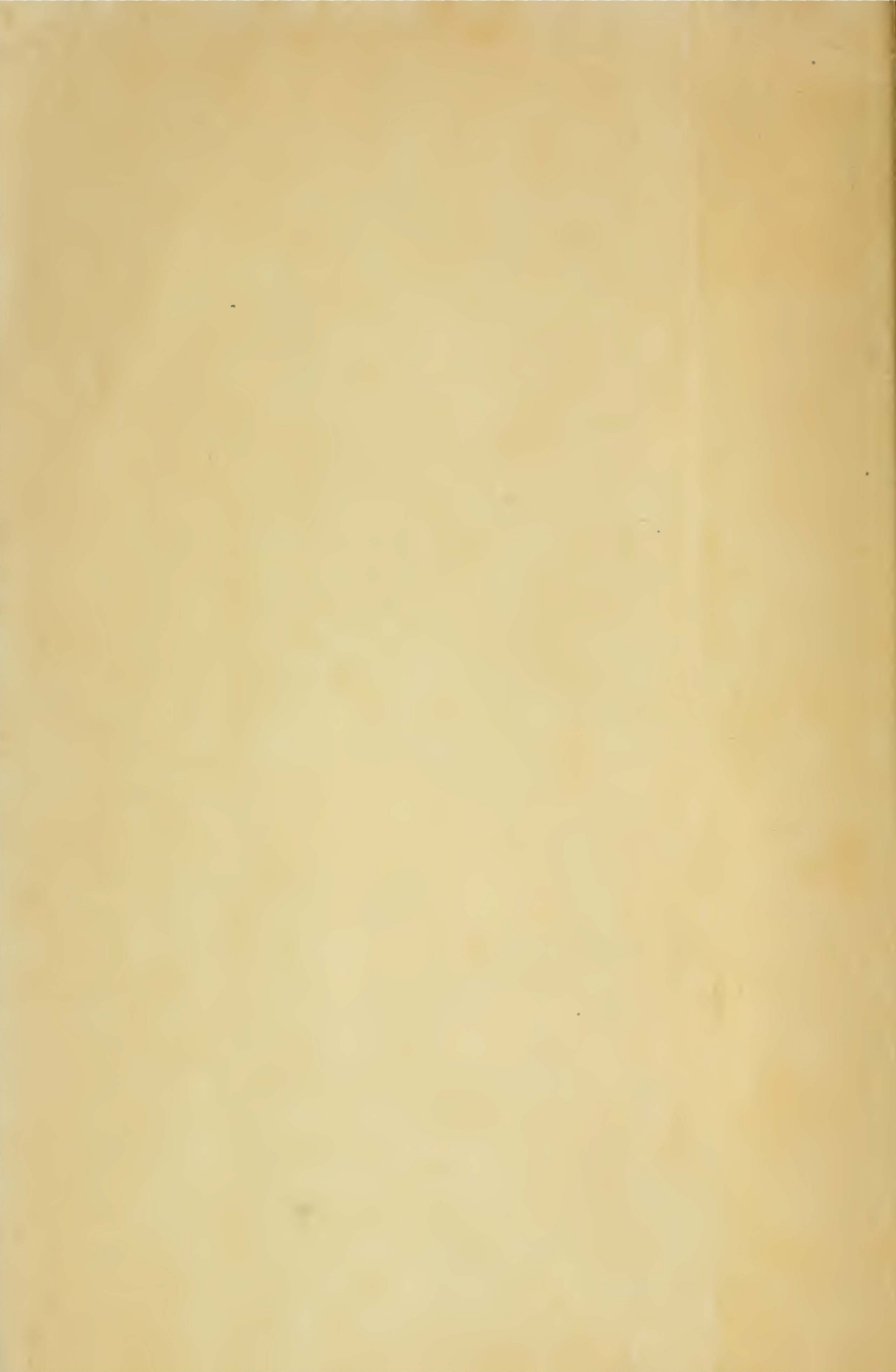




Fig. 1



Fig. 2



Fig. 3



Fig. 4



Fig. 5



Fig. 6



Fig. 7



Fig. 8



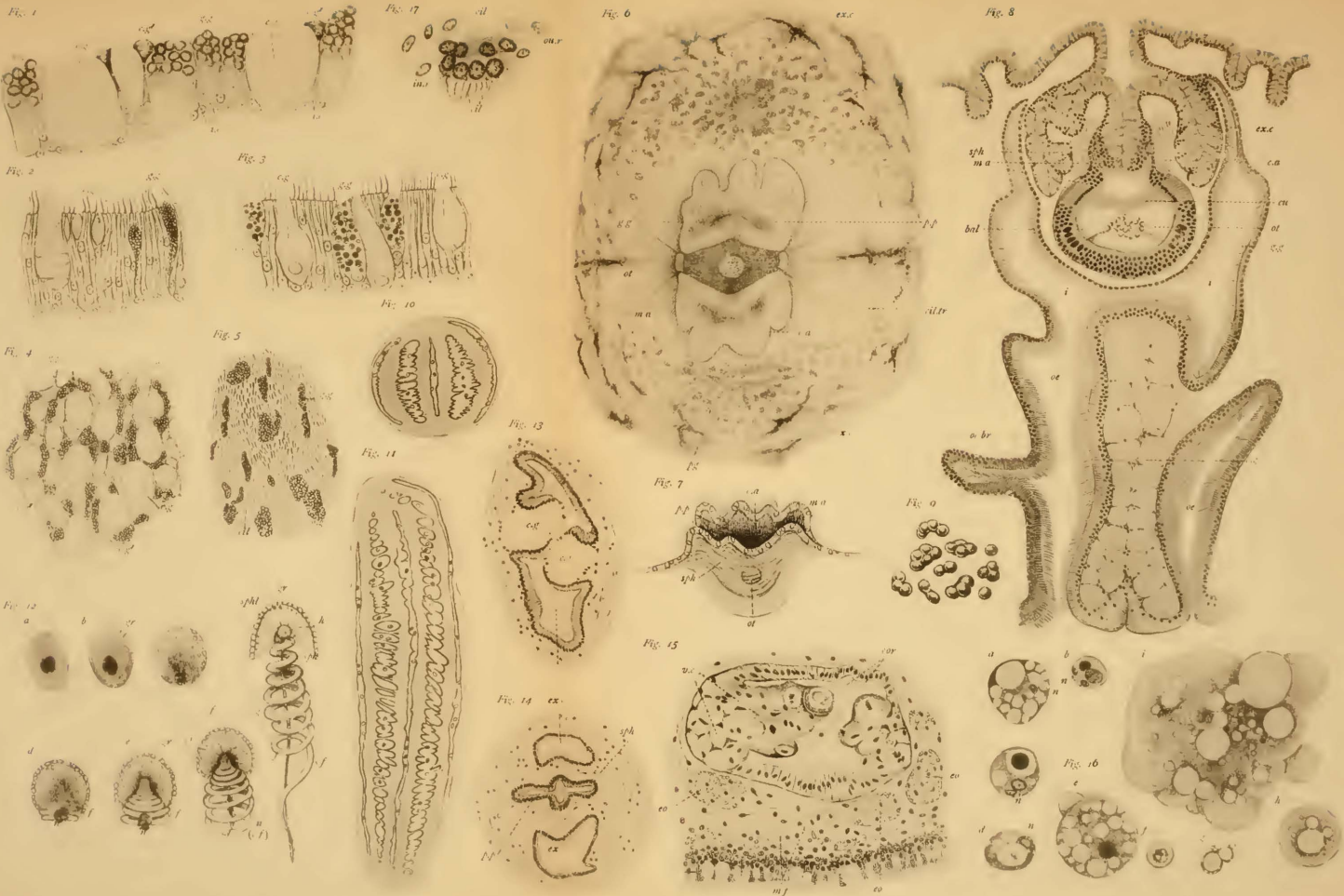
Fig. 9

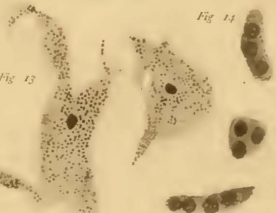
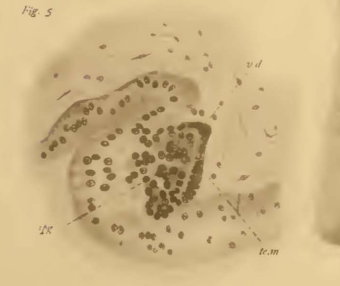
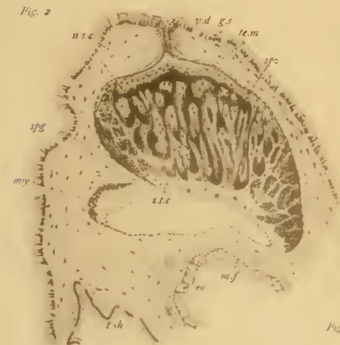
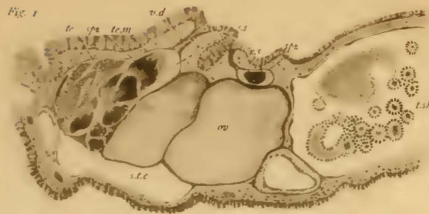


Fig. 10



Fig. 11





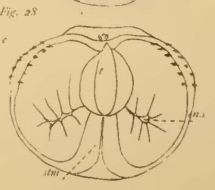
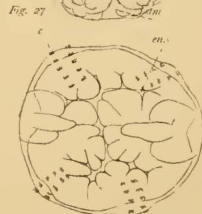
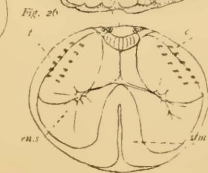
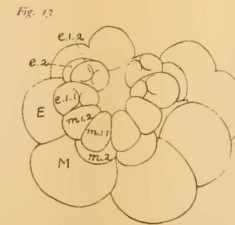
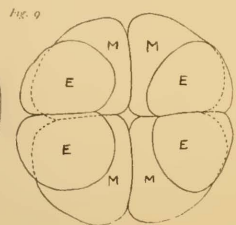
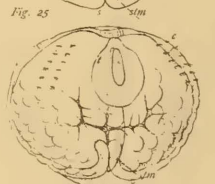
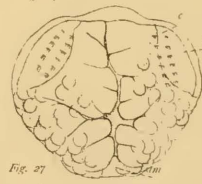
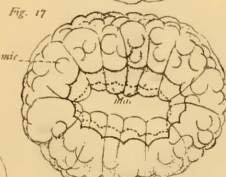
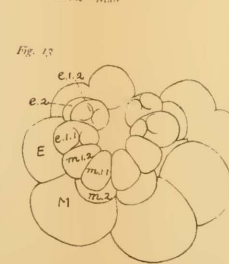
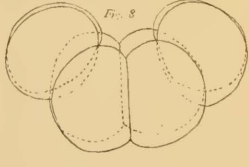
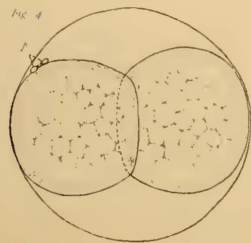
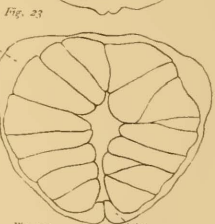
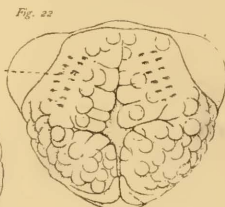
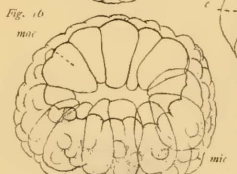
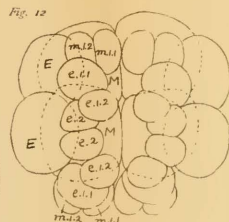
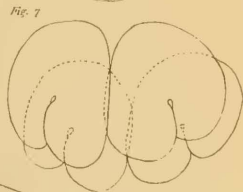
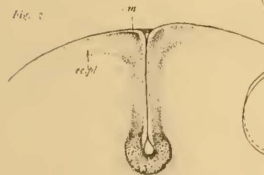
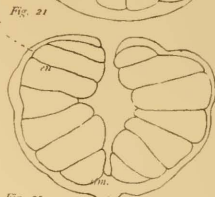
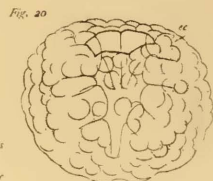
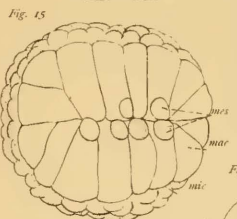
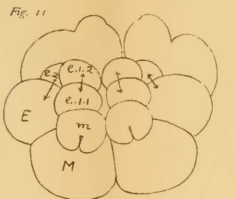
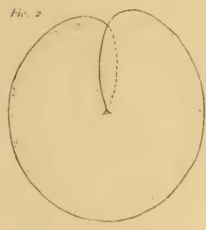
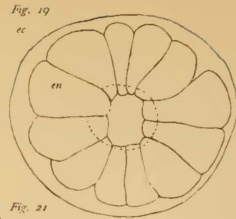
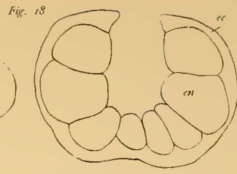
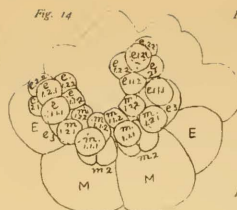
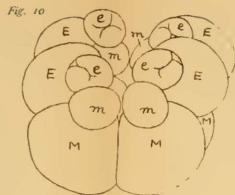
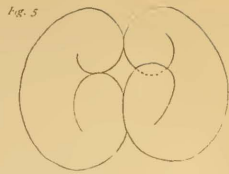
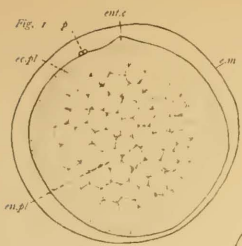


Fig. 1

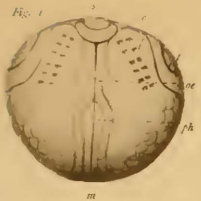


Fig. 2

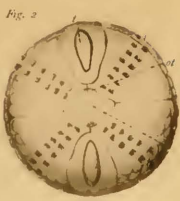


Fig. 3

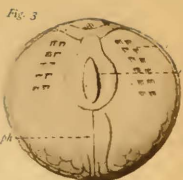


Fig. 4

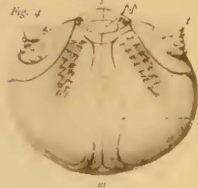


Fig. 5

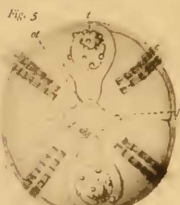


Fig. 6

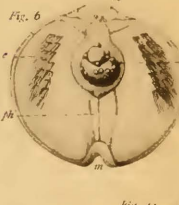


Fig. 12

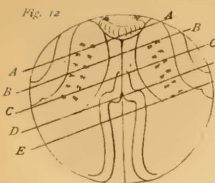


Fig. 20

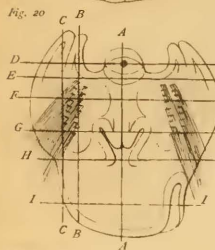


Fig. 14



Fig. 18



Fig. 15

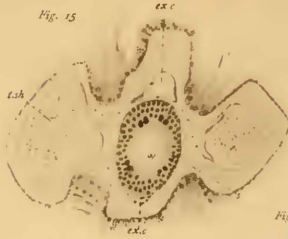


Fig. 19



Fig. 7

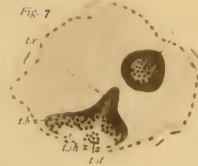


Fig. 9

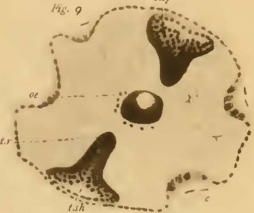


Fig. 11



Fig. 16



Fig. 8

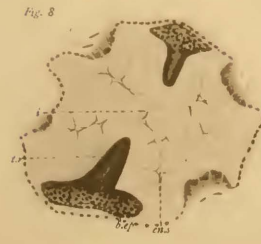


Fig. 10

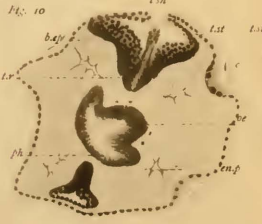


Fig. 13

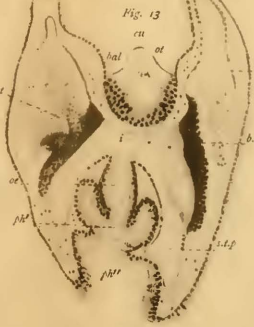


Fig. 17

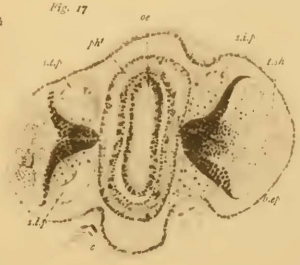
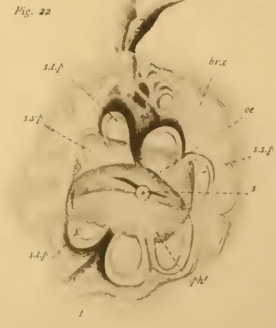


Fig. 22



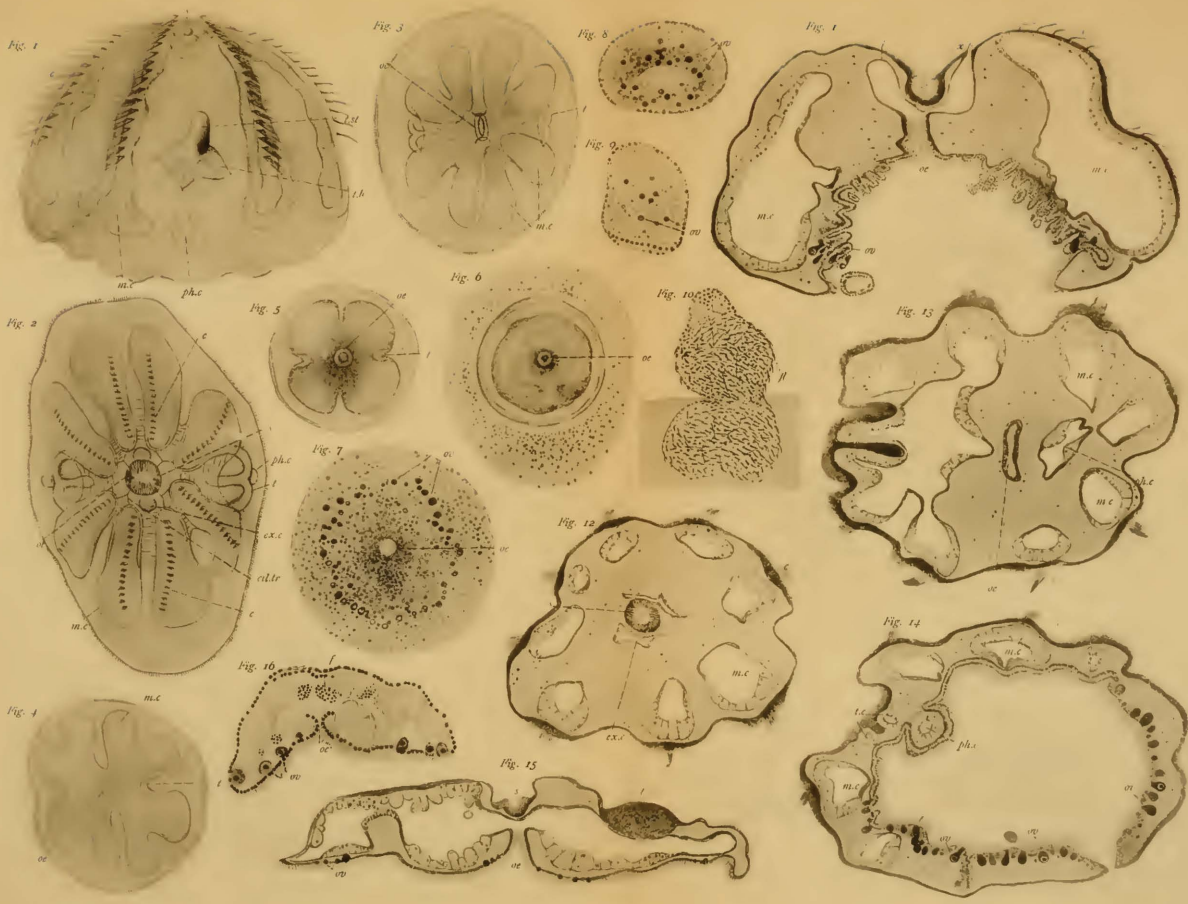


Fig. 1

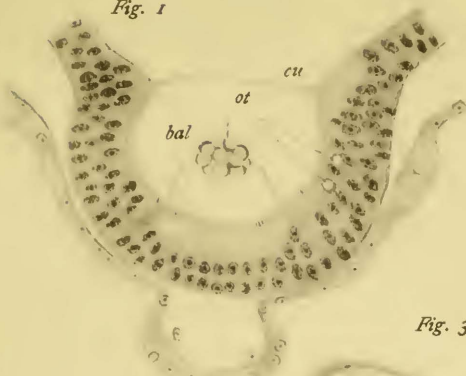


Fig. 8



Fig. 2



Fig. 3

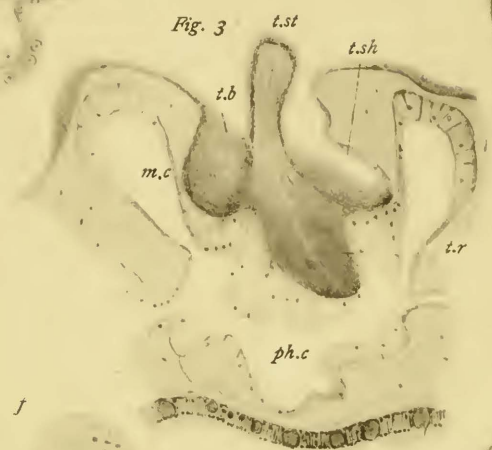


Fig. 9

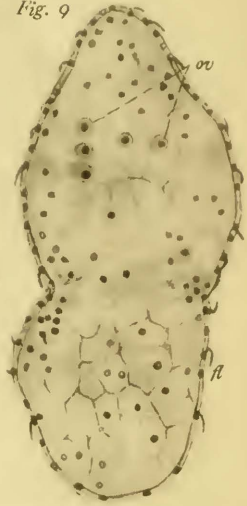


Fig. 5

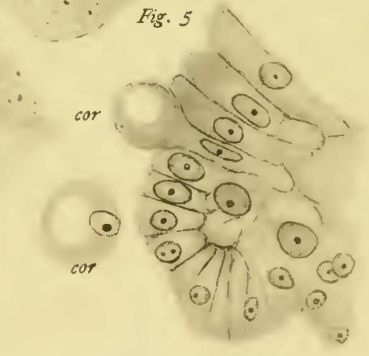


Fig. 4

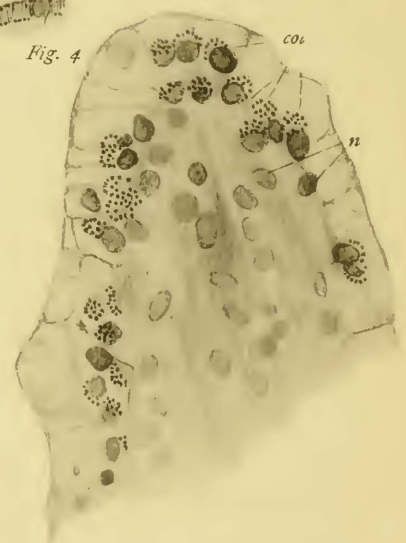


Fig. 6



Fig. 7



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