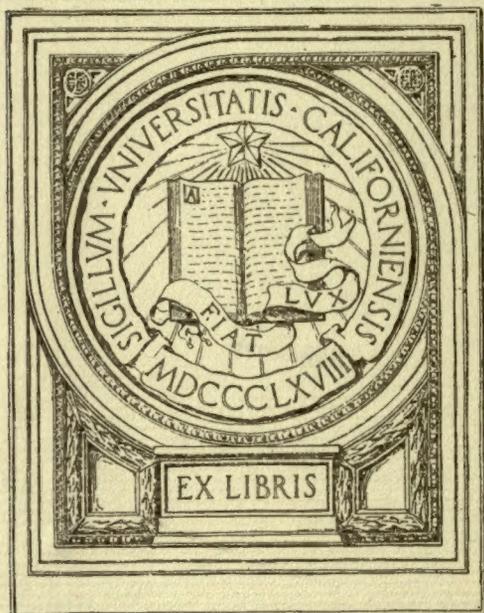




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THE DANISH  
INGOLF-EXPEDITION.

VOL. V, PART 2.

CONTENTS:

*TH. MORTENSEN: CTENOPHORA.*

PUBLISHED AT THE COST OF THE GOVERNMENT

BY

THE DIRECTION OF THE ZOOLOGICAL MUSEUM OF THE UNIVERSITY.



COPENHAGEN.

H. HAGERUP.

PRINTED BY BIANCO LUNO.

1912.



Univ. of  
California

THE DANISH INGOLF-EXPEDITION.

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VOLUME V.

2.

CTENOPHORA.

BY

TH. MORTENSEN.

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WITH 10 PLATES AND 15 FIGURES IN THE TEXT.



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UNIVERSITY OF  
CALIFORNIA

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Ready from the Press May 15<sup>th</sup> 1912.

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## Introduction.

It naturally follows from the difficulty of preserving Ctenophores in a tolerable condition only that this group of animals has been rather neglected by most of the great Expeditions. Thus the "Challenger"\* Expedition has evidently brought home no serviceable material, and the same appears to be the case with e. g. the Norwegian North Sea Expedition, the "Blake" Expedition a. o., even the material collected by the Plankton Expedition was only for a very small part in a condition which made it possible to identify it with certainty<sup>1)</sup>. The Danish "Ingolf" Expedition does not make an exception from the general rule. Most of the material was simply preserved in alcohol, which no Ctenophore can stand; if only formaline had been used, the results would certainly have been a good deal better, and results of considerably greater value might have been obtained. The Ctenophore-Fauna of the North Atlantic is certainly by no means so rich as that of the warmer regions, but it is certain that there is yet much to learn about it, both as regards the distribution of the forms already known and the occurrence of forms altogether unknown or not hitherto known from these regions. The recent discovery of a new form, *Pleurobrachia crinita* Moser, at Greenland indicates sufficiently the incompleteness of our knowledge of the North Atlantic Fauna of Ctenophores.

While there is after all not much prospect of finding new forms representing types of great morphological importance among the Ctenophores of the surface of the North Atlantic, the case is quite different with the deep-sea forms. Chun, in his report on the Ctenophores of the Plankton Expedition (p. 3) was the first to suggest that such might possibly exist, and he had the satisfaction of being also the first to prove their existence<sup>2)</sup>. On the German Deep-Sea Expedition he found two different forms of peculiar Deep-Sea Ctenophores, one of which has recently been described by Moser under the name *Mertensia Chuni*, the other still remaining undescribed. It may not be too hardy to suggest that many other Deep-Sea Ctenophores will prove to exist, and that also the North Atlantic will contain such seems equally probable. This highly interesting problem remains as yet unsolved; likewise the question of the vertical distribution of the Ctenophores has as yet scarcely received any attention. A quite new problem regarding Ctenophores, viz. the existence of forms adapted to life at the bottom as sessile or creeping organisms, has been raised by the unexpected discovery by Mr. Ad. S. Jensen of the extremely interesting sessile Ctenophore which I have preliminarily described

<sup>1)</sup> C. Chun. Die Ctenophoren des Plankton-Expedition. Ergebnisse d. Plankton Exp. d. Humboldt-Stiftung. II. K. 1898. p. 4—5. <sup>2)</sup> C. Chun. Aus den Tiefen des Weltmeeres. 2. Aufl. 1905. p. 545.

under the name of *Tjalfiella*<sup>1)</sup> *tristoma*, and of which the full description is included in this report, with the permission of Mr. Ad. S. Jensen and of the Editor of the "Ingolf" Expedition. By this discovery the view of the Ctenophores is upon the whole considerably widened; the Ctenophoran type, hitherto regarded as rather uniform, is now shown to have a very considerable adaptive power. It would be very singular if *Tjalfiella* should be the only Ctenophore which has adopted a sessile habit, and there may certainly be reason to expect the discovery of new sessile forms. The difficulty of the preservation has presumably been a main cause, why such forms have not hitherto been made known — had the *Tjalfiella* been simply preserved in alcohol, it would also have been impossible to recognise its characters. In any case it should be recommended to look out very carefully for such forms on future occasions.

The present report is divided into two main parts, the first containing the full description of *Tjalfiella*, the second dealing with the pelagic Ctenophores of the North Atlantic.

1) *Tjalfiella* from the "Tjalfe", the name of Mr. A. S. Jensen's vessel on his Greenland Expedition. Tjalfe is a renowned figure in Northern Mythology (the companion of the good Thor on his journey to Utgård).

\* The Ctenophora collected by the "Challenger" have not been made the object of a special report. In the "Summary of Results" are given some notes on the Ctenophores observed during the Expedition; most of them are in the form: "recorded in the note-books . . . Ctenophoræ", sometimes the names *Cydippe* or *Pleurobrachia*, *Eucharis* and *Beroë* being named, but always without indication of the species. Such notes are rather useless. Some value might be ascribed to the statement of the occurrence of a species of *Eucharis* on St. 217 (0° 39' S. 138° 55' E. 22/11 1875; near New-Guinea), as it may be suggested to have been the *Eucharis grandiformis* described by A. Agassiz and A. G. Mayer (Acalephæ from the Fiji Islands. Bull. Mus. Comp. Zool. 32. 1899), the only species of this genus hitherto known from the Pacific — if the identification of the genus has been correct, of which there is, however, no guarantee. Also the observation, at Stat. 165 A (36° 41' S. 158° 29' E.; between Australia and New Zealand) of "a very long, ribbon-like, animal of a golden green colour, supposed to be a *Cestus*" (Summary of Results. I. p. 587) is worth recalling, even if it is scarcely at the present moment possible to state which species of *Cestus* has been observed here.

Considerably more interest, however, may be attached to another observation recorded in the "Summary of Results". On p. 850 is mentioned from St. 217 "Dendrocælous Planarians, with digitiform processes", and in the most interesting record by Moseley on a large line of driftwood observed near New Guinea (Stat. 217) is mentioned among a number of other animals here observed "a small Dendrocælous Planarian with central mouth, diffuse ovaries, a superior penis, and single generative aperture (which) was in swarms upon everything, not only upon the dead matter, but all over the living crabs". There is in this description especially one thing, which indicates that this has not been a Planarian, viz. the "superior" penis, supposing "superior" to mean dorsal. I cannot but suggest that this supposed Planarian has really been *Coeloplana*; the "superior penis" would then evidently have been one of the tentacles.

On my asking Sir John Murray, whether it might be possible to get some specimens of these Planarians for examination, he kindly applied to the British Museum about the matter, and I had the pleasure to receive some specimens found among Crustaceans from that station. The examination of these specimens certainly left no doubt that they were really Planarians. The matter is, however, not definitely settled thereby. The specimens examined had no tentacles or processes, so that they could not have been described as having "digitiform processes" or a "superior penis". It seems then not unreasonable to suppose that there have really been some *Coeloplana* among the Planarians, which have, however, become lost on account of the difficulty of preservation.

It is, of course, impossible now to state anything definitely about this matter, but it will probably be conceded that there are here some points which seem to indicate that Moseley was really the first to observe *Coeloplana*, though without observing its Ctenophoran nature.

# I.

## Tjalfiella tristoma Mrtsn.

Pls. I—X.

Th. Mortensen. Tjalfiella tristoma n. g., n. sp., a sessile Ctenophore from Greenland. Preliminary notice. Vid. Medd. Naturh. Foren. København 1910. p. 249—253.

In 1880 Kowalevsky <sup>1)</sup> gave a description of the remarkable creeping Ctenophore, *Coeloplana Metschnikowii*, which he had detected in the Red Sea, and thus made known for the first time a Ctenophore which differed from the ordinary type in not being adapted to pelagic life. Since then also other divergent types of Ctenophores have been found. In 1886 Korotneff <sup>2)</sup> described the both creeping and swimming *Ctenoplana Kowalevskii* from the West Coast of Sumatra, which is provided with small, though distinct ribs, while in *Coeloplana* there are no ribs at all. In 1903 C. Dawydoff <sup>3)</sup> described a curious pelagic Coelenterate from near Amboina, *Hydroctena Salenskii*, which he thought to be an intermediate form between the Ctenophores and the Hydromedusæ (Narcomedusæ), much in the same way as another Pacific Coelenterate, *Ctenaria ctenophora*, was long ago declared by Haeckel to be an intermediate form between the Ctenophora and the Hydromedusæ. Finally in 1906 another most remarkable Ctenophore without swimming plates was described by Pedaschenko <sup>4)</sup> under the name of *Dogielia malayana*; it was found at the South-West Coast of Java. — Also the peculiar *Gastrodes parasiticum* described in 1888 by Korotneff <sup>5)</sup> may be mentioned. It was first regarded by Korotneff as a parasitic Medusa, later on (1891) <sup>6)</sup> as belonging to the Actiniæ. As shown by v. Heider <sup>7)</sup> it can scarcely be doubted, however, that it is a parasitic Ctenophore. Korotneff gave no information of the locality, where he had found the *Gastrodes*, stating only that it occurred in *Salpa fusiformis* and *S. confederata*, which are both very widely distributed, even cosmopolitan in the warmer regions. Probably the *Gastrodes* will then prove to be equally widely distributed. Through v. Heider its occurrence in the Mediterranean is stated.

<sup>1)</sup> A. Kowalevsky. Ueber *Coeloplana Metschnikowii*. Verhandl. d. zool. Section der VI. Versamml. russischer Naturf. u. Ärzte. Zoolog. Anzeiger. III. 1880. p. 140. <sup>2)</sup> A. Korotneff. *Ctenoplana Kowalevskii*. Zeitschr. f. wiss. Zool. Bd. 43. 1886. p. 242—50. Taf. VIII. <sup>3)</sup> C. Dawydoff. *Hydroctena Salenskii* (Étude morphologique sur un nouveau Coelentéré pelagique). Mém. Acad. Imp. St. Pétersbourg. 8. Ser. XIV. 1903. <sup>4)</sup> D. D. Pedaschenko. Eine neue tropische Coelenteratenform. Travaux Soc. Imp. des Naturalistes de St. Pétersbourg. Vol. XXXVII. 1906. p. 1—25. Taf. I—III. <sup>5)</sup> A. Korotneff. *Cunocantha* und *Gastrodes*. Zeitschr. f. wiss. Zool. Bd. 47. 1888. <sup>6)</sup> A. Korotneff. Zoologische Paradoxien. Zeitschr. f. wiss. Zool. Bd. 51. 1891. p. 613—618. Taf. XXX—XXXI. <sup>7)</sup> K. v. Heider. Über *Gastrodes*, eine parasitische Ctenophore. Sitz. ber. d. Gesellsch. Naturf. Freunde Berlin. 1893. p. 114—119.

All these forms which are of so very great interest both for the morphology and the phylogeny of the Ctenophora and have given rise to long discussions concerning the interrelations between the Ctenophora and other groups of animals, especially the Polyclads, are, with the exception alone of the somewhat problematic *Gastrodes*, as yet only known from the Coasts of the Indo-Pacific Ocean, those tracts so rich in all zoological wonders; not one of them is known to occur in the Atlantic Ocean (though *Gastrodes* will doubtless prove to occur there). — It is further a curious fact that all these remarkable types were discovered by Russian naturalists, so that it almost seemed to be their privilege to make such discoveries; to be sure, *Ctenoplana* has been rediscovered by Willey and *Coeloplana* by Abbott, but no new types<sup>1)</sup>, only some new species, were discovered by them. — At length, however, such a remarkably deviating type of Ctenophore has been discovered in the Atlantic, and this time by a Scandinavian Naturalist, Ad. S. Jensen. Thus the Atlantic Region has also been proved to be the home of at least one transformed Ctenophoran type, and even one of the most transformed and which affords quite unusually great interest, both from a morphological and a phylogenetic point of view.

The animal was found by Mr. Ad. S. Jensen on the stems of some *Umbellula Lindahlü* Köll. in the Umanak Fjord, West Greenland, where when trawling in a depth of 475—575 M., he came over a whole forest of this magnificent Pennatulid. His other duties not leaving him any time for observing the remarkable looking animal more closely, he preserved some specimens in formaline. On his return he asked me to undertake the study of the animal. I beg him to accept my sincerest thanks for leaving to me this most interesting task, and hope that he and my fellow-workers will find that I have treated the rare animal in a way not too much out of harmony with its unquestionably great morphological importance.

At first, the animal puzzled me very much, as, indeed, also my colleagues, with whom I discussed the question to which class of animals it belonged. Only two possibilities seemed to offer themselves — that it was a Coelenterate or a Tunicate. For the latter view something in the whole appearance was in favour; in fact there is, as I have said in my preliminary notice, something recalling the peculiar sessile Salp, *Octacnemus*; also for its being a compound Ascidian something might be said viz. the four pairs of knobs along the upper side, each having a small opening, while another single small opening was found in the middle of the upper side. It was, however, soon found that the anatomy of the animal did not in the slightest way support the suggestion of its being a Tunicate. There was then evidently no other possibility than that it was a Coelenterate. But also for a Coelenterate its organisation seemed most unusual. On studying its anatomy more closely I soon observed, however, that some roundish knobs on the sides of the animal contained embryos, and the most developed of these were found to be typical Ctenophores in the Cydippe-stage. Then the riddle was solved, and the whole anatomy of the animal proved to be in full accordance with its nature as a Ctenophore; though transformed in a most remarkable manner, it was not difficult to trace all its features to the typical Ctenophoran structure, especially the different developmental stages showing the way along which the transformations take place.

<sup>1)</sup> The *Heteroplana Newtoni* Willey regarded by the author as related to *Coeloplana* and *Ctenoplana* is, in any case, very doubtful as being really a Ctenophoran. (A. Willey. On *Heteroplana*, a new genus of Planarians. Quart. Journ. Micr. Sc. N. S. Vol. 40, 1898, p. 203—205).

The animals especially preserved by Mr. Ad. Jensen were only 4 in all. Two of these are preserved intact, as type specimens (represented in Pl. I. Fig. 1), while the two others were sacrificed for anatomical study. Wishing, of course, very much to have some more material, I examined carefully the remains found on the bottom of the tin in which the Umbellula's had been preserved — likewise in formaline — and to my great joy I found therein a good deal of specimens which had dropped from the Umbellulae, among which also some young stages and specimens in different stages of regeneration. Though, of course, less well preserved than the 4 first specimens — having rolled on the bottom of the tin, among a little bottom material from the base of the Umbellulae, during the whole voyage from Greenland to Denmark, — they were a most welcome addition to my material, without which I would not have been able to work out the anatomy of the animal so completely as has now been the case.

It was only later on that I came on the thought that possibly still more specimens might be found, if the heads of the Umbellulae were examined. Indeed, I found then in some of the larger ones several specimens of the Tjalfiella among the polyp-bases, and in one case also some specimens a good way out on the polyps. Unfortunately, all these specimens were very badly preserved, being partly more or less compressed between the polypes, partly because the Umbellulae had now been put in alcohol, whereby the Tjalfiellae had been much contracted and quite lost their jelly-like appearance. These specimens were then of no use for my studies of the anatomy of the animal; but they gave the interesting information that the Tjalfiella is not bound to the stem of the Umbellula, occurring also in the head, among or upon the polypes.

The question naturally arises here, whether there is possibly a kind of symbiosis between the Tjalfiella and the Umbellula. Though it is, of course, impossible to give a definite answer to this question before direct observations have been made on living material, it may be stated that, so far as evidence goes, there appears to be no direct symbiotic relation between the two animals. One fact seems to me to be especially important for deciding the question of symbiosis, viz. that a specimen of Tjalfiella was found to contain a shrimp in its digestive cavity. This shows that Tjalfiella does not depend on the Umbellula for its food. That those specimens which have taken a seat in the crown of the Umbellula may receive some protection thereby is quite possible (and that Tjalfiella is exposed to attacks from other organisms is clear enough from the facts set forth below, in the chapter on Regeneration) but this will, of course, not hold good for those specimens attached to the stems of the Umbellulae. On the other side it is hard to see how the Umbellula could derive any profit from the presence of the Tjalfiella, even if the latter catches a shrimp now and then. — The explanation of the occurrence of Tjalfiella on Umbellula most probably is this that on the soft bottom, where Umbellula occurs, there are so few objects to which the young Tjalfiella can attach itself, the Umbellula offering itself as the best suited for that purpose. If this suggestion be right, one must expect to find it in other localities attached to other objects, living or dead. Further observations are necessary for deciding this question.

The preservation of the animals in formaline was thus far a fortunate circumstance, as the whole shape and the jellylike consistence of the body was very well preserved. For the study of the histology of the animal this preservation was, of course, not the very best; still it was not the worst either, several minor histological details appearing irreproachably, only the staining being not quite

satisfactory. An after-fixation with corrosive sublimate, which I have tried on some of the specimens, appeared to have rather a good effect. Upon the whole it must be said that the conditions for studying the histology of the animal were not altogether bad and I hope it will be found that the information I have been able to give in this regard is not quite without value.

Turning now to the description of the animal I shall begin with the grown specimens, their anatomy and histology, taking thereafter the development and the anatomy of the young.

### A. Anatomy and histology of the grown animal.

The shape of the animal is most unlike that of any Ctenophore previously known. As seen from the figures on Pl. I it is elongated in the transverse or tentacular plane, rather compressed in the sagittal plane. In the middle of the nearly flat upper side is seen a small pore, which leads down to the otolith or statocyst (Pl. I. Figs. 6—8, s.), and along each side there are four, more or less prominent, knobs, of a rather compact nature — the genital organs. They are placed opposite one another, appearing thus paired, there being two pairs to each side of the statocyst. On each of them is a generally rather distinct, longitudinal slit-like opening (Pl. I. Figs. 6, 7, 9. i.). At each end, below the outer pair of genital organs, lies a large, yellow body, from which proceeds a thread-like prolongation; this is the tentacle apparatus. Each end of the body is erected into a curious vertical prolongation, like a chimney-top<sup>1</sup>), through which the tentacle may be seen to project. Below the genital organs there are on each side, in the larger specimens, a varying number of more or less prominent knobs, less compact looking than the genital organs; they are eggs or embryos, contained in their brood chambers. The transparent walls of the body, especially on the chimneys, are seen to contain irregular, branching canals, which prove to be part of the gastrovascular system. The underside of the animal forms an irregularly folded basal surface, in the middle of which is an elongate (in the tentacular plane), more or less open, sometimes even apparently quite closed slit; it leads to a rather large cavity with irregularly folded walls; from the roof of the cavity some thick folds hang down, and in the middle of these folds is found a narrow, transverse (in the sagittal plane) slit — the mouth opening (Pl. III. Figs. 5, 11.). The cavity is in open connection with the “chimneys” (Pl. III. Fig. 11 o. f., Pl. VI. Fig. 8 o. f.), which represent secondary mouths, the true mouth having become partially incapable of performing its functions through the sessile habit of the animal.

No trace of colour is found in the preserved specimens. As the formaline otherwise generally preserves the colour very well, it may be concluded that the living animal is quite colourless. That it is also quite clear and transparent (with the exception of the genital organs and the tentacle apparatus) is beyond doubt.

The size of the largest specimens was nearly 20<sup>mm</sup> in length (transverse plane), 5<sup>mm</sup> width (the sagittal plane); the height of the “chimneys” was ca. 10<sup>mm</sup>, the height in the middle of the body 5<sup>mm</sup>. (These measurements apply to the specimens when still in formaline; through the later transferring to alcohol they have become somewhat smaller).

<sup>1</sup>) In the preliminary description (loc. cit.) I have designated this vertical prolongation as a “funnel”. This is less fortunate, because the infundibulum is otherwise called the funnel and thus a confusion might easily take place. It is therefore thought better to speak of this tower-like vertical prolongation as the “chimney”.

There is no trace of costæ and swimming plates. The animal is thus decidedly unable to swim and must evidently rest for life on the Umbellula on which it has fixed itself as young. That it is capable of a slight creeping and gliding movement I think quite probable. The epidermis of the surface is ciliated, with some sensory bristles occurring among the cilia, and besides contains a number of mucus secreting cells; (the histological structure is upon the whole very like that of the epidermis in the "chimneys"). In several of the specimens the basal surface was covered by a thick layer of mucus. These facts seem to show that the animal cannot be fixed to the same spot on the Umbellula, where it first took its place. On the other hand there is no special arrangement of muscles in the basal disk.

The epidermis of the outer surface of the body is quite smooth<sup>1)</sup>, not ciliated, so far as I have been able to see. Its histological structure does not afford any exceptional features. It contains not very numerous, small gland-cells ("Körnerzellen").

The apical organ is very simple (Pl. VII. Figs. 1—2). It is a small groove, the walls of which consist of a high epithelium, carrying long cilia, on which the statocyst is resting. I have been unable to find any "balancers", and likewise the cilia do not appear to form a cupule over the statocyst. There is no trace of polar fields, and there are no ciliated bands ("nerves"). Excretory openings were not to be observed directly; but the presence of one pair of openings has been ascertained on sections (Pl. VII. Fig. 1), as mentioned below.

This highly rudimentary condition of the aboral sensory organ is in good accordance with the sessile habit of the animal. For an organism resting mainly in the same position through life there is, of course, not much use of an organ of the nature of a typical Ctenophoran aboral sensory organ, one of the main functions of which (to say the least) is that of being a static organ.

The invaginations over the genital organs, though decidedly of ectodermal origin, will be mentioned in connection with the genital organs.

The "chimneys" have the upper edge bent more or less outwards, collar-like, slightly and irregularly lobed. Along the inner, adapical side of each chimney the narrow tentacle sheath proceeds upwards, opening near its upper edge (Pl. I. Fig. 5, Pl. III. Fig. 7, Pl. VI. Fig. 9). The inner walls of the chimneys are raised into rather prominent longitudinal ridges (Pl. III. Fig. 7, Pl. VI. Fig. 3).

The epidermis of the inside of the chimneys is distinctly ciliated. It is composed of three different kinds of cells: clear mucous cells, granular cells and undifferentiated interstitial cells; the latter alone carry the cilia (Pl. VIII. Figs. 1, 5). The granular cells contain numerous small round grains, which stain very strongly with eosine<sup>2)</sup>. (In sections stained with Mann's "Wasserblau-Eosin" these grains are very prominent in the otherwise faint blue tissue). The clear cells are seen in the fresh material (treated with formaline only) to be strongly swollen so as to rise like small cupules over the surface of the epithelium; the often quite slimy appearance of the skin here (and even more so on the basal surface and in the oral cavity) is evidently due to these cells. Seen from the surface the epidermis of the chimneys shows a conspicuously reticulate structure, the meshes being formed by

<sup>1)</sup> In the sections the epidermis appears generally rather much folded; this being due to the contraction by the transferring of the specimens to alcohol, xylol and paraffine, it has been thought correct to omit the folds in the reproduction of sections (Pl. IV—VI).

<sup>2)</sup> Comp. Samassa. Zur Histologie der Ctenophoren. Arch. f. mikr. Anat. Bd. 40. 1892. p. 163.

the interstitial cells, the clear spaces by the mucous cells (Pl. VIII. Fig. 1). Among the common cilia are found some coarser bristles, not exceeding the cilia in length; I think there can be no doubt that they represent the sensory bristles so generally met with in Ctenophorans, though they are shorter here than usual. (Comp. e. g. Samassa. Op. cit. Taf. VIII. Fig. 14. Hertwig. Über den Bau der Ctenophoren. Taf. I. Fig. 5<sup>1</sup>). In any case I have not been able to discern them as being composed of agglutinated cilia with the highest magnifying powers at my disposal.

As stated above the lumen of the "chimneys" continues directly into the basal (or suboral) cavity; the longitudinal ridges of the chimneys also continue directly into the folds of the walls of this cavity; they are, however, much less developed here than in the "chimneys", and more reticulate. On the contrary the roof of the suboral cavity is folded even to an extreme degree (Pl. III. Fig. 11). The histological structure of these folds is not essentially different from that of the "chimney"-walls, only the granular cells are much more abundant. (Pl. VIII. Fig. 3).

Evidently the suboral cavity, and especially the folds hanging down from its roof, has undertaken the functions of a stomach; the absorption of the food takes place here, whereas in the typical Ctenophorans it is the pharynx which has this function, the true (entodermal) stomach (the "infundibulum"), generally not receiving the food material directly, only the chymus<sup>2</sup>).

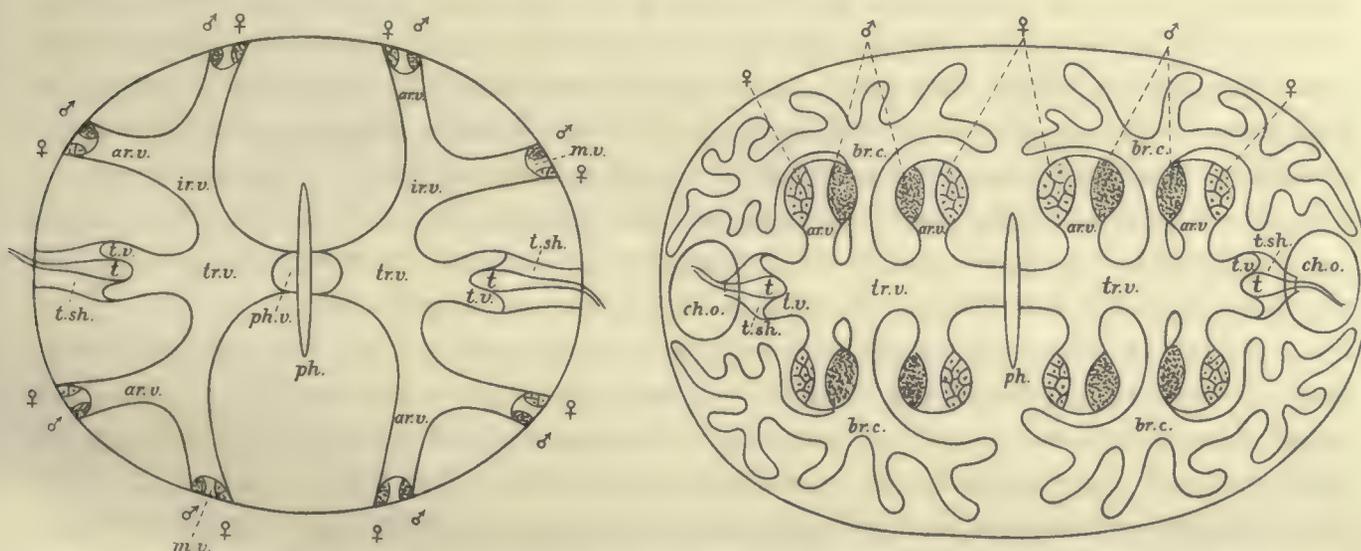
In the middle of these digestive, circumoral folds the true mouth opening is found; it has the shape of a narrow slit, being in the sagittal plane, viz. at right angles to the long (transverse) axis of the body (Pl. III. Fig. 11, o). It is only seen on pushing aside the folds, by which it is normally covered. It leads into a short pharynx which, as appears from the section represented in Pl. IV. Fig. 4, is compressed in the sagittal plane as usual in Ctenophores. The walls of the pharynx are densely ciliated and contain only few granular and gland cells (Pl. VII. Fig. 2). At its upper end the pharynx opens into the very low infundibulum (stomach), the aboral wall of which consists of a low epithelium with the nuclei arranged in a single layer, and which is apparently not ciliated. The apical organ lying close to the aboral wall of the infundibulum there is no room for an infundibular canal ("Trichtergefäß"), and the excretory vessels therefore originate directly from the infundibulum (Pl. VII. Fig. 1). There are two simple excretory vessels, lying on each side of the apical organ in the sagittal

<sup>1</sup>) Quoted from the separate edition; in Studien zur Blättertheorie, von O. Hertwig u. R. Hertwig. Heft III. Jena 1880.

<sup>2</sup>) I cannot accept the terminology adopted by Chun. As shown definitely by the development the part which he designates as "Magen" is of ectodermal origin, and accordingly represents the pharynx (or stomodæum); the true stomach, of entodermal origin, is the infundibulum, or as he names it, "Trichter". To speak of a "primary" and "secondary" Entoderm, as does Chun (Ctenophoren des Golfes v. Neapel. p. 117), does not alter the fact that the part of the gastrovascular system which he terms stomach is really of ectodermal origin. What has caused this unfortunate terminology is doubtless the fact that the pharynx has undertaken more or less completely the function of absorbing the food. But if this is accepted as a valid reason for designating the pharynx as the stomach we should consequently also name the basal or suboral cavity of *Tyalpella* the stomach — but as this cavity is really outside the mouth, I think nobody would accept that terminology. (In most of the recent text-books the terminology of Chun is justly rejected). We must acknowledge the fact that in the Ctenophorans the function of absorbing the food has been transmitted from the stomach to the pharynx, and in *Tyalpella* even to the folds outside the mouth.

In the young *Bolina* Chun (Die Dissogonie; Festschr. f. Leuckart. p. 98) has found the Entoderm-cells of the meridian vessels "mit festen Nährpartikeln erfüllt, welche sie intracellular verdauten. Partikel des Chitinskelettes von Krustern und Bündel quergestreifter Muskeln waren oft so reichlich in ihnen aufgespeichert, dass man auf Schnitten durch die Zwittergefäße der Jugendformen ganz fremdartige und verwirrende Bilder erhielt". Likewise Abbott (The Morphology of *Coeloplana*. Zool. Jahrb. Abt. f. Anat. Bd. 24. 1907, p. 54) records that in *Coeloplana* "In the peripheral region (of the gastrovascular system) various metaplastic bodies become very evident: globules of fat, . . . In addition all varieties of ingested food matter may be found, such as diatoms, as well as other foreign bodies, apparently half digested". These observations show that it is, however, no unexceptional rule that the pharynx of Ctenophores has undertaken the absorbing function.

plane. That both of them open to the exterior I do not doubt, though I have not directly observed both openings. In the series of sections after which Pl. VII. Fig. 1 has been drawn it is directly seen that the left canal opens to the exterior (apparently on a small papilla, which may, however, be due only to contraction on the preservation); on the right side there is certainly also an exterior opening, but the lumen of the canal was not traceable the whole way from the outer opening to its opening into the infundibulum. Neither have I been able to make the canals out in a more satisfactory way in other series of sections. Still I think there can be little doubt of both canals really opening to the exterior, the more so as they have been directly observed to do so in the young *Cydippid*-larvæ. They are distinctly ciliated (Pl. VII, Fig. 5). The openings are not shifted obliquely to the right or left of the sagittal plane as is otherwise the case in Ctenophores, and there appear to be no ampullæ; but the position of the canals in the sagittal plane is in accordance with what obtains in typical Ctenophores, the difference being only that the canals are not dichotomously branched at their upper end. (For the relations of the pharynx, infundibulum and apical organ, comp. also Pl. VI. Figs. 2 and 9). In some of the sections I have observed small excrement-like masses lying in the excretory canals. Also spermatozoa have been observed lying in them.



Figs. 1--2. Diagrams of the gastrovascular system and genital organs of a typical, tentaculate, Ctenophore (Fig. 1) and of *Tjalfiella* (Fig. 2). ar. v. adradial vessel (in *Tjalfiella* represented by the genital vessel); br. c. branching gastrovascular canals; ch. o. "chimney" opening; ir. v. interradian vessel; m. v. meridian vessel; ph. pharynx; ph. v. pharyngeal vessel; t. tentacle; tr. v. transverse vessel; t. sh. tentacular sheath; t. v. tentacular vessel.

The gastrovascular system. From the infundibulum proceeds to each side in the transverse (tentacular) plane a rather large vessel which continues to the tentacle, sending a branch into each side-half of the tentacle-base, as is the usual condition in Ctenophores. From this main vessel (the transverse canal) further proceeds a small branch towards each genital organ, into the lumen of which it opens. Finally a large branch divides off from the main vessel below each subtentacular genital organ; this branch continues into the walls of the body, where it ramifies, forming thus the branching canals so conspicuous through the transparent epidermis, especially on the "chimneys". (Pl. III, Figs. 9 and 10 show the relation of the genital canals and the branching canal to the main vessel; the open-

ings of the canals into the genital organs and the tentacle base can only be seen in sections. Comp. Pl. IV. Figs. 3—4. Pl. V. Figs. 6, 7, 11, 12. Pl. VI. Fig. 7). The transverse main vessel, of course, corresponds to the transverse, perradial, main vessel of typical Ctenophores; the interradial vessels are not represented, the genital vessels, which evidently correspond to the adradial vessels of typical Ctenophores, proceeding directly from the main vessel. Meridian vessels are not developed, and likewise there are no pharyngeal vessels ("Magengefäße"). The two diagrams (Figs. 1—2) may serve to bring out clearly the relations between the gastrovascular system of *Tjalfiella* and typical Ctenophores.

As seen from the figures on Pl. I the branching gastrovascular canals in the walls of the body do not form anastomoses, or at least only exceptionally. (In Fig. 8, Pl. I a single anastomosis is observed). The branches on the two sides of the "chimneys" do not unite on the outer side; likewise the two branching canal systems on the same side of the body do not unite in the middle line (over the sagittal plane).

The structure of the gastrovascular canals is that typical in Ctenophorans, two lateral thickenings forming prominences into the lumen of the canals, while the upper and lower (outer and inner) wall is formed of low epithelium; this structure is found in the whole of the branching gastrovascular canals in the body wall as well as in the main vessel (Pl. VIII, Fig. 2; comp. also the different sections represented in Pl. IV and V). The two prominent ridges consist of more or less strongly vacuolated cells. (Though the vacuoles may partly be due to the preservation it is beyond doubt that part of them are real enough; also in other Ctenophores the cells of these ridges are generally highly vacuolated). The nuclei are spread irregularly in the ridges, while in the low epithelium of the two other sides of the canals the nuclei are arranged rather regularly in a single layer (Pl. VIII, Fig. 2).

Cilia do not appear to occur in the gastrovascular canals; at least I have been unable to find any traces of ciliation here, while in the pharynx e. g. it was very easy to observe.

Rosettes, which had, of course, to be sought for in the thin walls of the branching canals, appear to exist as in other Ctenophorans. I have not succeeded, it is true, in getting a fully satisfactory view of them, but of their existence I have become convinced. In one case I have seen the whorl of cilia of a rosette most distinctly projecting into the lumen of the canal.

Here may be included an observation regarding the food of *Tjalfiella*. In one specimen was found in the suboral cavity a shrimp of ca. 1<sup>cm</sup> length, filling out the whole cavity, the tail lying partly within the one chimney. It was lying with the back downwards. As it was already half decomposed it would scarcely be possible to identify the species, and it was therefore not dissected out. This observation proves that Crustaceans, and not especially the smaller forms, make at least part of the food of this Ctenophore; whether it also catches other animals as prey must remain an unsolved question for the present. That it must catch them by means of its tentacles seems beyond doubt. — It is worth noticing that the food of *Tjalfiella* consists of Crustacea (partly at least), thus being in accordance with what is the case also in other Ctenophores (except the Beroids, which prey on other Ctenophores); these latter, however, take only small pelagic Crustaceans (and occasionally other pelagic animals), according to the observations of Chun (Monogr. p. 240), with which my own observations on *Bolina* and *Pleurobrachia* agree, while *Tjalfiella* takes larger, non pelagic, Crustaceans. For the rest it is scarcely probable that it keeps to the Crustaceans alone; it would appear more probable

that it takes any kind of animals which it may have occasion to catch. That its tentacles must afford a rather powerful catching instrument is evident from the fact that it can capture animals with so strong powers of movement as shrimps.

The tentacles (Pl. I, Pl. III, Figs. 7, 10, 12) are simple, without accessory filaments. They are rather variable in thickness, on account of the different stages of contraction on preservation. The tentacle basis is short and rounded, slightly lobed where the tentacle proceeds (Pl. III, Figs. 10, 12). In a few instances I have observed a small secondary tentacle below the primary (Pl. III, Fig. 12). The whole tentacle apparatus is of a conspicuous yellow colour, due to the colloblasts which cover both the basis and the tentacle, as usual in the tentaculate Ctenophores. The colloblasts (Pl. VIII, Fig. 8) are of the typical form; the spiral filament is inserted in the muscle layer of the tentacle in the usual way; the central filament appears to be short. For finer histological observations on the structure of the colloblasts the material was, of course, not suited.

In sections the axis of the tentacle is seen to consist of a solid muscle cord (Pl. V, Fig. 2 t. Pl. VI, Fig. 3 t. Pl. VIII, Fig. 4), without any special central core as is found in the primary tentacle of *Coeloplana*, according to Abbott<sup>1</sup>). The structure of the tentacle basis is shown by the figs. 1—7, Pl. V, and especially by figs. 7 and 9, Pl. VI. As appears [from these figures the structure is in its main features in full accordance with that described by Chun and Hertwig for *Hormiphora* a. o. Cydippids. The muscle cord of the tentacle is seen (Pl. VI, Fig. 9) to proceed from a fanshaped root occupying the middle part of the tentacle basis. To each side of the tentacle root is a cavity which may be traced by means of sections to the main vessel (Pl. V, Figs. 1—10); they represent the tentacular vessels. They are lined with a high, more or less vacuolated epithelium corresponding to that found in the ridges of the gastrovascular canals and in the genital organs (see below p. 12). On the outer side of the whole is found a thick, very conspicuous layer of colloblasts<sup>2</sup>) (Pl. VI, Fig. 7), the formation of which is seen to proceed from the sides, the fully formed colloblasts occupying the middle part, from which they gradually pass on to the tentacle as it continues growing out from the base. At the inner edge the thick colloblast-forming layer is seen to pass directly into the low epithelium, quite endothelial in structure, which lines the tentacle sheath. The finer histological structure of the tentacle root, and the development of the muscles of the tentacle I have not been able to trace in a satisfactory way; it does not, however, appear to be exactly as described by Hertwig (Op. cit.) in *Callianira*.

The genital organs form one of the most prominent features of the animal and at first sight appear to be of a structure quite unusual among Ctenophores. On a closer study, however, they are found to be built after the usual Ctenophoran type, the only essential difference being that they are here restricted to short, round bodies, while in the typical Ctenophores they continue along the meridian vessels for a longer or shorter distance. By the reduction of the costæ and the shortening of the main (longitudinal) axis of the body it necessary follows that also the meridional vessels are reduced and the genital organs, being bound to these vessels, must be located on the end of the inter-

<sup>1</sup>) James F. Abbot. The Morphology of *Coeloplana*. Zool. Jahrb. Abt. f. Anat. Bd. 24. p. 59.

<sup>2</sup>) It is this layer of colloblasts which Willey has taken for chloragogenous cells in *Ctenoplana* (A. Willey. On *Ctenoplana*. Quart. Journ. Micr. Sc. N. S. Vol. 39. 1897).

radial (genital) vessels, the point from which the meridian vessels would proceed, if present, and accordingly they must become quite short.

As seen from the sections the genital organs contain a rather large cavity which is the direct continuation of the genital (interradial) vessel, the branch going from the main vessel to each genital organ. (Pl. IV, V and VI; the connection between the genital cavity and the main vessel is seen in Pl. IV, Fig. 3, the right subsagittal organ below, and likewise in Pl. V, Figs. 11 and 12). In the side-walls of this cavity the genital products develop, arranged in the way typical for Ctenophorans, viz. the eggs developing on the adradial side, the spermatozoa on the interradial side of the genital organs. (Comp. Pl. IV, Pl. VI, Figs. 1 and 3, also text figures 1-2, p. 9). In Pl. IV, Figs. 2-4, the left subsagittal genital organ appears to be in contradiction to the rule; it is, however, only apparently so. On following this organ through the different sections it is seen that it is really built after the usual plan, only the ovary has been exceptionally developed, occupying secondarily also the greater part of the interradial side, pushing the testis partly over to the adradial side, thus making some disorder in the arrangement of the parts of the organ; in the Fig. 2 part of the ovary is seen in the right place. In the other specimens sectioned no such disorder was found.

The genital cavity, the homologue of the meridian vessels, is lined with a more or less vacuolated epithelium, very similar to that of the tentacle vessels and of the ridges in the ramifying gastro-vascular canals, to which it also corresponds in morphological value. It is generally very high over the ovary, considerably lower over the testis. The nuclei are often arranged very beautifully in a regular row near the edge of the epithelium (Comp. Pl. IV, Figs. 2-4). The arrangement of the ovary and the testis within the single genital organ and their relation to the genital cavity is easily understood from the fig. 4 of Pl. VI. It very much recalls the Fig. 3, Pl. IV of Hertwig (Op. cit.), which represents a section through a meridional vessel of a young *Beroë*; that the ovary and testis are here separated both above and below, while in the quoted figure of the *Tjalfella* they are close together above is no essential difference; in other sections they may be separated as e. g. shown in Pl. VI, Fig. 3, in the right genital organ. It may not be superfluous to point out this close resemblance in the structure of the genital organs to that of other Ctenophorans.

The development of the genital products is partly to be followed in the sections. In Pl. VI, Fig. 6, some larger cells are seen in the germinal zone of the ovary, with large nuclei and a very conspicuous nucleolus, which stains very strongly with eosine (the sections being stained with "Wasserblau-Eosin" after Mann). These doubtless represent young eggs. In later stages they protrude into the genital cavity, being surrounded by the large entodermal cells lining the genital cavity (Pl. VI, Figs. 3-4). Whether these cells are ultimately transformed into a jelly-like mass surrounding the egg, (such as occurs in other Ctenophores), when it leaves the ovary to fall into the genital cavity, I cannot tell, having found no quite ripe eggs. The size of the ripe egg therefore cannot be given either. — The development of the spermatozoa is easily followed. The germinal zone is found at the lower edge of the testis (Pl. VI, Fig. 4), from here the different stages of development are found gradually upwards (Comp. Pl. VI, Fig. 5; this figure has not been reproduced in the natural position, in which the thin portion points downwards). The young spermatozoa are arranged in very conspicuous packets, as described by Willey in *Ctenoplana*. (Also in *Beroë* a somewhat similar arrange-

ment was found by Chun; Ctenoph. d. Golfes v. Neapel. Taf. XVI, Fig. 48). The ripe spermatozoa are found in the upper part of the testis. They break through the entodermal lining into the genital cavity, where they may be found in large quantities in the sections (Pl. VII, Fig. 9). The peculiar fact observed by Chun (Dissogonie p. 98, Taf. XIII, Fig. 2, 6) that in *Bolina* "die Schwänze der Spermatozoen zu keilförmig gestalteten Bündeln vereint sind, welche allmählich sich zwischen das Gefäßepithel einzwängen und schliesslich nach der Leibeshöhle durchbrechen" has not been observed here. I have not found the material suited to working out the minor histological details of the development of the spermatozoa.

The figures 5—6, Pl. VI, are of value for determining the question about the origin of the genital cells in *Tjalfiella*. It is seen there, especially very distinctly in fig. 5, that the germinal zone is a direct continuation of the low entodermal epithelium lining the lower wall of the genital cavity. It appears that on the limit between this low epithelium and the higher epithelium which covers the genital organ a constant proliferation of the cells takes place, most of the young cells being added to the germinal layer. It can scarcely be denied that all evidence is in favour of the entodermal origin of the genital cells in *Tjalfiella*. This case is thus quite in accordance with the view maintained by Chun that the genital cells of the Ctenophores are of entodermal origin, which view is also supported by the researches of Garbe<sup>1</sup>). The opinion of Hertwig (Op. cit.) later on maintained anew by Samassa<sup>2</sup>) that they are of ectodermal origin seems to me definitely refuted by Chun; the ectodermal invaginations of *Callinira bialata* which have caused this opinion appear to be a kind of sense organs peculiar to this species and have not been found in any other Ctenophore as yet. — It may be worth recalling here the series of glands which occur along the subventral ribs in *Eurhamphæa vexilligera* Gegenb. and which secrete a red fluid, when the animal is touched. (Comp. Const. N. Jonescu: Über die Ctenophore *Eurhamphæa vexilligera*. Jen. Zeitschr. f. Naturwiss. Bd. 43. 1908. p. 685—691. Taf. XXIV). The structure of these glands being as yet unknown, it is, of course, impossible to say anything definitely about their homologies. But it might perhaps not be unreasonable to suggest that they could have some relation to the ectodermal sacs of *Callianira*. That Chun (Ctenoph. Golfes v. Neapel, p. 296) is inclined to suppose a genetic relation between *Eurhamphæa* and *Callianira* is also worth mentioning in this connection. Though Jonescu denies the existence of any nearer relation between these two forms, the suggestion of Chun certainly deserves a more careful investigation.

More recently a third view of the origin of the genital cells of the Ctenophores has been maintained by Karl Cam. Schneider<sup>3</sup>), viz. that they are of mesodermal origin. It does not appear to me that the reasons produced by Schneider for this opinion are very convincing, as also B. Hatschek (Das neue Zoologische System, 1911. p. 13) finds them "noch nicht beweiskräftig"; being, however, not profoundly acquainted with histology, I do not venture on a detailed criticism of his statement. I would only point to some facts, which appear to me very unfavourable to his theory of the meso-

<sup>1</sup>) Aug. Garbe. Untersuchungen über die Entstehung der Geschlechtsorgane bei den Ctenophoren. Zeitschr. f. wiss. Zool. Bd. 69. 1901. p. 472—491. Taf. XXXVI—XXXVII.

<sup>2</sup>) P. Samassa. Über die Entstehung der Genitalzellen bei den Ctenophoren. Verhandl. d. naturh.-medic. Vereins zu Heidelberg. N. F. Bd. V. 1893. (This paper has not been available to the author).

<sup>3</sup>) Karl Camillo Schneider. Histologische Mitteilungen. I. Die Urogenitalzellen der Ctenophoren. Zeitschr. f. wiss. Zool. LXXVI. 1904. p. 388—399. Taf. XXIV.

dermal origin of the genital cells. That I have found nothing in *Tjalfiella*, which might suggest a wandering of primordial genital cells from the mesoderm into the genital organs, is, of course, not sufficient evidence against such theory; but I fail to see, how a figure like Pl. VI, fig. 5, could be explained otherwise than I have done, viz. that it shows directly the germinal cells originating through a proliferation of the entodermal epithelium of the genital cavity. Schneider also admits that (in *Beroë*) "an den lateralen Randpartien der Gonaden die Abgrenzung keine übermässig scharfe ist" (Op. cit. p. 393). Further, when he adduces the observations of Willey on the genital organs of *Ctenoplana* as important supports of his view, this loses a good deal of its weight from the fact that several severe objections may be raised against Willey's work, as shown below. Schneider's view (Op. cit. pag. 395) of "die aufsteigend morphologische Differenzierung" of the genital organs in the Ctenophores, four "Differenzierungsschritte" being distinguished, starting from Porifera, seems to me in consequence rather ill founded. — For my own part I cannot doubt the correctness of Chun's view of the entodermal origin of the genital cells in Ctenophores.

In the preliminary description of *Tjalfiella* I have stated that the genital organs have external ducts as in *Ctenoplana*. A closer study of the sections has proved that such is not the case; the ripe sexual products, as shown above, fall directly into the gastrovascular system (the genital cavity) in the same way as in other Ctenophores. The supposed genital ducts are only ectodermal invaginations, sacs which are quite closed towards the genital organs and separated from them through a thin layer of mesodermal tissue. (Comp. Pl. IV, Fig. 1; Pl. V, Figs. 6—7, 12—13; Pl. VI, Fig. 1 and especially Pl. VII, Fig. 11). In the bottom of the sacs there is an elevation, like a knob; this elevation limits one side of the bottom of the sac, which is clad with a high epithelium, in which cell limits appear as rather distinct radiating lines. The nuclei are arranged partly in a nearly regular layer along the outer edge, partly and more irregularly along the basal edge of the epithelium. These cells are provided with long cilia (Pl. VII, Fig. 11). The other part of the bottom of the sac is lined with simple, low epithelium which continues some way up along the outer side of the elevation which limits the ciliated part. The walls of the duct through which the sac opens to the exterior are of the same structure as the outer epithelium, with rather numerous gland-cells. The opening may be of very different width (— comp. e. g. Pl. VI, Fig. 1, i. with Pl. VII, Fig. 11); it may then not be unreasonable to suppose, that it can be actively closed or opened by means of the muscles extending into the lips of the opening (Pl. VII, Fig. 11).

It appears evident that these peculiar organs cannot have anything to do directly with the genital organs, in spite of their position, one over each genital organ. That they must have some kind of sensory function can scarcely be doubted — what function, it will be useless to speculate over from the information available at present. They recall the invaginations over the genital organs in *Callianira bialata*, to which they may possibly be homologous. The structure of those sacs, however, appears to be less complicated than in *Tjalfiella*, but they are ciliated, the cilia being "sogar in besonders grosser Anzahl vorhanden" in the sacs. (Hertwig op. cit. p. 78). Chun (Dissogonie. p. 95) also points out that "die charakteristische Körnerstructur, welche die Drüsencellen der Coelenteraten und speciell auch jene der Ctenophoren anszeichnet, durchaus den Wimperzellen der

Säckchen fehlt". I may also refer to the red glands of *Eurhamphœa vexilligera* in this connection, though nothing more exactly can be said about their possible homology so long as the structure of the glands in this latter form is unknown.

The observations on the structure of the ectodermal sacs of *Tjalfiella* would seem to throw light on the supposed genital ducts in *Ctenoplana* described by Willey (Op. cit. p. 329—331, Pl. 21, Figs. 7—9). Though I must agree that the three figures quoted, when combined, show a duct from the genital organ to the exterior, I cannot but express some doubt about the correctness of the observations of Willey regarding this point. *Ctenoplana* otherwise agrees with *Tjalfiella* in several important characters and is doubtless nearly related with it. The suggestion then naturally presents itself that the supposed genital ducts of *Ctenoplana* might be organs homologous to the ectodermal sacs of *Tjalfiella* (— their greater number in *Ctenoplana*, 3 to each genital organ, would certainly be no serious objection to the homology with the single organs of *Tjalfiella* —). It will doubtless also be conceded that, since the highly transformed *Tjalfiella* has been shown to be in full accordance with the typical Ctenophores in regard to the structure of the genital organs and the way in which the genital products are ejected, it seems very remarkable that the much less transformed *Ctenoplana* should have acquired a way of ejecting the genital products (or at least the spermatozoa) so radically different from what obtains in all other Ctenophores (— allowing that it remains as yet unknown how the case is in *Coeloplana* —). Until renewed researches have been made in the light of the observations here given on the ectodermal sacs of *Tjalfiella*, it seems to me that the problem about the genital ducts of *Ctenoplana* cannot be regarded as definitely solved. (Comp. the further remarks on *Ctenoplana* in Chapter D.).

The musculature is of the usual Ctenophoran type. The general appearance of the muscles upon the whole very much resembles that of Pl. XVII, Fig. 17 in Chun's Monograph. They are arranged in the walls of the chimneys in three main directions, viz. longitudinal, circular and radiating, the latter going directly between the epidermis of the outer and inner side of the chimney; threads are, however, also found, which run in all other directions. In the other parts of the body the arrangement of the musculature is essentially the same. It is worth pointing out that there is no special arrangement of the muscles in the basal part, adapted to perform creeping movements of the animal.

The threads are branched at their ends in the usual way, though not to a very extensive degree. They are very fine, measuring only ca. 0.001—0.003<sup>mm</sup>. I have not observed with certainty any anastomoses between the muscles. The finer histological structure of the muscles I have not been able to investigate in a satisfactory way on the material available. — Between the muscles are found some other histological elements, viz. amœboid-looking cells with pseudopod-like prolongations, corresponding to those described and figured by Chun (Ctenoph. d. Golfes v. Neapel. Taf. XVII, Fig. 17--19); more numerous are some peculiar small aggregates of cells in linear or more irregular arrangement (Pl. VIII, Fig. 9). They are sometimes running out into muscle-like prolongations, sometimes without such prolongations. I suppose that they represent development stages of muscles, corresponding to those described and figured by Samassa in *Beroë* (Zur Histologie d. Ctenophoren, p. 212—214, Tab. XI, Fig. 58).

To enter on a discussion of the nervous system, one of the most difficult problems in Cteno-

phores, would not be appropriate on the basis of the material available. This question can only be discussed appropriately, when material treated *lege artis* is at hand. It must however be pointed out that no indications of the existence of distinct ganglia, as are described by Abbott in *Coeloplana* (Op. cit. p. 61, Fig. B) were found.

## B. Development; Anatomy of the Cydippid-stage.

When ripe the eggs fall into the cavity of the genital organ, from which they must be transferred through the main vessel to the ramifying canals and then transported in some way or other to the place, where they are going to hatch. Though no direct observations have been made as to this, it cannot be doubted that it must happen along this way. How the transport is made, remains uncertain, but it may be suggested that the eggs wander by active amœboid movements, since cilia have not been found within the gastrovascular canals. To be sure, it can scarcely be taken as definitely proved that cilia do not occur in the gastrovascular canals, the histological preservation being insufficient for proving the non-existence of cilia in some places; but the fact that they are easily observed in other places (e. g. in the pharynx and in the chimneys) makes it very probable that they really do not exist in the gastrovascular canals; this supposition also gets an important support from the fact that cilia are not found in the gastrovascular canals of *Coeloplana* (Abbott; op. cit. p. 54). (In typical Ctenophores the low epithelium in the gastrovascular canals is ciliated, while the high cells of the ridges carry no cilia). That the eggs wander through active movements is the more probable, since in other Ctenophores direct movements of the eggs have been observed both by Kowalewsky, Agassiz and Chun, the latter author giving the following description of the movements as observed in *Eucharis*, *Lampetia* and *Cestus* (Monogr. p. 100) "... Bewegungen..., welche, darin bestehen, dass das Ektoplasma sich contrahirt, bald an dieser, bald an jener Stelle der Peripherie sich in grösserer Menge ansammelt und das Endoplasma hin- und herpresst. Es fehlte nur noch, dass die verdichteten Stellen der Peripherie sich zu Pseudopodien ausziehen, um die Ähnlichkeit mit einer amöbenartigen Bewegung zu vervollständigen". Through such movements it may be understood that the eggs can wander from the genital organs to the brood-cavities.

The fertilisation must take place within the gastrovascular canals, the eggs evidently not leaving the animal. Since the spermatozoa are also found in quantities in the canal system, both eggs and spermatozoa developing contemporaneously in the same genital organ, as appears from the sections, it seems hard to see how self-fertilisation can be avoided. Another thing is that it cannot be doubtful that foreign spermatozoa may have access to the eggs. I have observed spermatozoa within the excretory canals, which proves that they are liberated this way (perhaps also through the mouth and the chimneys); the foreign spermatozoa probably must enter through the chimneys and the mouth, perhaps also through the excretory canals.

The brood-cavities in which the development of the embryos takes place are probably situated in the end branches of the ramifying gastrovascular canals. I have, however, been unable to prove this definitely on the sections; but the canals are seen to abut against the brood-chambers, not continuing beyond them, so I feel rather convinced that such is the case. Further observations

on fresh material are necessary for solving this question also. — The arrangement of the brood-cavities is quite irregular (Comp. Pl. I, Fig. 9). They are confined to the sides of the body, in larger specimens also occupying part of the chimney-wall in the lower part; higher up on the sides of the chimneys than the level of the genital organs I have not found them (comp. Pl. IV, Figs. 2—4; e. c.). In larger specimens they may be so crowded as to lie in a double layer; I have counted up to 35 in one specimen. The embryos occur in all different stages of development, arranged without any order whatever, in the same specimen.

The first stages of the development, cleavage etc., I have not been able to work out — not because such younger stages were not found, but because the thick egg-membrane has prevented the penetration of the preserving fluid, the young cells being thus not satisfactorily fixed. I think I have observed the large, clear entodermal cells typical for Ctenophoran development; but upon the whole these young stages were not sufficiently well preserved for being worth figuring.

Stage I. The youngest embryos sufficiently well preserved for showing anything clearly are those represented in Pl. II, Figs. 1—3 and 7, this stage being designated as stage I. The shape is quite spherical, the diameter being ca. 1.2<sup>mm</sup>. At the apical pole of the embryo is seen an epithelial thickening, elongated in the sagittal plane (Pl. II, Fig. 3, s.). It is the apical organ, the two elongations representing the polar fields. The shape is quite similar to that shown in Taf. VII, Fig. 20 of Chun's Monograph, representing a young *Beroë Forskålii*. The costæ have made their appearance as four pairs of radiating, thickened lines, in which there is already a distinct grouping of the cells in transverse series; from each of these groups a comb originates, though not yet seen in this stage. As seen in side view (Pl. II, Fig. 2) the costæ reach nearly halfway down on the embryo. At the level of the lower end of the costæ is seen a pair of epithelial thickenings with a vertical keel in the middle; these represent the rudiments of the tentacle apparatus. On the oral side there is a distinct furrow in the transverse plane, reaching scarcely halfway up to the tentacle-rudiments (Pl. II, Figs. 1—2). The mouth-opening is not seen, the edges of the transverse furrow lying close together. In the slightly younger stage represented in Fig. 7, Pl. II, the mouth is very distinct, the transverse furrow having as yet scarcely begun to form. (In this stage the aboral side is as in figs. 2—3, the costæ being only a little less developed). The four radiating lines seen in this figure I suppose to be due to the arrangement of the large entodermal cells; it cannot, however, be decided, the sections giving no information thereof on account of the bad preservation of the entodermal elements. I would refer to such figures as Taf. VII, Fig. 11 and 14, Taf. VIII, Fig. 9—10 of Chun's Monograph as affording the probable explanation of these radiating lines. Whether the radiating darker tracks seen in Fig. 6, Pl. II should be explained in the same way or perhaps represent the mesoderm-strips I do not venture to maintain; the sagittal tracks might be due to the pharynx, which most probably is the explanation of the vertical (sagittal) tracks seen in Figs. 1 and 4, Pl. II.

The embryos in this and the other stages show a number of small, irregularly placed, white spots. I suppose they are only effects of preservation (coagulated matter), but as I cannot give definite proof thereof, I have thought it right to mention the fact and represent it in the figures of this stage.

The egg-membrane lies quite close to the surface of the embryo; only over the transverse

furrow it becomes free of the epidermis and thus can be seen in side view (from the transverse plane) (Pl. II, Fig. 2 m.).

Stage II. In the next stage (II), represented in Pl. II, Figs. 4—6, the size is the same as in the former stage, ca. 1.2<sup>mm</sup> in diameter, and the shape is also spherical as before. The combs have been formed, though quite short as yet. The costæ are distinctly shorter than in the foregoing stage, being more concentrated — a very conspicuous feature; it should however be pointed out that the number of the combs is rather variable, so that the difference in the size of the costæ may be partly due to this fact. Also the tentacle rudiments are somewhat nearer the apical pole than in the preceding stage (comp. figs. 3 and 6, Pl. II). The transverse furrow is much deeper, but has still not nearly reached the tentacle rudiment. As seen from Pl. III, fig. 8, which represents an embryo of this stage opened, the furrow has already a considerable depth. The apical organ has been rather deeply sunk, the body forming four rounded elevations round it. The egg-membrane still adheres closely to the epidermis, except over the apical invagination, the transverse furrow and the costæ (comp. Pl. II, Fig. 5, Pl. III, Fig. 8 m.; also Pl. IX, Figs. 1—5).

On account of the thick, very resistant egg-membrane it is very difficult to have these young stages imbedded and sectioned. Only by cutting a hole in the membrane have I been able to obtain sections, which are somewhat satisfactory. The histological preservation is, as regards the entodermal cells, very poor, so that no information can be given about the entoderm of the embryo; but the ectoderm is tolerably preserved, the sections thus giving some information of interest.

In Pl. IX, Figs. 1—5 are represented some horizontal sections at different levels through an embryo in the stage II; they are easily understood on being compared with Pl. II, Figs. 4—6 and Pl. III, Fig. 8. In Fig. 2 the pharynx is cut on the level where it passes into the transverse furrow, which latter in the following sections gradually lengthens until (Fig. 5) it reaches the periphery, thus dividing the body (in the lower part) into two lobes. The walls of the furrow are rather thick, the nuclei being arranged irregularly in two—three layers. In Pl. VII, Fig. 4 is represented a longitudinal section through the pharynx in this stage; it is seen to be distinctly ciliated. At the upper end the walls continue into a thin layer of entoderm. A corresponding thin layer of entodermal cells is seen in Pl. VII, Fig. 6 just below the apical organ; it represents the roof of the infundibulum. Farther out both these entodermal membranes pass into the large, vacuolated entodermal cells, which are too badly preserved for figuring.

A vertical section through the apical organ of this stage is represented in Pl. VII, Fig. 6. The epithelium has already been very considerably thickened. A group of otoliths (ot.) are seen lying in the cavity of the depression apparently borne upon a bunch of cilia, which I think must be regarded as homologous to the balancers of other Ctenophores. Other otoliths are also seen still lying between the epithelial cells; they have each a rather distinct nucleus, in accordance with the observations of Samassa (Op. cit. p. 181, Taf. IX, Figs. 16, 17). The cells within the depression carry a dense coat of short cilia. At the edge of the depression there is a zone (c. z.) of high clear cells, with the nuclei arranged rather regularly in a single layer near the outer surface, and which carry long, very distinct cilia. They are the cells which form the cupule, the cilia being as yet isolated and not converging over the otocyst. This zone is very distinctly limited both towards the epithelium of the depression

and towards the epithelium outside the depression, which has likewise the nuclei arranged rather regularly in a single layer. — The section described of the apical organ of this stage upon the whole corresponds very well to that through the apical organ of *Callianira bialata* represented by Hertwig (Op. cit. Taf. V, Fig. 8), showing that the organ in the earliest stages has exactly the same structure as in typical Ctenophores. — There is yet no indication of the excretory canals and pores.

The costæ are formed as simple thickenings of the ectoderm, slightly depressed; in the cavity thus formed between the epidermis and the egg-membrane lies the comb (Pl. IX, Figs. 1—3, Pl. VIII, Fig. 6). The nuclei are somewhat larger than those of the epidermis; they are arranged more or less regularly in a single layer near the basis of the cells. It is an important fact that each comb is formed from the first beginning by a considerable number of cells, not by a single cell as was found by Chun (Monogr. p. 111, Taf. XVI, Fig. 22) to be the case in *Eucharis multicornis*.

The tentacles are seen to originate as thickenings of the ectoderm; in horizontal sections they have the shape of a T (Pl. IX, Figs. 2—3. tb.); the thicker part in the middle represents the tentacle itself, from the wing-like expansions originates the thick colloblast-forming layer covering the sides of the tentacle-base. In Pl. VIII, Figs. 10—11 are represented two vertical sections through the tentacle rudiment of this stage, fig. 10 of the lateral, fig. 11 of the thick, median part. The development of the tentacle muscles has not yet begun. It would appear to be evident from these sections that the tentacle apparatus originates alone from the ectoderm as maintained by Chun (Monogr. p. 14) and Hertwig (Op. cit. p. 45), and quite recently by Hatschek (Das neue zoologische System. 1911; p. 9). There is no trace of either mesodermal or entodermal elements taking part in its formation<sup>1)</sup>. — As seen in the two figures quoted the tentacle sheath has begun to form as a simple folding of the ectoderm over the tentacle rudiment.

Of the mesoderm in this stage I can only give the negative information that no undoubted mesoderm cells could be observed in the sections and that no muscles have been formed as yet.

It should not be omitted to state that the epidermis in the sections of these stages is not in so complete condition as is shown in the figures, being broken in several places, but, of course, the restorations are made only after careful studies, being in full correspondence with reality. It may also be said here that in the sections of this and the following stage all wrinkles of the epidermis, which are evidently quite accidental results of the preservation, have been omitted.

Stage III. In this stage (Pl. II, Figs. 8—11, Pl. III, Figs. 1—2, 4, 6, Pl. VIII, Figs. 12—14, Pl. IX, Figs. 6—14, Pl. X, Figs. 1—9), by far the most important of the embryonal stages, the embryo is a fully formed Cydippid with all the structural features characteristic of this form typically developed. Though they are still enclosed within the egg-membrane, they are upon the whole rather well preserved (— the membrane lies more loose and is ruptured in some of the specimens —), so that it has been possible to study their anatomy rather fully, by sections as well as by direct preparation under the microscope. I may thus give a detailed account of this stage, which gives the clue to the anatomy of the grown animal and also gives valuable hints as to its relations to other Ctenophores.

<sup>1)</sup> Comp. E. Metschnikoff, Vergleichend embryologische Studien. 4. Über die Gastrulation und Mesodermbildung der Ctenophoren. Zeitschr. f. wiss. Zool. 42. 1885. p. 653. P. Samassa. Zur Histologie der Ctenophoren. Arch. f. mikrosk. Anat. Bd. 14. 1892. p. 189, 192—193. K. Camillo Schneider. Lehrbuch d. vergleichenden Histologie d. Tiere. 1902. p. 185.

The shape of the embryos is now rather different from that of the previous stages; they are distinctly elongate in the transversal plane, as seen in Figs. 8—9, Pl. II, and towards the oral side they are narrowed, being thus pear-shaped when seen from the transverse plane (Pl. II, Fig. 10). Contemporaneously they have increased somewhat in size, being now ca. 1.5<sup>mm</sup> long (transverse diameter) by ca. 1.2<sup>mm</sup> broad (sagittal diameter). The now fully developed costæ are sunk down in deep lodges, the four radial parts of the body arching out between the costæ and partly covering them, so that the combs protrude from four deepenings. The four radial archings also rise over the apical organ, which is rather deeply sunk (Pl. II, Figs. 8—9).

The transverse furrow is now very deep and reaches so far upwards as to include the opening of the tentacle sheath (Pl. II, Fig. 10). The lobes may be pressed together or more or less opened, even so widely that the basal surface comes to be quite flat (Pl. III, Fig. 6). (The same may be observed in the young of *Eucharis*. Comp. Chun. Monogr. p. 128. Pl. IV, Fig. 10). When the lobes are thus opened, the mouth-opening is seen in the bottom of the furrow as a transverse slit (viz. transverse to the furrow). (Pl. II, Fig. 11). — The larva in this stage agrees in several important respects with the larval form of the Lobatae, especially that of *Eucharis multicornis* as described by Chun (Monograph, p. 122. Pl. IX, especially figs. 1—2).

The apical organ has now reached its full development. It is deeply sunk (Pl. II, Fig. 10, Pl. III, Fig. 1, Pl. VIII, Fig. 13, Pl. X, Fig. 9), a narrow channel limited by the four aboral elevations of the body leading down to it (Pl. III, Fig. 1). The sections figured in Pl. VII, Figs. 3 and 10 give some information on its finer structure (to compare with Pl. VII, Fig. 6 representing its structure in the foregoing stage). The main difference from the foregoing stage is that there has now been formed a complete cupule over the otolith, which latter has been considerably augmented. The zone of cells forming the cupule is still quite distinct. Whether the cells in the bottom of the depression are ciliated in this stage I have not been able to see quite distinctly; but I can scarcely doubt that the zone between the nuclei of the epithelium and the otolith shown in Pl. VII, Fig. 10 partly, at least, consists of a mass of cilia corresponding to that seen in the figure of the organ in the foregoing stage (Pl. VII, Fig. 6); in a pair of the sections I think I can discern in some places a limit between the cilia and the epithelium, as it is represented in Pl. VII, fig. 6. Any trace of balancers could not be detected. Seen from above (Pl. X, Fig. 11) the walls of the organ are folded inwards in the transversal axis, while in the sagittal axis there is seen an apparently kidney-shaped body to each side of the organ (Pl. X, Fig. 11, p. f.). These bodies represent the polar fields, which lie wholly within the depression, though above the apical organ itself. On preparing the whole apical organ out the real shape of the polar field is seen to be nearly that of a horseshoe (Pl. X, Fig. 10). Of its finer histological structure no satisfactory information can be given; sections through it are shown in Pl. VII, Figs. 7 and 8. — As stated above (p. 7) I have been unable to find any traces of the polar fields in the grown animal; it thus appears that these organs degenerate later on; also the cupule and the cells forming the cupule appear to have degenerated in the grown specimens.

In Pl. III, Fig. 2 are represented some fine lines radiating from the apical organ to the upper end of the costæ. There can certainly be no doubt that they correspond to the ciliated epithelial strands connecting the apical organ with the costæ in other Ctenophores, regarded by Chun as

representing nerves. Of their finer structure I can give no satisfactory information; in sections they are seen to be slightly sunk (Pl. X, Fig. 7, the two small depressions of the epidermis at the apical side; they are not quite simple depressions, but have a little elevation in the middle corresponding to the fact, that there are two lines in each).

The excretory canals and pores have been formed, viz. a single, not branching canal to each side of the organ, in the sagittal plane, opening through a pore situated nearly in the median line (Pl. VII, Fig. 10). On preparations of the organ in toto I have not been able to discern more than one opening with certainty (Pl. X, Fig. 11, excr. o.); but sections leave no doubt of the existence of both. (Comp. also Pl. VII, Figs. 7—8, representing horizontal sections through the apical organ).

The costæ have now reached their highest development. They consist of 7—11 (or perhaps a few more) iridescent combs each, the number varying somewhat; there is no difference in the sub-sagittal and subtransversal costæ as to the number of combs, and there is no indication of new combs being added at the upper end after this stage has been reached. The combs are very long and lie so close together that their number can only be made out with certainty from the cell-groups, by which they are formed. As seen by the Fig. 7 Pl. VIII, representing a vertical section through a pair of combs, they have the characteristic angle at the base (comp. Chun. Monogr. p. 81). The basal cells are folded over the inner end of the comb, which thus proceeds from a deep ridge, this arrangement being the result (or perhaps the cause) of the close aggregation of the combs, there being no room for the basal cells to take the arrangement which occurs in other Ctenophores. The position of the costæ in deep lodges is well shown by the sections Pl. IX, Figs. 6—11 and Pl. X, Figs. 2—6; this explains how the costæ in vertical sections may be seen lying apparently quite within the body (Pl. X, Figs. 7—9). The two costæ lying in each lodge are separated by a narrow keel (Pl. IX, Figs. 6—10).

The tentacle apparatus is deeply sunk, enclosed by the tentacle sheath, which opens through a rather long and narrow canal, directed obliquely downwards, the opening being, as stated above, within the transverse furrow. The tentacles are fully developed and generally lie coiled up within the tentacle sheath (Pl. II, Figs. 8—11, Pl. III, Fig. 4), the latter being then considerably swollen. Sometimes, however, I have found them protruding through the sheath and penetrating into the furrow, the egg-membrane not allowing it to occupy any other room. It is a simple cord, covered by colloblasts, which are, however, much less numerous than in the grown specimens (comp. also Pl. X, Figs. 2—4). The thick epithelium covering the tentacle basis has taken up its function as the colloblast-forming layer, having the same appearance as in the grown specimens (Pl. X, Fig. 3, to compare with Pl. V, Figs. 1—5, Pl. VI, Fig. 7); at the margin this thick layer passes directly into the thin wall of the tentacle-sheath (Pl. IX, Figs. 10—12).

The transverse furrow which, as stated above, has reached so far upwards as to include the opening of the tentacle sheath, is deep and wide (Pl. III, Figs. 1, 4; Pl. X, Figs. 1—9); when closed as in the specimen represented in the sections in Pl. X, its walls are much folded. In the middle, near the mouth, the large folds, so characteristic of the grown animal, have begun to appear. The epithelium of the furrow is considerably thicker than the outer epithelium (comp. the sections figured on Pl. X), and has already been differentiated, the gland cells having been formed in considerable number. It is distinctly ciliated. The nuclei lie mostly at the base of the cells.

The pharynx (Pl. III, Fig. 1, Pl. VIII, Figs. 12—14, Pl. VII, Fig. 3, o. e.) has the walls rather strongly folded, except in the uppermost part, the folds protruding into its lumen. It is very probable that only the upper, smooth part corresponds to the pharynx of the grown animal, in which there are likewise no folds (Pl. VII, Fig. 2); the lower part with the folds would then develop into the large folds surrounding the mouth in the grown animal. This question I am not able to solve definitely, having only insufficient material of the following stages, in which this development must take place<sup>1</sup>).

The infundibulum (Pl. VII, Figs. 3, 10, Pl. VIII, Figs. 12—13) is quite short, with thin, non-ciliated, walls; from each side of it, in the sagittal plane, proceeds upwards a narrow canal, which opens to the exterior — the excretory canal.

The general appearance of the gastrovascular system is easily seen on removing the epidermis of the embryo. (Pl. III, Figs. 1, 4, 6). Under each pair of costæ protrudes a large sac (e. s.) there being four such sacs in all. At their base they are united two and two below each tentacle apparatus; the cavity of the sacs is in direct connection with the infundibulum through the main cavity formed by their uniting in the middle line (Pl. VIII, Figs. 12—13). — It is easily seen that these four large sacs correspond with the four entodermal sacs of other Ctenophoran embryos. (Comp. Chun, Monograph, p. 115—116, Taf. VIII). In the sections the walls of the entodermal sacs are seen to consist partly of very large, vacuolated cells, partly of a quite low epithelium. In the outer part of the sacs the large cells are distinctly arranged in two separate groups (comp. Pl. IX, Fig. 13, Pl. X, Figs. 2—5), the structure being thus already the same as that of the gastrovascular canals of the grown animal. (Also in other Ctenophores the differentiation of the cells of the entodermal sacs begins at the corresponding stage of development. Chun, loc. cit.). The tentacular vessels have not acquired their definite shape as yet; the large entodermal cells are seen to fill out the two sides of the tentacle base (Pl. X, Figs. 3—5), but there is no lumen discernible as yet.

The genital organs have not yet been formed, and I have been unable to find in the sections any grouping of young cells which might be interpreted as representing the first rudiments of them.

The musculature has already reached a considerable development, as seen by the sections (Pl. VIII—X; comp. also Pl. VII, Figs. 3, 10). It is especially well developed in the lobes.

On reaching this stage of development the embryo is ready to leave the brood chamber. Having ruptured the egg-membrane, and probably at the same time the covering epidermis of the

<sup>1</sup>) The structure of the pharynx of *Mertensia ovum*, as described in the second part of this memoir, does not leave any doubt as to how these structures in *Tjalfiella* must be interpreted. In *M. ovum* there is a narrow upper part without folds, compressed in the sagittal plane; below this part the pharynx widens considerably, the strongly developed pharyngeal (or stomodæal) folds ("Magenwülste") occupying the lateral (transversal) walls. The upper narrow part, which may be distinguished as the oesophagus, evidently corresponds to the narrow canal leading from the "suboral" cavity to the infundibulum in *Tjalfiella*, designated above (p. 8) as the pharynx (Pl. IV, Fig. 4; Pl. VII, Fig. 2); this part should then likewise be designated as the oesophagus (as it is, in fact, designated in the figures). The lower part, the pharynx s. str., corresponds to the whole of the "suboral" cavity of *Tjalfiella*, the large folds, situated laterally (transversely) to the "mouth", being beyond doubt homologous to the pharyngeal folds of *Mertensia* and the other Ctenophores. It follows further that what has above (p. 8, Pl. III, Fig. 11. o) been designated as the true mouth-opening, is really only the opening from the pharynx into the oesophagus. To the mouth-opening in typical Ctenophores corresponds in *Tjalfiella* the opening in the basal surface + the two "chimney"-openings. — It was only after the above had been printed that these facts became clear to me on examining some specimens of *Mertensia ovum*.

parent animal (— this can doubtless only take place through the enlargement of the size of the embryo —) it moves freely about in the usual way of Ctenophores — but probably only for a very short time, as seems to be shown by the fact that the youngest fixed stage is scarcely larger (2<sup>mm</sup> transverse diameter) than the Cydippid-embryo still lying within the egg-membrane (1.5<sup>mm</sup>). The young Cydippid then attaches itself to the *Umbellula* by the opened lobes; the secretion of the gland cells found in the epidermis of the lobes may probably be of some use in the attachment. The ends of the transverse furrow are now produced towards the aboral side (Pl. III, Fig. 3); at some distance from the end, below the opening of the tentacle sheath, the two lobes unite with their edge, the upper part of the furrow thus being separated from the larger under part. It is easily understood how these separated-off lateral parts grow upwards carrying with them the tentacle sheath and thus form the “chimneys” so characteristic of the grown animal. The upper ends of the furrow thus become directly converted into the “chimney” openings. The change of their position from vertical in the young to horizontal in the grown must be due to the part where the edges of the lobes unite growing faster than the upper (adapical) side of the “chimney.”

The costæ have already disappeared totally. Their role is only to carry the young to a place some short distance away from the parent animal, they being thus reduced to be a temporary means of dispersal. The very close packing of the combs, which must evidently check their locomotive power considerably, is in fair accordance with the reduction of their functionary importance.

The gastrovascular system has undergone an important change from that found in the Cydippid stage. As seen by the Fig. 3, Pl. III, the large entodermal sacs have begun to branch at their outer end, which proves that they transform directly into the branching canals of the grown animal. From their base are seen to protrude a pair of smaller sacs. I do not doubt that they will give rise to the genital vessels and the genital organs. The definite proof of this cannot be given here, the specimen figured being unfortunately the only one found in the stage of metamorphosis from the Cydippid-larva to the grown form, and I have not thought it right to sacrifice this highly important specimen for section. The apical organ of this specimen could thus not be studied more closely either, though it would have been very interesting to see, whether it has already begun to degenerate at this stage. Another structure, the origin of which it would be highly interesting and important to have made known, is the sense organ lying in the invagination above each genital organ in the grown animal. The solution of these questions must be postponed till further material comes to hand.

The question whether dissogony occurs or not may be answered more definitely. It certainly appears very improbable that dissogony takes place, seeing that the genital organs have not yet begun to form in the Cydippid ready to leave the egg-membrane, and the free-swimming period of the animal being probably only quite short, judging from the size of the youngest metamorphosed specimen. Further, the observations of Chun (Dissogonie p. 102—103) have shown that the dissogony of *Bolina* and *Eucharis* takes place only under the influence of the high temperature of the surface waters, not occurring during the winter season, and is not known either in the *Cestus* larvæ, which during the summer months occur only in deep water, coming to the surface in the winter months, and it would thus seem very improbable that dissogony should occur in *Tjalfiella*, which lives in the depths of the cold waters of Greenland.

### C. Regeneration.

Several of the larger specimens of *Tjalfiella* in hand are remarkable through having the two halves of the body unequally developed, the very different size of the two "chimneys" being especially a conspicuous feature. The one chimney may be only half the size of the other, as in the specimen represented in Pl. I, Fig. 4, or even much smaller as in the specimen represented in Pl. I, Fig. 8 — or it may be totally wanting as seen in Pl. I, Fig. 7. That the latter case is not due to damage done to the specimen through capture is shown by the fact that the edges of the furrow have united below the place of rupture. There can be no doubt that the figures quoted represent specimens in different stages of regeneration. In the fig. 7 the regeneration has just begun, there being still no trace of the organs lost, viz. the tentacle apparatus, the outer pair of genital organs and the whole of the branching gastrovascular canals of that half of the body. In the specimen figured in Pl. I, fig. 8, the regeneration has already been carried a considerable step farther. Both the tentacular apparatus and the genital organs have been formed anew, though the tentacle itself appears not to be developed as yet, and also the genital organs are still quite small. The branching gastrovascular canal has also been formed, giving off already three main branches. In the specimen represented in Fig. 4 the regeneration is nearly carried to the end; but the size of the whole right half and all its organs as compared with the left sufficiently shows that also this specimen is in process of regeneration. (Also the fig. 9, Pl. III, is from a specimen in regeneration).

The histological processes of the regeneration have not been studied, the material in hand being not sufficient for that purpose. That such a study will prove most interesting is beyond doubt. Thus e. g. the formation of the genital organs and the sense organs attached to them might well be studied in this way.

The question arises here whether perhaps the animal divides itself by autotomy, the two halves thus regenerating the part wanting. This question must evidently be answered in the negative. If such were the case, the division would doubtless invariably take place along the middle line (the sagittal plane), as appears to be really the case in the specimens represented in Pl. I, Figs. 4 and 8 — though the smaller size of the subsagittal genital organ of the not regenerating side makes it a little uncertain whether the division line was really in the middle of the animal. But the specimen represented in Pl. I, fig. 7 gives sufficient proof that no voluntary division has taken place here. The division here has taken place between the subsagittal and subtransversal genital organs, only the latter together with the tentacular apparatus and the "chimney" having been lost. It is evident that a self-division along this line is not well imaginable. Specimens are also found in which the line of fraction has been quite oblique; in one specimen there is only one large genital organ, all the other being regenerated. There can thus be no doubt that the regeneration is caused not through autotomy but by damage done to the animal, perhaps by fishes or Crustaceans feeding upon it. The high percentage of specimens in regeneration among the material in hand shows that they must be very exposed to such damage.

The very great regenerative power thus shown to exist in this animal is the more interesting as, according to Chun (Monograph. p. 241), the Ctenophores otherwise do not appear to be capable to

regenerate even unimportant parts removed from their body. In his famous memoir "Die Dissogonie" (p. 103) Chun even more definitely states that "den Ctenophoren nach den übereinstimmenden Berichten aller Beobachter ein Regenerationsvermögen abgetrennter Theile durchaus abgeht". That this is, however, not an unexceptional rule, is proved also by the facts recorded below of *Bolina infundibulum*. This Ctenophore I have found to be in possession of even quite a remarkably great regenerative power. Also *Beroë cucumis* appears to be capable of regenerating large and important parts of the body, though I have made no direct experiments with this form. From this I would be inclined to think that Chun is not right in his statement, it seeming rather singular that the *Bolina* should differ so conspicuously from other Ctenophores (except *Tjalfiella*) in this respect.

#### D. Affinities of *Tjalfiella*.

Turning now to the question of the relations of *Tjalfiella* to other Ctenophores, the attention is naturally first directed towards the other aberrant Ctenophores known, viz. the two genera *Ctenoplana* and *Coeloplana*, constituting the order **Platyctenida**.

It is easily seen that there are several points of resemblance between *Tjalfiella* and *Ctenoplana*. The costæ are deeply sunk in *Ctenoplana* as in the young *Tjalfiella*. According to both Korotneff and Willey the costæ of *Ctenoplana* are withdrawn by means of a specially developed muscular system; as it is shown below that the peculiar muscular system ascribed to *Ctenoplana* by Korotneff and (partly) by Willey is nothing but the tentacle, withdrawn into the sheath, it becomes very improbable that such special retractor muscles of the costæ really exist. The fact that the young *Tjalfiella* has its costæ sunk in a similar way (without being retracted by muscles) would seem to indicate that it is also their natural position in *Ctenoplana*. I would suggest that the supposed retraction is only the lying down of the combs, when swimming is interrupted. — Korotneff's suggestion (Op. cit. p. 250) that the combs of *Ctenoplana* have lost their function as swimming apparatus and become "ein Schutzapparat, wie die Borsten der Anneliden" is, of course, refuted by Willey's direct observation of their being used in the usual way.

A feature specially worth mentioning is that *Ctenoplana* can fold itself up in the transverse plane, having thus two large lobes, which it can open or lay together, just as is the case in the young *Tjalfiella*.

Also in the structure of the gastrovascular system there is a considerable resemblance between the two forms. As seen from the figure 3, (p. 26), copied from Korotneff, there is a pharyngeal cavity with richly developed folds as in *Tjalfiella*. Korotneff regards this cavity as the stomach, the folds being regarded as "Darmäste" (Op. cit. p. 241). The oesophagus and infundibulum are mainly alike in both forms; both have a richly developed branching peripheral gastrovascular system (anastomosing in *Ctenoplana*, not anastomosing in *Tjalfiella*), and both lack the meridional canals. — On the other hand there would appear to be also some very essential differences in the gastrovascular system. The branching peripheral canals are stated by Korotneff to arise from the folds of the pharyngeal cavity, while according to Willey (p. 328) "the two end-lobes are in open communication with the peripheral canal system". There can certainly be no doubt that the observations of Willey regarding this

point are correct, and thus the peripheral canal system has the same origin in both *Tjalfiella* and *Ctenoplana* — assuming that the “endlobes” of Willey are those between the two outer pairs of costæ in his Fig. 1. In the very diagrammatical figure 11 of Willey’s paper these lobes would sooner be taken to represent the tentacle vessels, as what Willey later on mentions as the “terminal lobes” decidedly represent the tentacle vessels. It seems that Willey has not reached full clearness on this point; but I cannot doubt that the branching canals really arise from the outer lobes, not from the tentacle vessels.

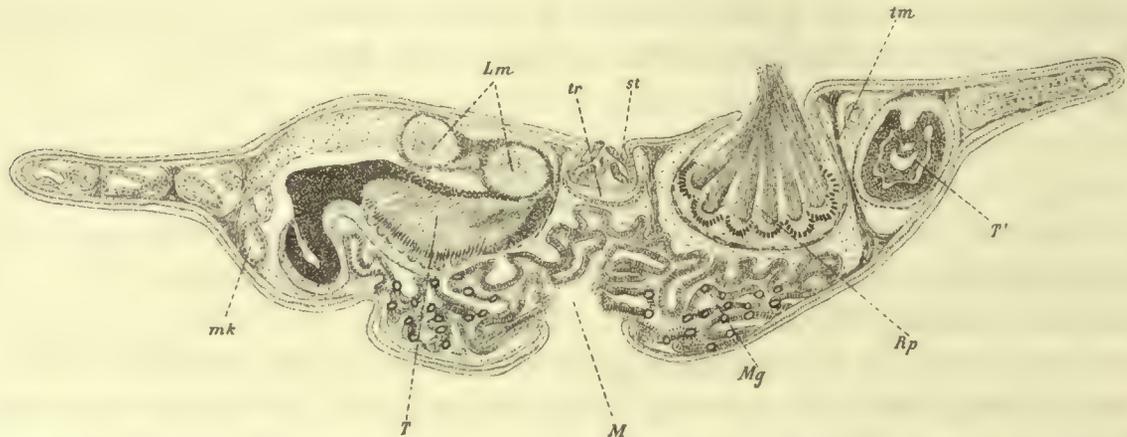


Fig. 3. Vertical section, somewhat oblique, in the transversal plane, through *Ctenoplana Kowalevskii*. (After Korotneff. Op. cit. Taf. VIII. Fig. 3). The letters are those of Korotneff. Lm. “grosse Längsmuskeln” (= tentacle); M. Mund; Mg. Magen (= folds of the pharyngeal cavity); mk. “Magenkanal” (— probably sections of the tentacle); Rp. Rippenplättchen; st. “Sinnestentakeln”; T. grosse Tentakeln; tm. dorsoventrale Muskeln; tr. Trichter (infundibulum).

Regarding the histological structure of the peripheral canal system I venture to suggest that there will prove to be perfect accordance between the two forms. It is true, Korotneff states them to be lined all round with a simple, uniform epithelium (comp. his fig. 9) and Willey (Op. cit. p. 328) even states that they appear in sections “merely as the spaces partitioned off by the dorsoventral trabeculæ, which Korotneff describes as dorsoventral muscles”. But in the figure 4, copied from Willey (Op. cit. Pl. 21, Fig. 5), a rather distinct indication of the two walls of high epithelium is seen in the space directly below the genital organ, as described above for *Tjalfiella*. I do not doubt therefore that the histological structure of this canal system will prove to be identical with that of *Tjalfiella*, so that the peripheral canal system, upon the whole, is evidently another essential point of resemblance between *Ctenoplana* and *Tjalfiella*.

The central part of the gastrovascular system, however, appears to differ very considerably in the two genera, both in its general configuration and in its anatomical and histological structure. A very conspicuous feature is the possession of a pair of large lobes in the sagittal plane. This is a feature entirely unknown in typical Ctenophores; but in *Coeloplana* a corresponding pair of lobes occur, from which a system of branching canals arise; it might then perhaps not seem unreasonable to suggest that also in *Ctenoplana* they give rise to branching canals. In *Tjalfiella* there is no trace of such sagittal lobes from the gastrovascular system, probably as a consequence of the compression of the body in the sagittal plane, while in the flattened, widened body of *Ctenoplana* and *Coeloplana* there is room enough for this structure. This is the first difference of any importance

noticed in the inner anatomical structure between *Tjalfiella* and *Ctenoplana*. But there would seem to be other important differences.

According to Willey's description the gastrovascular system of *Ctenoplana* is characterized by the possession of a pair of peculiar "gastric glands" and some not less peculiar "gastric proliferations" from the walls of the terminal gastric lobes; the cells of these proliferations "appear to assume the properties of chloragogenous cells, and numerous yellowish refringent concretions occur in and amongst them" (Op. cit. p. 330). (Comp. the fig. 5 of Willey's paper, here reproduced in fig. 4). It appears to me beyond doubt that these "terminal gastric lobes" are the tentacle vessels, their lumen being lined with large, clear entoderm cells, as in *Tjalfiella* a.o. Ctenophores.

The supposed chloragogenous cells are the colloblasts of the thickened tentacle base (— which may, indeed, well recall chloragogenous cells —). Quite the same evidently is the explanation of the structure thus described by Korotneff (p. 244):

"Au einer Seite des Tentakels befindet sich eine feinkönige, vielleicht drüsige und sich stark färbende Bildung; die andere Seite besteht aus einem schwammigen Gewebe". (Comp. Fig. 3). — The "gastric gland" is thus described by Willey (p. 330) "As the median walls of the neighbouring terminal lobes fuse together on nearing the median canal which connects them with the stomach, the minute cellules which compose the greater part of the proliferations in question are replaced by long pyramidal cells which compose a compact gland, having a radiating structure due to the peculiar arrangement of the cells. I will call this a gastric gland, and hope that at some future date light may be thrown upon its nature". I think I am able to throw

the light wanted upon this peculiar structure; though no figure is given of it, the description seems to me to leave no doubt but that it is only the tentacle-base, the radiating structure being due to the arrangement of the muscles in the tentacle-root.

After this explanation of the two supposed peculiar structures of the gastrovascular system of *Ctenoplana*, it is evident that there is a very close similarity between *Ctenoplana* and *Tjalfiella*, also in the gastrovascular system, the only difference of greater importance being the absence of the sagittal lobes in *Tjalfiella*. (The absence of anastomoses between the peripheral canals in *Tjalfiella* can scarcely be a character of primary importance).

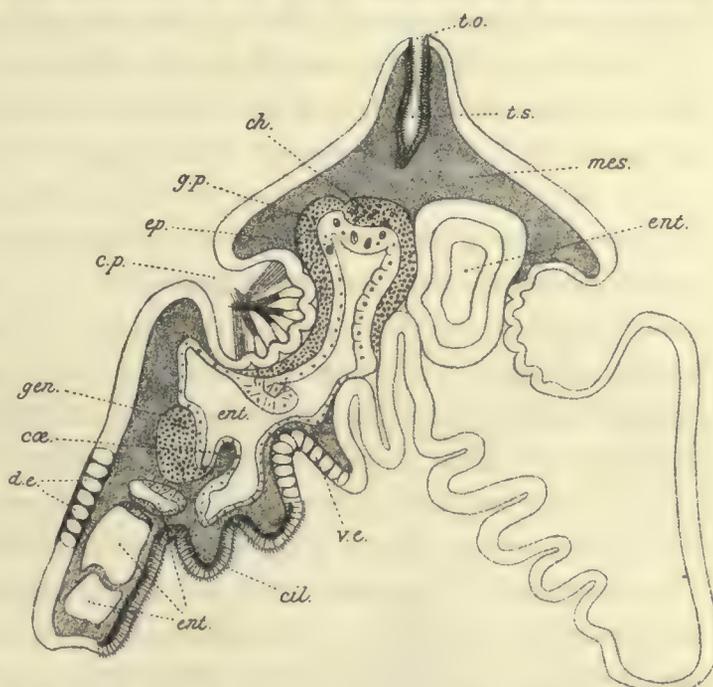


Fig. 4. Sagittal Section (somewhat oblique) through *Ctenoplana*, reproduced from Willey, Op. cit. Pl. 21, fig. 5. The letters are those of Willey. ca. genital caecum; ch. "chloragogenous cells" (= colloblasts); cil. ciliated epithelium of ventral surface; c.p. "Ctenophoral plate" (= costa), retracted; d.e. dorsal spongy vacuolar non-ciliated epithelium; ent. "coelenteron"; ep. digestive epithelium; gen. "genital proliferation on the wall of the genital caecum"; g.p. "gastric proliferation"; mes. mesenchymatous tissue; t.o. opening of tentacle sheath; t.s. tentacle sheath; v.e. non-ciliated glandular epithelium of the ventral surface.

It should still be mentioned, in connection with the gastrovascular system, that, according to Willey (p. 328), there is no excretory opening in *Ctenoplana*, while in *Tjalfiella* there is, at least, one. It would not seem improbable, however, if further researches will prove such openings to exist also in *Ctenoplana*.

A great difference would appear to exist between *Tjalfiella* and *Ctenoplana* in regard to the muscular system. Korotneff (p. 247) describes no less than three different muscular systems in *Ctenoplana*: 1. a dermal muscular system, 2. dorsoventral muscles and 3. a system of longitudinal muscles ("selbständige Muskulatur der Ruderplättchen und Tentakeln"). The first of these systems evidently corresponds to the usual Ctenophoran musculature, as appears from the description. The dorsoventral muscles would appear to correspond, partly at least, to the radially arranged muscles of other Ctenophores, though Willey may be partly right in maintaining (p. 328) that they are only the dorsoventral trabeculæ between the branches of the peripheral canals of the gastrovascular system. (These trabeculæ, however, will doubtless prove to contain muscles also). Much more remarkable is the longitudinal muscular system, which would appear to be something otherwise quite unknown among Ctenophores, as pointed out by Korotneff. There are two pairs of longitudinal muscles; "jedes Paar korrespondiert mit seiner Seite und dient dazu die betreffenden Rippenplättchen in Bewegung zu bringen, d. h. die letzten aus- und in die Taschen hineinzuziehen. Dabei aber verwächst jedes Paar, bevor es sich an die Plättchentasche anheftet, zu einem gemeinsamen Muskelbündel, welcher im Querschnitte ein mondähnliches Aussehen bekommt. Nach dem Anheften behält der Muskel dieselbe Form einige Zeit, um später sich wieder zu theilen, bis an die folgende Plättchentasche. In der Mitte zwischen zwei Taschen liegt jederseits ein Tentakel, dessen Muskulatur auch von den Längsmuskeln geliefert wird; dabei erfolgt dieselbe Verschmelzung von dem entsprechenden Muskelpaar, wie es für die Rippenplättchen soeben beschrieben ist". — Similarly Willey writes: "The muscles of the tentacles form part of the voluminous musculature, which, so far as I can make out, affects the retraction of the aboral sense-organ and of the ctenophoral plates, which can be completely drawn into the body". "At a short distance on either side of the median stomachal plane the sections in contracted specimens are almost entirely occupied by the convoluted bundles of muscles"

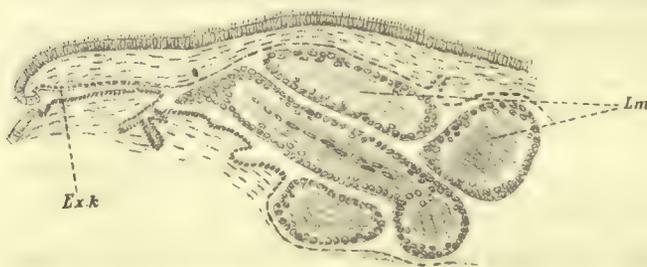


Fig. 5. Section through the supposed "excretory canal" (Ex. k.) and "longitudinal muscles" (Lm.) of *Ctenoplana*. (After Korotneff. Taf. VIII. Fig. 4).

(p. 328—29). From a closer inspection of the figures of this muscular system given by Korotneff I have become fully convinced that this remarkable, complicated structure is nothing but the tentacle, retracted and curled up within the tentacle sheath. In the figure 3 of Korotneff reproduced above (Fig. 3) a pair of such "muscles" are seen lying above the tentacle base, evidently within the tentacle sheath; still more convincing is the Fig. 4 of Korotneff, reproduced in Fig. 5; it is

quite beyond doubt that this figure represents a section of the tentacle curled up within the sheath, not an excretory canal and longitudinal muscles as Korotneff thinks. — That the "excretory canal" is really the opening of the tentacle sheath was observed by Willey; as seen from the above quoted passage he did not, however, understand the nature of the "longitudinal muscles", so that when

Abbott (Op. cit. p. 44) says: "As Willey suggests, there is no doubt that Korotneff was describing a section through the tentacles.... The muscular fibres of the tentacle stalk might well be taken for longitudinal muscles", Abbott has probably himself understood the whole matter; but Willey, who speaks of "the convoluted bundles of muscles" can scarcely have had the right view of it, since his convoluted "muscle bundles" can evidently be nothing but the curled-up tentacle. — The histological structure of the "longitudinal muscles" is also in full accordance with the supposition of their being the tentacle; the "nuclei" round the periphery of the bundles are the colloblasts, the "Fasern" the real muscles of the tentacle. What Korotneff regards as the tentacle is only its basal part.

Herewith I think that the true nature of this remarkable muscular system of *Ctenoplana* has been shown; there is then obviously no essential difference in regard to the muscular system between *Tjalfiella* and *Ctenoplana*, or between these forms and the typical Ctenophores.

While, thus, neither the gastrovascular nor the muscular system of the two forms differs very essentially and not at all so considerably as would appear from the description of *Ctenoplana*, the matter seems different with the genital organs.

The genital organs of *Ctenoplana* were not found by Korotneff; but Willey discovered in his specimens of *Ctenoplana Korotneffi* the male genital organs, four in number, situated between the subtentacular and the subsagittal costæ, at the outer end of the "terminal lobes" of the main gastrovascular system, before the beginning of the branching peripheral canals, as may be concluded, though Willey does not state this expressly. As points of resemblance with *Tjalfiella* may be noticed, their being single glands, not series of glands as in typical Ctenophores; further that their cavities (the "genital coeca" of Willey) are in direct connection with the gastrovascular system; also their position appears to be mainly the same in the two forms. That there are only four genital organs in *Ctenoplana*, eight in *Tjalfiella*, is, of course, a very conspicuous difference; but it is not unparalleled among the Ctenophores; thus in *Euchlora rubra* (Köll.) the genital products are developed only in the subtentacular vessels, while in *Euchlora filigera* Chun they are developed in all eight meridional vessels; this conspicuous difference is, however, not held by Chun as of more than specific value, and accordingly this difference between *Ctenoplana* and *Tjalfiella* cannot be taken to be of very great importance. More remarkable is the statement that in *Ctenoplana* the genital organs represent only the testes, a feature quite unparalleled among Ctenophores. Willey suggests (p. 329, Note) that *Ctenoplana* may be a protandric hermaphrodite, which might account for his being unable to find the female genital organs. I would think this suggestion much more probable than that the animal is unisexual. It would, however, be very desirable to have this question examined closely on fresh material; I confess that the figures of the genital organs given by Willey, especially Fig. 9 (reproduced here in Fig. 6), do not seem to me very convincing. In fact "the genital coecum" in this figure with its

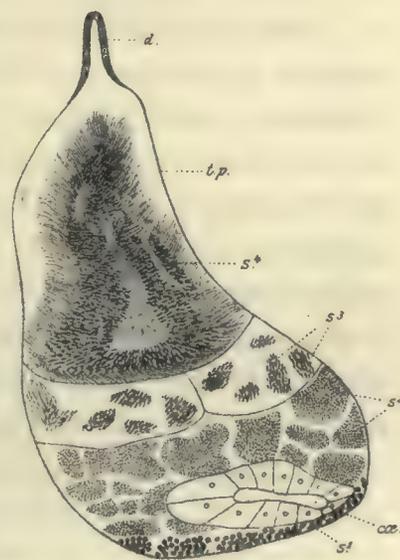


Fig. 6. Section through genital organ of *Ctenoplana* (reproduced, in  $\frac{3}{4}$  size, from Willey, Pl. 21, fig. 9). The letters are those of Willey. cæ. genital coecum. d. genital duct. s<sup>1</sup>—s<sup>4</sup>. different stages of the development of the spermatozoa. t. p. tunica propria.

lining of large cells recalls the prominent part of the ovary in *Tjalfiella*, shown e. g. in Pl. IV, Fig. 3, the left genital organ on the upper side of the figure. I do not venture, of course, to maintain that this "genital coecum" really represents the ovary, but I must maintain that it cannot be considered as definitely proved that the genital organs of *Ctenoplana* are unisexual, and for my own part I think it very probable that they will prove to agree completely with those of *Tjalfiella* in regard to the presence of both testis and ovary in the same organ.

Another point in the structure of the genital organs of *Ctenoplana* is that they are surrounded by a tunica propria. In *Tjalfiella* I have been unable to find anything which might be termed thus, and it is also totally unknown in other Ctenophores. As Willey's figures are, upon the whole, not very elaborate, I confess that I cannot feel quite convinced of the existence of this tunica propria; in any case, it seems to me very desirable to have this point made the object of further researches.

The most remarkable statement about the genital organs in *Ctenoplana* is, however, that they open to the exterior through one or more ducts each. Though the figures 7—9 of Willey's paper seem to show this to be really the case, I would recall the well known ectodermal invaginations over the genital organs in *Callianira*, and especially those of *Tjalfiella*. In these two cases it is beyond doubt that they have nothing especially to do with the genital organs. The fact that *Ctenoplana* is the only Ctenophore known which appears to have such genital ducts, which are thus a quite unparalleled feature among Ctenophores, makes it, at least, very desirable to have the matter reexamined. — If they are really genital ducts, it may perhaps be explained as a special adaptation of a structure homologous to the invagination over the genital organs existing in *Tjalfiella*.

Having thus shown that the apparent great differences in the gastrovascular system and muscular system between *Ctenoplana* and *Tjalfiella* are due to misconceptions in the description of *Ctenoplana*, and that there is likewise very probably fair accordance between their genital organs, at least in the main points, I think it evident that these two forms are indeed nearly related, the differences being mainly of adaptive nature, due to the different habits of the animals. The disappearance of the costæ, the rudimentary condition of the apical organ and the development of the peculiar chimneys in *Tjalfiella* are quite evidently adaptations to its sessile habit. Finally, the lacking of the sagittal lobes of the gastrovascular system in *Tjalfiella* is in accordance with the compressed shape of its body. Differences not to be thus explained are: the structure of the tentacles (unbranched in *Tjalfiella*, branched in *Ctenoplana*), the character of the peripheral canals of the gastrovascular system (anastomosing in *Ctenoplana*, simply branched in *Tjalfiella*), the existence of only four genital organs in *Ctenoplana*, while *Tjalfiella* has eight. Also the presence of genital ducts in *Ctenoplana*, if it proves to be a fact, is a feature not to be explained as an adaptation to the habit of animal. These differences are, however, not of primary importance. That *Ctenoplana* and *Tjalfiella* form two very well distinguished genera nobody, I think, will deny; but I think it equally evident that these two genera, in spite of their very different appearance, are nearly related and belong to the same family.

The anatomy of *Coeloplana* is not sufficiently known for a detailed comparison with *Tjalfiella*, but through Abbott's very important paper "The morphology of *Coeloplana*" (Zool. Jahrb. Abt. f. Anat.

24. 1907)<sup>1)</sup> several important additions have been made to our knowledge of this highly interesting Ctenophore.

There is no folding plane, the animal having acquired a quite Planarian-like habit. The gastro-vascular system affords some essential points of resemblance to *Tjalfiella*. The stomodæum contains in its outer part (the pharynx) a rich system of folds, the inner part (the oesophagus) being narrow and provided with long cilia as in *Tjalfiella* and *Ctenoplana*. From the infundibulum two unbranched tubes rise towards the dorsal side, both unbranched and both opening to the exterior; "as in the typical Ctenophores these arise in such a position that along the tentacular plane the lower one is to the right, the upper one to the left of that plane". In *Tjalfiella* (the grown animal) only one of the tubes has been definitely shown to open to the exterior, the opening lying nearly in the sagittal plane. In *Ctenoplana* no opening has been found. In any case they all agree in the tubes being simple, and I suppose future researches will show them to agree also as regards the opening of the tubes and the position of these openings.

As in *Tjalfiella* and *Ctenoplana* there is a branching peripheral canal system arising from the main branches of the gastrovascular system. As in *Ctenoplana* a pair of sagittal lobes proceed from the infundibulum, and these lobes give rise both to the peculiar dorsal respiratory tubes and to branching canals which anastomose with the other peripheral canals. The histological structure of the canals appears to be as in *Tjalfiella*, judging from Taf. 9, Fig. 14, of Abbott's memoir. — There thus seems to be accordance in the main points regarding the structure of the gastrovascular system in all the three genera, the non-existence of the sagittal lobes in *Tjalfiella* being probably an adaptation to its body shape, and thus of secondary importance; likewise the fact that the peripheral canals are anastomosing in *Ctenoplana* and *Coeloplana*, not anastomosing in *Tjalfiella* seems to me of minor importance. — (Regarding the origin of the sagittal lobes as explained by Abbott for *Coeloplana* (Op. cit. p. 64–65) I confess that I feel rather convinced of the incorrectness of this explanation, in which the pharyngeal vessels, not existing in *Tjalfiella*, play an important role; but to enter on this point here I find of little use, especially so long as the development of *Coeloplana* is completely unknown). Regarding the genital organs, which have not yet been observed, it may not be unreasonable to expect that they will prove to agree in the main points with those of the two other genera, and that their relation to the gastrovascular system in both *Coeloplana* and *Ctenoplana* will prove to be essentially as in *Tjalfiella*.

<sup>1)</sup> Abbott's "Preliminary Notes on *Coeloplana*", in Annot. Zoolog. Japonenses. IV. 1902. p. 103–108, contain some information not included in his final paper. Thus e. g. the following highly interesting statement (p. 105): "It not only crawls in any direction whatever but it frequently goes in more than one direction at once and the two halves, starting off for opposite sides . . ., often stretch the middle part to the breaking point". — Further the statement "where one is found, others are quite sure to be, and the situations in which they are found are sometimes strongly suggestive of multiplication by division, tho no evidence has been obtained yet as to that point" is worth recollecting in connection with the above remarks on the regeneration of *Tjalfiella*.

Concerning the tentacles it is stated that "the secondary branches are covered with batteries of nettle cells". In the final paper (p. 56) these branches are stated to be "covered with typical Ctenophoral adhesive cells (lassocells, colloblasts) that sometimes, when the tentacle is fully extended, appear to be arranged in groups or batteries" — no mention being made of the "nettle cells", which are evidently due only to a less precise terminology. This fact has, unfortunately, occasioned a separate generic name for the Japanese *Coeloplanas*. Schouteden in his paper "Les affinités des Ctenophores et Polyclades" (Ann. soc. Zool. et Malacol. de Belgique. XI. p. 1905. CXVII), establishes for these forms, mainly on the supposed presence of nematocysts, otherwise unknown among Ctenophores (the often quoted exception, *Euchlora rubra*, according to Samassa, Op. cit. p. 173, has not nematocysts) a separate genus, *Pseudocoeloplana*. This name, evidently, must be dropped again as a synonym only of *Coeloplana*.

It is thus seen that the genera *Tjalfiella*, *Ctenoplana* and *Coeloplana* agree in several important characters: the numerous folds of the pharyngeal cavity, the branching peripheral canals and the lacking of the meridional canals of the gastrovascular system, the unbranched excretory canals and (probably) the single genital organs. All these characters distinguish them sharply from all the rest of the Ctenophores. The rudimentary character or total loss of the costæ might not a priori be taken as a proof of the near relation between these forms, as it is evidently an adaptive character; but since it is in accordance with the other characters, it tends to accentuate the near relation between the three forms.

Much more different from *Tjalfiella* are the two other forms made known recently as transformed Ctenophores, viz. *Dogielia malayana* Pedaschenko and *Hydroctena Salenskii* Dawydoff. It will be desirable to give some remarks on these two forms also on the present occasion, in order to show whether they have possibly any relation to *Tjalfiella*.

*Dogielia* at the first sight recalls the gastrovascular system of a Cydippid, agreeing therewith in all main points, as the describer, Prof. Pedaschenko, has not failed to remark. (Comp. Fig. 7, reproducing Fig. 1. Tab. I, of Pedaschenko's memoir). The vertical plates at the ends of the vessels



Fig. 7. *Dogielia malayana*, ca.  $\frac{1}{40}$ . From Pedaschenko, who, however, places the animal in the inverted position.

("Körperäste") contain the genital organs, arranged in the usual way, the male genital organs along one side, the female organs along the other side; doubtless they represent the costæ of typical Ctenophores, as maintained by Pedaschenko. They do not, however, carry swimming plates; accordingly it is suggested that the animal moves only through the contraction of the muscular elements found in the jelly. These muscular elements are rather well developed, the author distinguishing both longitudinal and circular muscles. But the jelly itself is remarkably little developed, and still more remarkable is the ectoderm of the animal. "An der Gallertoberfläche ist weit nicht überall ein gesondertes Epithel zu sehen, sei es als eine ihr aufliegende sehr feine Membran oder als einzelne sehr

abgeplattete Zellen. An einigen Stellen findet man zwar an der Peripherie Zellen, jedoch hängen sie mit der Gallerte zusammen. Sie liegen in der Gallerte, wenn auch in ihrer oberflächlichsten Schicht und sind von ihr durch keine Demarkationslinie getrennt... Bald findet man sie auf Schnitten einzeln, bald mehrere auf einer geringen Strecke. Es sind aber auch grosse Strecken der Gallertoberfläche durchaus kernfrei. Diese Thatsachen führen mich zur Vermuthung dass die Gallerte ein Produkt des äusseren Epithels hauptsächlich ist, welches dabei im oralen Körperabschnitte zum grössten Theil aufgebraucht wird". (p. 22—23). — This condition of the ectoderm is, indeed, exceedingly remarkable. The two photographic figures of sections (Tab. II, Fig. 4 and Tab. III, Fig. 6) accompanying Pedaschenko's memoir decidedly give the impression that the animal has no ectoderm at all; only some slight remains of jelly are found in the more protected spots. Instead of this paradox — an animal without ectoderm — the true explanation of *Dogielia malayana* seems to me to be that it is really the gastrovascular system alone of a Cydippid, the whole jelly and ectoderm (and

the swimming plates) having been lost through the handling of the animal in the net. The more remarkable circumstance here is not the disappearance of the jelly and the skin, but the fact that the gastrovascular system has remained in connection as a sort of "skeleton"; though remarkable enough it is, however, much less improbable than the existence of an animal without skin.

The *Dogielia* thus explained is no longer one of the most aberrant Ctenophores made known; it very probably belongs to the Cydippids. Possibly it will prove to represent a separate genus within this group, so that the name *Dogielia* may perhaps be retained (— the relation of the interradial vessels to the tentacular sheaths seems somewhat unusual —); but the order "Actenæ" established for it by Peda-schenko, in any case must be dropped. To *Tjalfiella* it has evidently no near relation.

While there is no doubt that the *Dogielia* is really a Ctenophore, or at least part of a Ctenophore, the Ctenophoran nature of the *Hydroctena Salenskii*<sup>1)</sup> is very problematic. In the presence of an apical sense-organ it certainly recalls in some degree the Ctenophores; but the fact that there are two otoliths is a prominent difference from the Ctenophores, which have always only one otolith. Another fact recalling the Ctenophores is the existence of only two, aboral, retractile tentacles, lodged within well developed tentacle sheaths. They possess a strong muscular core as do the tentacles of the Ctenophores, in decided contrast to the Hydromedusæ. But here the resemblances stop; and the differences are certainly much more important. There is a well developed velum and manubrium but no costæ; no colloblasts are found, but cnidoblasts. The whole histological structure is quite different from that of Ctenophores. I fully agree with A. G. Mayer (*Medusæ of the World*. II. 1910. p. 459) that the resemblances between *Hydroctena* and Ctenophores are "merely parallelisms, none of which indicate a genetic relationship with Ctenophoræ". *Hydroctena* is a Narcomedusa, resembling the genus *Solmundella* in all respects, excepting its apical sense-organ, peculiar structure of the tentacles and the absence of marginal sense-organs, the resemblance being rendered closer by the recent discovery by Woltereck<sup>2)</sup> that the larva of *Solmundella* has a ciliated, apical pole-plate. Thus the only feature remaining exceptional for a Narcomedusa is the muscular core of the tentacles. — The parallelism sought by Dawydoff between *Hydroctena* and *Ctenoplana* in the structure of the excretory vessels is accordingly, at most, an analogy, viz. in case these vessels really do not open to the exterior in *Ctenoplana*, as is maintained by both Korotneff and Willey, but which can, by no means, be regarded as an established fact. — In his note "Systematische Stellung von *Hydroctena salenskii*" (*Zool. Anzeiger*. XXVII. Nr. 18. 1904. p. 569) K. C. Schneider maintains *Hydroctena* to be a true Ctenophore; the undeniable resemblances to the Hydromedusæ are regarded as "Konvergenzercheinungen". Schneider "homologisiert ohne weiteres die sog. Subumbrella samt Velum mit dem

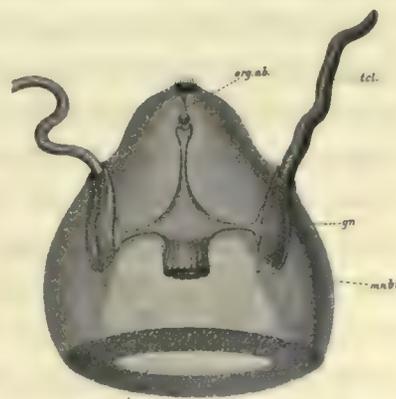


Fig. 8. *Hydroctena Salenskii* (after Dawydoff). gn. tentacle sheath; mnbr. manubrium; org. ab. apical organ; tcl. tentacle; vl. velum.

<sup>1)</sup> C. Dawydoff. *Hydroctena Salenskii*, (Étude morphologique sur un nouveau Coelentéré pelagique. *Mém. Ac. Imp. d. Sci. St. Pétersbourg*. 8. Sér. XIV. Nr. 9. 1904.

<sup>2)</sup> R. Woltereck: Bemerkungen zur Entwicklung der Narcomedusen und Siphonophoren. *Verh. d. deutsch. Zool. Gesellsch.* 1905. p. 115.

Ctenophorenschlund", because their histological structure is not in accordance with that generally found in the Hydromedusæ, while they more resemble what obtains in Ctenophores. The resemblances to Hydromedusæ are thus restricted to "die velumartige Einkrümmung des unteren Körperrandes, der ausserdem durch etwas reichlichere Muskelentwicklung und entsprechende Verdickung des Nervensystems zu einem inneren Ringnerven ausgezeichnet ist, und ferner auf die Anwesenheit eines kurzen sogenannten Magenstiels" — which are regarded as of no importance. "Subumbrella, Velum und äusserer Velumrand sind in ihrer bekannten Ausbildung, als Bewegungsorgan und Sinneszentrum, für die Medusen so wesentliche Charaktere, dass deren vollkommener<sup>1)</sup> Mangel bei *Hydroctena* ohne weiteres jede phylogenetische Ableitung der letzteren von den Hydromedusen ablehnen lässt. Es kann sich nur um eine Anähnelung, eine Konvergenzerscheinung (Pseudovelum), handeln". *Hydroctena* is thus "einzig und allein an die Ctenophoren, in keiner Weise aber an die Cnidarier, anzuschliessen. Sie stellt eine merkwürdige, zweifellos jugendliche, daher besonders schwierig zu beurteilende aberrante Ctenophore, ähnlich *Coelo-* und *Ctenoplana*, dar, für die man eine besondere Ordnung wird aufstellen müssen, ohne dass aber die Notwendigkeit erwächst, auf Grund des Mangels von Ruderplättchen eine ganz neue Klasse einzurichten. Für die Erkenntnis der verwandtschaftlichen Beziehungen der Ctenophoren zu den Turbellarien erscheint *Hydroctena* zurzeit bedeutungslos".

It does not appear to me necessary to discuss Schneider's arguments for the Ctenophoran nature of *Hydroctena*; his whole reasoning appears rather too much influenced by the preconceived idea that *Hydroctena* should be a Ctenophore. I would only point out that it seems, in the present state of knowledge, unjustifiable to lay so much stress on some points in the histological structure as is done here, while at the same time another important histological fact (the cnidoblasts) is regarded as of no importance. Schneider has, in fact, produced no additional evidence for the Ctenophoran character of *Hydroctena*. — To *Tjalfiella* it has no relation whatever, and no more to *Ctenoplana* or *Coeloplana*. The same applies to the *Ctenaria ctenophora* of Haeckel; this latter form, however, need not be discussed here anew.

One form must still be mentioned, which has been maintained as a relative of *Coeloplana* and *Ctenoplana*, viz. the *Heteroplana Newtoni* of Willey (On *Heteroplana*, a new genus of Planarians. Quart. Journ. Micr. Sc. N. S. 40. 1898. p. 203). I confess that I am quite unable to see in the description of this animal given by Willey the slightest reason for associating it with *Coeloplana* and *Ctenoplana*. The anatomy is very incompletely known; it is stated, however, that there is a cerebral ganglion and a large number of marginal eyes. On the other hand, there are no tentacles and no apical organ; there are some branching intestinal canals and the mouth is placed in the middle of the length of the body, otherwise nothing is known about the gastric system. "Through the whole body, and especially prominent in the anterior and posterior regions, is a close reticulum formed by the anastomosis of fine moss-like tubules which probably constitute the genital apparatus". — That there is here not the slightest indication of a Ctenophoran nature I think will be universally agreed. In spite of the anatomical structure, however, Willey states that "on account of its remarkable relations of symmetry I (he) should place this genus in the order Archiplanoidea, established by me (Willey) for the reception of *Coeloplana* and *Ctenoplana*, because ... it would appear to be more nearly related to a biradial than to a bilateral type like the Planarians. This seems to follow from a

<sup>1)</sup> I am responsible for the emphasis here.

consideration of such a form as *Ctenoplana*". Willey claims to have proved conclusively that the tentacle axis of *Ctenoplana* corresponds to the longitudinal axis of the flat-worms. But *Ctenoplana*, when creeping, has not one of the tentacles directed forwards, it creeps with one side foremost, viz. after the sagittal axis. *Heteroplana* moves "in a somewhat one-sided fashion, and the number of marginal eyes on the forwardly directed lobe is more than twice that on the corresponding lobe on the opposed side of the frontal region". *Heteroplana* "is almost directly derivable from a biradial type of the same grade of organisation as *Ctenoplana*. But in *Heteroplana* the direction of locomotion (creeping) has been definitely localized, and the side (namely the right side) to which the preference has been given has for that very reason predominated over the other (left) side. In other words, in *Heteroplana* there is hypertrophy of the right side and atrophy of the left".

Instead of entering on a discussion of Willey's profound reflections on the relations of symmetry I will only give a reproduction of the sketch of *Heteroplana* given by Willey (Fig. 9). Is not the only reasonable explanation of the figure this, that it represents a Planarian which has, in some way or other, lost the left half of its body and is now about to regenerate it? The fact that Willey did not find more than one specimen is certainly not against such an explanation. Herewith I think we may safely leave this animal out of the discussion.

*Gastrodes parasiticum* Korotneff there is no reason to discuss here; its affinities to other Ctenophores being quite obscure; I think it would be hard to find any special relation between it and *Tjalfiella*. The question about the systematic affinities of *Gastrodes* can upon the whole scarcely be solved before its development has been studied.

Having thus critically examined the different forms of real or supposed, aberrant Ctenophora and pointed out how far they show structural resemblances to *Tjalfiella*, the question remains whether perhaps a nearer relation can be shown to exist between any of the groups of typical Ctenophores and *Tjalfiella*. This question must, I think, be answered in the affirmative.

Taking first the Beroids, it must be conceded that the well known proliferations from their meridional canals in some way remind one of the branching peripheral canals in *Tjalfiella* (and *Coeloplana* and *Ctenoplana*). Further the peculiar development of the polar plates of *Beroë*<sup>1)</sup> recalls the condition found in *Ctenoplana*, as pointed out by Willey (*Ctenoplana* p. 332). However, the presence of tentacles in *Tjalfiella* shows beyond doubt that it has no real relations to the Beroids; it is needless then to point out the other characters in which they differ from each other. The resemblance in the branching canals of the gastrovascular system are merely a superficial analogy, as is also the resemblance between the polar plates of *Ctenoplana* and *Beroë*.

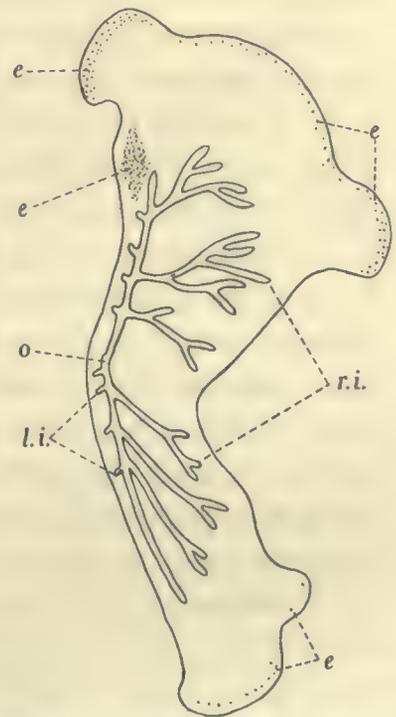


Fig. 9. *Heteroplana Newtoni* Willey. (From Willey. Op. cit.) e. eyes; l. i. "left rudimentary intestinal diverticula"; o. position of mouth on ventral surface; r. i. right intestinal diverticula.

<sup>1)</sup> Perhaps not found in all Beroids; it remains uncertain whether the species of the genus *Pandora* have the polar plates thus developed — in any case *P. mitrata* Moser appears to have simple polar plates. Moser, *Japanische Ctenophoren*. *Abh. Bayr. Akad. d. Wiss. I. Suppl. 4.* 1908. p. 35. (*Beitr. z. Naturgesch. Ostasiens*, herausg. v. Doflein).

While it would scarcely be possible to point out other resemblances between *Tjalfiella* and the Cestidæ than those necessarily following from the fact that both are Ctenophores, the case is different with the Lobatæ (— including the Ganeshidæ —). On comparing the young *Tjalfiella* in the Cydippid-stage with a young Lobate, we find a conspicuous resemblance in the oral lobes, though they are not quite so early developed in the Lobatæ (in any case in *Eucharis multicornis* and *Bolina infundibulum*, the only two forms whose development has been studied more closely as yet). Further the shape of the aboral side of the young *Tjalfiella* resembles that of the young Lobatæ, and in both the aboral organ is more or less sunken. These points of resemblance can certainly not be done away with as being merely cases of analogy, the more so as they occur in the young stages only; they might well be regarded as indicating a real relation between these forms. On the other hand the very great difference in the gastrovascular system shows that the affinity cannot be so very close; the two groups may have originated from a common source, but they have then developed further along very different lines. Bourne, to be sure, thinks that the peripheral canals of *Ctenoplana* may be compared with the canals of the lobes of Lobatæ, which would then also apply to *Tjalfiella* (Op. cit. p. 17). With this, however, I can not agree. The canals of the lobes of Lobatæ represent only prolongations from the meridional canals, which reach their highest perfection in this order; in *Tjalfiella* and the two allied forms, *Ctenoplana* and *Coeloplana*, there are no meridional canals at all, the peripheral branching canal being outgrowths directly from the large interradial lobes. —

It remains to examine the possible relations between *Tjalfiella* and the Cydippidæ. The fact of the young *Tjalfiella* being a typical Cydippid undoubtedly shows that its ancestors, like those of all the other tentaculate Ctenophores, were Cydippids, and more especially forms like the Mertensiidæ, having the tentacle axis longer than the sagittal axis. This suggestion is confirmed by the most interesting deep-sea Ctenophore recently described by Moser<sup>1)</sup> under the name of *Mertensia Chuni*. This remarkable form has a pair of oral lobes recalling very much those of the young *Tjalfiella*, being in the same position and very much of the same form. The polar plates are small. Further it has a rich net of branching canals from the pharyngeal vessels, and also from the meridional vessels fine proliferations arise; finally the inner wall of the pharynx is closely covered with hollow, partly ramified "Zotten"<sup>2)</sup>. Though the branching canals can scarcely be directly compared with those of *Tjalfiella*, it is evident that this form among all the typical Ctenophores made

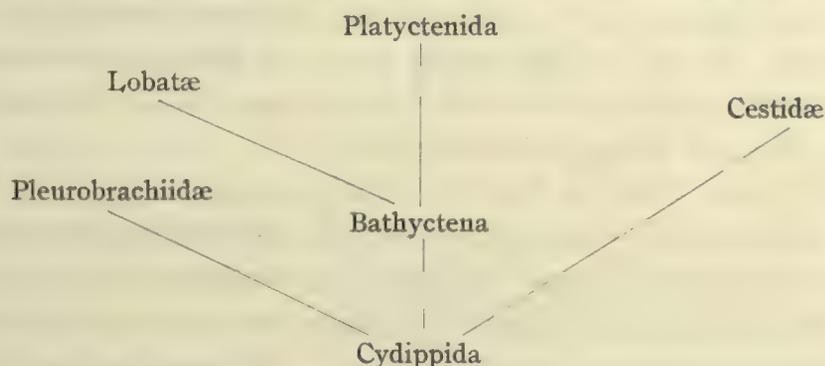
<sup>1)</sup> Die Ctenophoren der deutschen Südpolar-Exped. Deutsche Südpolar-Exp. 1901—1903. XI. Bd. Zoologie Bd. III. 1909. p. 126—130.

<sup>2)</sup> It seems very remarkable that Dr. Moser has referred this peculiar deep-sea form to the genus *Mertensia*. The only species of the genus *Mertensia* hitherto known, *M. ovum* (Fabr.), has certainly never been fully described, or adequately figured (the beautiful figure given by Torrey in his Ctenophores of the San Diego Region (Univ. Calif. Publ. Zool. Vol. 2, II. 1904. Pl. I. Fig. 1) under the name of *Mertensia ovum* is certainly not that species, as pointed out by Moser (Op. cit. p. 126)) but so much is known, however, that it has no oral lobes and no proliferations from the pharyngeal vessels (perhaps there are such on the meridional vessels; — comp. the remarks on *M. ovum* in Part II of this memoir); further the tentacle sheaths do not open orally as in the deep-sea form — and still other differences might be pointed out. That the deep-sea form represents a very distinctly characterized genus seems to me beyond doubt. I may propose the name **Bathyctena** n. g. I do not even feel certain that it can remain in the family Mertensiidæ, but on a discussion of this question I shall not enter. By the way, I may further be permitted to make a little remark on account of the description of *M. Chuni*. Dr. Moser suggests that the thick pharynx walls and the reduction of the lumen of the pharynx, the strong lips which are able to close the mouth tightly, the narrow tentacle sheaths and the position of their very small openings at the oral, instead of at the aboral pole as is otherwise the rule, are special adaptations to the life in the deep-sea which "befähigen . . . den kolossalen Druck des Wassers und dessen Eindringen in ihre Körperhöhlen einem grösseren Widerstand zu leisten". — This suggestion can scarcely be right — the idea that a jellylike animal could upon the whole make any resistance to the pressure of the water in a depth of ca. 3000 m seems not very probable, even if the jelly is ever so resistant.

known as yet is the one showing most resemblance to *Tjalfiella*; it would then not seem unreasonable to suggest, that *Tjalfiella* and its nearest relations *Ctenoplana* and *Coeloplana*, come from the Cydippids through forms like *Bathyctena* (*Mertensia*) *Chuni*. And probably the Lobatae are also derived from such forms.

While the three aberrant Ctenophores thus seem to come from the Cydippids, they are, of course, so much specialized that it is impossible to unite them with this order. They evidently form an order for themselves, the *Platyctenida*. Whether they should also be united into one family, cannot be decided at present. It seems evident that *Ctenoplana* and *Tjalfiella* are the most nearly related of the three, while *Coeloplana* would seem to stand more apart; thus far there would be no difficulty in adopting the two families: *Ctenoplanidæ* and *Coeloplanidæ* established by Willey (On *Ctenoplana*; p. 341), *Tjalfiella* then evidently belonging to the former family. But so long as our knowledge of the anatomy of *Ctenoplana* and *Coeloplana* is so insufficient, and their development even quite unknown, the question of the families must be left undecided.

The probable interrelations of the tentaculate Ctenophores may be graphically expressed as follows:



## E. Phylogeny.

The demonstration that the *Platyctenida* are the most specialized of all Ctenophores, instead of the most primitive, has a very important bearing on the much discussed question about the relation between Ctenophores and other groups of animals, especially the Planarians.

It seems unnecessary to enter on a discussion of the theory of the affinities between Ctenophores and Echinoderms, as first expressed by L. Agassiz<sup>1)</sup> and later on carried out in more detail by A. Agassiz<sup>2)</sup> and Metschnikoff<sup>3)</sup>. I may refer to the remarks of Chun (Monograph, p. 245—256). So far as I know, this theory<sup>4)</sup> has not been adopted since then by anybody. Likewise there

<sup>1)</sup> L. Agassiz. Contributions to the Natural History of the Acalephæ of North America. Part II. On the Beroid Medusæ of the shores of Massachusetts, in their perfect state of development. 1849. (p. 366).

<sup>2)</sup> A. Agassiz. North American Acalephæ. (Ill. Cat. Mus. Comp. Zool. II. 1865. p. 11—12); Embryology of the Ctenophoræ (Mem. Amer. Acad. X. 1874, p. 384—387); Embryology of the Starfish (Mem. Mus. Comp. Zool. V. 1877. p. 83).

<sup>3)</sup> E. Metschnikoff. Studien über die Entwicklung der Siphonophoren und Medusen. (Zeitchr. f. wiss. Zool. XXIV. 1874. p. 70—77).

<sup>4)</sup> The main point of this theory is the homologizing of the gastrovascular canals of Ctenophores with the ambulacral vessels of Echinoderms. The configuration of the entoderm with the protruding, but not yet separated off, enterocoel vesicles in the young Echinoderm larva is found to resemble that of the entoderm + the (ectodermal) pharynx in the young Ctenophore, this resemblance forming the main proof of the theory. The Ctenophores are regarded as "prophetic animals" which explain "the separation of the digestive cavity into two distinct parts". "The separation of a sort of alimentary canal, in Ctenophoræ, from the rest of the digestive apparatus, exactly corresponding to what exists in Echinoderm larvæ; . . . although in the adult starfish, or Sea-urchin, or Ophiuran, there is no apparent connection between the ambulacral and the digestive system, yet in the young larvæ we can see that this connection exists, the water system being formed by diverticula from the digestive cavity". (A. Agassiz: North American Acalephæ. p. 11—12).

is no reason to enter here on a discussion of the affinities of the Ctenophores to the Coelenterates and their possible derivation from either the Hydromedusæ (especially the Cladonemidæ), the Narcomedusæ or the Actiniæ, nor to discuss the curious view held by K. Cam. Schneider<sup>1)</sup> that the Ctenophores are related to the Porifera, founded mainly on the fact that both possess "ein echtes Mesoderm, das in engster genetischer Beziehung zum Ektoderm steht" (Op. cit. p. 3a7). It is the theory of the affinities between Ctenophores and Polyclads, which concerns us here, on account of the light which *Tjalffella* throws on *Ctenoplana* and *Coeloplana*, those two forms which have played so important a role in the discussions of this question. It will be necessary to give a short account of this theory and its history.

The first to express the view of a nearer relation between Ctenophores and Planarians was Selenka, who in his "Zoologische Studien. II. Zur Entwicklungsgeschichte der Seeplanarien" (1881)<sup>2)</sup> points out several important parallels in the embryological development of the two groups; he concludes therefrom (p. 31) "dass die marinen Polycladen oder überhaupt die Turbellarien aus ctenophoren-ähnlichen Wesen hervorgegangen seien, indem letztere aus der schwimmenden in die kriechende Bewegung übergangen". He suggests that possibly among the Rhabdocoela transitional forms may be found; whether *Coeloplana* (which had then quite recently been described by Kowalevsky) is such a transitional form "lässt sich vorläufig nicht beurtheilen".

Soon after the same theory of the close affinity between Ctenophores and Polyclads was set forth by A. Lang, independently of Selenka, in his paper "Der Bau von *Gunda segmentata* und die Verwandtschaft der Plathelminthen mit Coelenteraten und Hirudineen"<sup>3)</sup>, the conclusion being "mit einem Worte, dass sie (the Polyclads) kriechende Ctenophoren sind" (p. 215). — In his great Monograph "Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzenden Meeresabschnitte" (p. 645—666)<sup>4)</sup> Lang again discusses this theory in a very detailed manner, altering his views from the first paper only in some minor points. An elaborate comparison of the morphology and embryology of the two groups is given as support of the theory, which appears directly confirmed through the existence of an intermediate form like *Coeloplana*. — The theory is also discussed by Chun<sup>5)</sup>, who does not, however, take a definitive position towards it.

Starting with the axial relations of the body of Polyclads and Ctenophores, Lang points out that the main axis, which is vertical in Ctenophores, has been bent in Polyclads<sup>6)</sup>. In the embryos of Polyclads it is vertical as in Ctenophores, the cerebral ganglion (apical organ) lying vertically over the mouth; behind the ganglion is a vertical branch from the gastrovascular system representing an excretory vessel. In the course of development the ganglion moves forward, entraining the excretory vessel, which develops into the anterior branch of the gastrovascular system. Thus the position of the brain below this branch is naturally explained. The important fact that in young stages there is over the excretory vessel "eine Lücke im Ektoderm, durch welche das darunter liegende Entoderm

<sup>1)</sup> K. Camillo Schneider: Histologische Mittheilungen. I. Die Urogenitalzellen der Ctenophoren. Z. wiss. Zool. 76. 1904.

<sup>2)</sup> See also his note "Zur Entwicklungsgeschichte der Seeplanarien" in Biol. Centralblatt. I. 1881. p. 229—239.

<sup>3)</sup> Mitth. a. d. Zool. Stat. Neapel. III. 1882. p. 187—250. Taf. XII—XIV.

<sup>4)</sup> Fauna u. Flora d. Golfes v. Neapel. Monographie XI. 1884.

<sup>5)</sup> C. Chun. Die Verwandtschaftsbeziehungen zwischen Würmern und Coelenteraten. Biol. Centralblatt. II. 1882. p. 5—16.

<sup>6)</sup> In the treatise on *Gunda segmentata* Lang homologized the longitudinal axis of the Polyclad body with the main axis of Ctenophores, the original position of the mouth in Polyclads thus being taken to be at the posterior end of the body, as is nearly the case in *Cestoplana*. This view is corrected in the Monograph of the Polyclads (p. 646).

freigelegt wird" (p. 652) is a confirmation of the homology between this vessel and the excretory vessel of Ctenophores. Anything corresponding to the other excretory vessel of Ctenophores is not found in the grown Polyclads, (where it would have to be sought for below the brain) but Lang has found an indication of it in the early stages of development. The two accompanying diagrams, copied from Lang show these features clearly.

The main axis given, the other plans are easily found. The excretory vessels lying always in the sagittal plane, it is accordingly the longitudinal axis of the Polyclads which corresponds to the sagittal axis of Ctenophores, the transverse axis of the latter being then also transverse in Polyclads. From this then naturally follows that the nuchal tentacles of some primitive Polyclads (Planoceridæ) are regarded as homologues of the tentacles of Ctenophores, being placed in the transverse plan.

The gastrovascular system of Polyclads and Ctenophores corresponds in several important points. There is in both a large ectodermal pharynx ("Pharyngealtasche" in Polyclads); to the "krausenförmiger Pharynx" in the more primitive, the "rüssel" in more specialized Polyclads, correspond the "Magenwülste" of Cteno-

phores; the fact that in the primitive Polyclads the pharynx is glandular is in accordance herewith. — The pharynx opens in the Polyclads into a "Hauptdarm", of entodermal origin, corresponding exactly to the infundibulum of Ctenophores. From this proceeds in both groups the main stems of the gastrovascular system; in the Polyclads there may be many paired stems, but in the more primitive forms they are few in number, though never less than four pairs. In *Coeloplana* the gastrovascular canals are branching and anastomosing as in Polyclads. In none of the groups is an anal opening found. The histological structure is mainly alike in both; also in Polyclads there is a line of thickened epithelium in the branches of the gastrovascular canals. Finally both agree in the important physiological fact, that the food is absorbed in the pharynx.

The genital organs are of entodermal origin in both<sup>1)</sup> and both are hermaphrodite. In the Polyclads the testes are situated on the ventral side, the ovaries on the dorsal side of the gastrovascular canals, while in Ctenophores they lie respectively in the right and left side of the meridional canals. Important differences are found, however, in regard to the genital organs of the two groups; while the sexual products of Ctenophores are ejected through the gastrovascular system, there are in

<sup>1)</sup> In the paper on *Gunda segmentata* Lang does not doubt the entodermal origin of the genital organs; in the Monograph he is in doubt about this point.

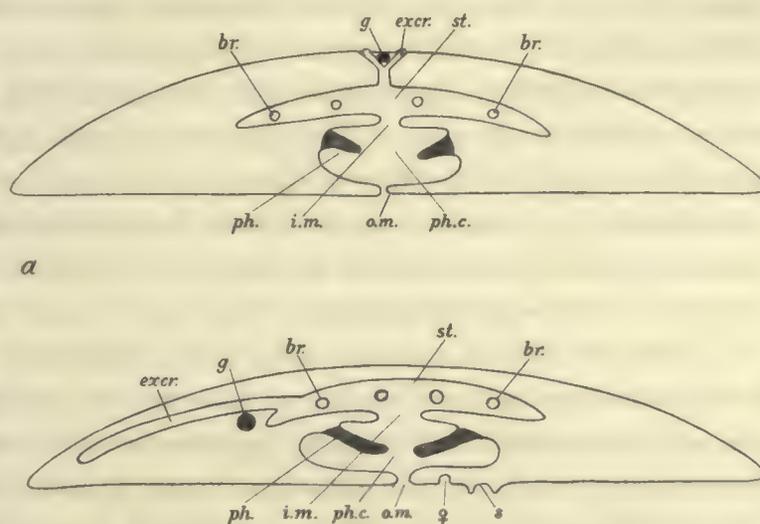


Fig. 10. Diagrammatic longitudinal section of a hypothetical ancestral form (a) and of a primitive form of Polyclads (*Anonymus*) (b); the former corresponds very nearly to *Coeloplana*. br. places, where the branching gastrovascular canals proceed from the stomach; excr. excretory vessel, in fig. b. the anterior branch of the gastrovascular system; g. ganglion (apical organ); i. m. inner mouth-opening; o. m. outer mouth-opening; ph. pharyngeal folds; ph. c. pharyngeal cavity; s sucking disk; st. stomach (infundibulum). ♀ female genital opening. (Slightly modified from Lang. Monogr. p. 102).

the Polyclads separate genital ducts, and even copulatory organs are found. These are, however, of a very peculiar primitive type, as might be expected in forms where they are acquired as new organs.

The nervous system affords some difficulties for the comparison on account of its doubtful character in Ctenophores. It seems, however, beyond doubt that the cerebral ganglion of Polyclads corresponds to the apical organ of Ctenophores, even if the latter is not directly to be regarded as being a nervous apparatus. It develops as an ectodermal thickening in Polyclads and in a central position; it is only later on in the development that it is separated from the ectoderm, contemporaneously moving forwards; in the more primitive forms, e. g. *Planocera*, it remains rather remote from the anterior end of the body. According to Chun the eight main nerves of Polyclads are the homologues of the eight ciliated ridges of Ctenophores. It is a consequence of the forward wandering of the brain that the two posterior nerves become the main longitudinal nerves. The otolith, so highly characteristic of Ctenophores, has no homologue in Polyclads; in some Rhabdocoela there is, however, an otolith above the cerebral ganglion.

The histological structure shows rather conspicuous conformity. The epidermis has essentially the same structure in both groups; to the very characteristic granular cells of Ctenophores the rhabdite cells of Polyclads are evidently homologous. On the other hand there is nothing in Polyclads corresponding exactly to the colloblasts, which is easily understood from the fact that the tentacles, when at all present, in Polyclads have completely lost the function as prehensile organs. — The Polyclads are certainly ciliated over the whole surface, which is not the case in typical Ctenophores; but here *Coeloplana* forms the connecting link, being ciliated as the Polyclads<sup>1</sup>. — The muscles are of the same type in both groups, branched at the ends; that the musculature is considerably more developed in Polyclads than in Ctenophores is only what should be expected from their different mode of life.

Concerning the movement of the Polyclads the highly interesting fact is pointed out that the more primitive forms (*Anonymus*, *Planocera*) do not always proceed with the anterior end forwards; they may also move sideways — in good accordance with their supposed origin from radiate ancestors. With this also corresponds the fact that in the primitive forms eyes are found all round the margin of the body.

In the development there is conspicuous accordance in the cleavage and gastrula-formation (epiboly); in both groups the gastrula-mouth develops into the definite mouth, the opposite pole becoming the sensory pole. On the other hand the mesoderm appears to develop in a different way in the two groups. In the larvæ finally there is a peculiar feature, not without importance for the comparison of the two groups, viz. that on the processes of the Polyclad-larvæ the cilia are arranged in transverse rows, the cilia of each row moving contemporaneously — recalling the combs of the Ctenophores. Lang hints at the possibility of homologizing the eight processes of the Polyclad-larvæ with the costæ of Ctenophores, pointing out, however, as a main difficulty that they are not in the same relative position to the axes of the body as the latter.

With full right Lang states (Monogr. p. 665) that this hypothesis "scheint bei dem gegenwärtigen Stand unserer morphologischen Kenntnisse diejenige zu sein, die den Ursprung der Bilaterien

<sup>1</sup>) According to the recent researches of Abbott *Coeloplana* is only ciliated on the ventral side.

aus Strahlthieren — ein Postulat der neueren Morphologie — in der am meisten befriedigenden Weise erklärt, indem sie sich ebenso sehr auf den Thatsachen der vergleichenden Anatomie und Ontogenie, als auf biologische und physiologische Erwägungen stützt, und nicht eine unabsehbare Reihe unbekannter hypothetischer Zwischenformen... erfordert". On the other hand he does not conceal the fact that there are as yet considerable difficulties to the theory. These are mainly the excretory system and the development of the mesoderm; also the homology of the nervous system is somewhat less satisfactory. — Regarding the excretory system Chun has suggested that the rosettes of Ctenophores may possibly be the homologues of the excretory cells of Polyclads; Lang, however, is not very inclined to think this correct, as he has never found the flame-cells lying in the epithelium of the gastrovascular system in Polyclads (— though this is found in *Gunda segmentata* —), and the rosettes are not connected with ducts opening to the exterior. For the mesoderm Lang gives some theoretical considerations (Monogr. p. 660) which might seem to reconcile the discrepancies on this point, but he does not himself seem very satisfied therewith. The solution of these questions must be left for future researches.

Not less important would be the close study of *Coeloplana*, known at that time only from Kowalevsky's short notice, which gives no information about its nervous system, musculature, genital or excretory organs. Its branching and anastomosing gastrovascular canals correspond with those of the Polyclads, but there is no mention of a pharynx; if this is really lacking, "so entfernt sich *Coeloplana* in diesem Punkte ebenso sehr von den Polycladen wie von den Ctenophoren" (p. 648). "Ein unabweisbares physiologisches Postulat ist ferner das, dass bei *Coeloplana* die Anpassung an die kriechende Lebensweise eine grosse Veränderung in der Anordnung der Muskulatur und damit des motorischen Nervensystems nach sich gezogen habe. Da die Rippengefässe fehlen, müssen ferner auch die Geschlechtsorgane anders angeordnet sein als bei den Ctenophoren" (p. 650). It would be equally interesting to learn, whether perhaps copulatory organs have been formed.

It did not last long before this Selenka-Lang's theory, which really looks so very attractive, got important support from other sides. In 1885 Metschnikoff published his researches "Über die Gastrulation und Mesodermbildung der Ctenophoren"<sup>1)</sup>, in which he shows that the mesoderm is not formed by cells wandering in from the ectoderm, as was previously supposed, but as a separate formation, being divided off from the oral pole of the (entodermal) macromeres and transferred during the further development to the aboral pole, where it develops into four radiating thickenings. Thus the formation of the mesoderm is found to be essentially in accordance in the two groups.

Already the next year another splendid confirmation of the theory appeared in the discovery of *Ctenoplana*, through Korotneff. The phylogenetic importance of this remarkable new form is fully appreciated by Korotneff, who thus summarizes his view of *Ctenoplana* and *Coeloplana*: they are "zwei Übergangsformen, welche an verschiedenen Seiten der Scheidelinie zwischen den Ctenophoren und Planarien stehen: die *Ctenoplana* neigt sich mehr den Ctenophoren, die *Coeloplana* den Planarien, obschon die beiden Formen zu derselben Zeit sehr nahe verwandt sind"<sup>2)</sup>. The relations of *Ctenoplana* to the Ctenophores on the one side, and to the Polyclads on the other, are in the main these: The flattened body in which a dorsal and a ventral side are differentiated (as in *Coeloplana*),

<sup>1)</sup> E. Metschnikoff. Vergleichend embryologische Studien. Zeitschr. f. wiss. Zool. Bd. 42. p. 648—656.

<sup>2)</sup> Zeitschr. f. wiss. Zool. Bd. 43. p. 249—250.

is a Planarian character, as is also the general ciliation (— the existence of ciliation on the dorsal side being, however, denied later by Willey —); the presence of costæ, on the other hand, is decidedly a Ctenophoran character. The gastrovascular system is in accordance with that of the Polyclads (and *Coeloplana*) through the branching and anastomosing of the peripheral canals; on the other hand, it differs from both Ctenophores and Polyclads in lacking a pharynx — Korotneff having quite misunderstood the structure of the pharynx, (comp. p. 25). Also in the musculature he finds a great difference from both Ctenophores and Planarians — “aber es wird kaum bestreitbar sein, dass die Muskulatur am meisten den ausseren Einflüssen widerstehen und deswegen schreibe ich (Korotneff) den Eigenthümlichkeiten dieses Systems bei der Ctenoplana keine besondere Wichtigkeit (genetisch) zu”. — It is curious to see, how Korotneff tries to remove the apparent great difficulty arising from the remarkable muscular system, which he has described; the difficulty is certainly better removed by the demonstration that his “muscular system” rests on a complete misconception, (comp. p. 28—29).

In spite of these misconceptions and though no information is given of so important a structure as the genital organs the view of Korotneff that *Ctenoplana* represents, as well as *Coeloplana*, a transitional form between Ctenophores and Polyclads appears well enough founded. Further support for Lang's theory is given by Samassa in his paper “Zur Histologie der Ctenophoren” p. 235—238. He there points out that the histology of Ctenophores and Polyclads is even more in accordance than supposed by Lang; also the homologizing of the nervous system in the two groups he finds fully justified. He further maintains that the Polyclads are decidedly the most primitive of the Turbellarians against L. v. Graff, who in his work “Die Organisation der Turbellaria Acoela” 1891 (p. 49—52) expresses the opinion, against “die unbewiesene Ansicht dass die Turbellarien (mit den Polycladen als Wurzel) von den Ctenophoren abstammen”, that the Acoela are the most primitive of Turbellarians, the Acoela being derived from such undifferentiated forms as *Trichoplax*. — Also later on (in Bronn. Klassen u. Ordn. d. Tierreichs. Bd. IV. Abt. I. C. Turbellarien. 1904—1908) v. Graff decidedly maintains the same opinion, with the exception that *Trichoplax* is not here regarded as an ancestral form of the Turbellarians.

The theory of the derivation of Polyclads from Ctenophores thus apparently rested on a much firmer basis, than when it was worked out by Lang; for a rather long time it remained nearly<sup>1)</sup> undisputed, until in 1896 Willey turned the whole theory upside down<sup>2)</sup>.

In discussing the theory Willey first points out that the axial relations between Ctenophores and Polyclads, as represented by Lang, rest on a misconception. “Ctenoplana unequivocally proves, as I (Willey) think, that the tentacle plane or funnel-plane of it and the Ctenophores corresponds to the sagittal plane of bilateral animals, and not to the transverse plane” (p. 332). Chun, who was at first in doubt as to the criterion by which to homologize the planes of Ctenophores with those of the Bilateria, came through the discovery of the peculiar *Thoë paradoxa*, in which at first only one (“directive”) tentacle is developed, to the conviction that the tentacle axis is homologous to the long axis of Bilateria. Through regarding *Ctenoplana* Willey comes to the same conviction. “In Cteno-

<sup>1)</sup> Comp. p. 46, the remarks on Korschelt & Heider's (Lehrbuch d. vergleichenden Entwicklungsgesch. d. wirbellosen Thiere) and Hatschek's (Lehrbuch d. Zoologie) position towards the theory.

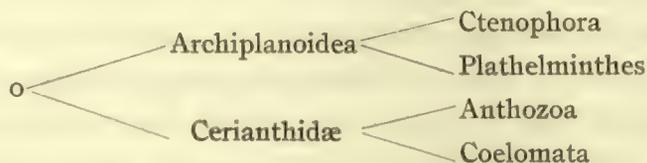
<sup>2)</sup> A. Willey. On Ctenoplana. (Quart. Journ. Micr. Sc. N. S. 39).

plana the tentacle axis and the stomachal axis are equipolar; but if we consider about which axis the paired structures are situated, we are simply forced to acknowledge that the plane of the tentacles corresponds to the sagittal plane — in other words that the tentacle axis of *Ctenoplana* and *Ctenophora* correspond to the longitudinal axis of *Bilateralia*". — Lang's theory "rests in the first instance on the assumption that the pinnate tentacles of *Ctenophores* and *Coeloplana* are homologous with the sensory tentacles of *Polyclades*"; but it must be emphasized that "under no circumstances and from no point of view are the tentacles of *Ctenoplana* bilaterally disposed, but they are biradially disposed". It is true that when *Ctenoplana* creeps, its tentacles look as if they were transversely disposed "and it may seem difficult to imagine an ancestor of bilateral animals with an unpaired tentacle in front and an unpaired tentacle behind. But the point is that we have got to imagine this, because in the animals with which we are dealing there are no such relations as anterior and posterior, right and left" (p. 335). Willey accordingly finds it much more probable that the nuchal tentacles of *Polyclades* are the homologues of the "sensory tentacles" of *Ctenoplana*, which are again homologous to the polar fields of typical *Ctenophores*.

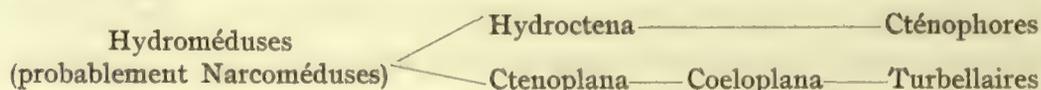
The researches of Willey lead him to the conclusion that *Ctenoplana* must be regarded as "an ancestral form, and not, as some Zoologists seem to suppose, a highly modified creeping *Ctenophore*... That the *Planarians* and *Polyclades* in particular have close affinities with the *Ctenophora* there can be no doubt, but it is very much open to question, whether the former are derived from the latter. The view that the *Polyclades* are so derived seems a reversal of the natural order of events, which point to the littoral fauna as the origin both of the pelagic and the abyssal fauna". Considering the bilateral symmetry of *Polyclads*, and especially their well developed nervous system, they can scarcely be imagined to be derived directly from amorphous forms (like *Trichoplax*) "but rather from animals which possibly, like *Ctenoplana*, possessed a biradial symmetry. *Ctenoplana* approaches more nearly to a condition of bilateral symmetry than the *Ctenophores* do, in that it possesses very clearly differentiated dorsal and ventral surfaces. And this is exactly what we should expect to find in the littoral or sublittoral ancestor of such purely pelagic forms as the *Ctenophora*, the pelagic habit, as is well known, often tending to produce a more or less radial symmetry. On the other hand, a biradial form, like *Ctenoplana*, possesses the potentiality of assuming a strictly littoral life, in which the ventral surface is the permanent locomotor surface, such an existence leading to a condition of bilateral symmetry, according to well-understood physiological principles". "The ctenophoral plates must have put in their appearance for the first time in some form or other; and although it is at present beyond the limits of our knowledge to explain how they arose, yet it is not right to conclude that the ctenophoral plates of *Ctenoplana* are degenerate or reduced structures merely because they are smaller than the ctenophoral rows of the *Ctenophora*. It is a groundless assumption to say that *Coeloplana* and *Ctenoplana* are modified creeping *Ctenophores*. *Ctenoplana* is an expert crawler, it is expert at hanging on to the surface film of water, and it is indeed an expert swimmer. Everything it attempts it does well in the old primeval fashion, and there is nothing degenerate about it" (p. 338).

*Coeloplana* and *Ctenoplana* thus are neither *Ctenophores* nor *Planarians*, but represent a separate order, the *Archiplanoidea*, equivalent to the orders *Turbellaria*, *Trematoda* etc. From the *Archiplanoidea* are derived both *Ctenophores* and *Plathelminthes*. In the same way the *Anthozoa* and

Coelomata are thought to have originated from the Cerianthidæ, the result thus being the diphyletic origin of Bilateralia, as expressed in the following diagram.



Mainly in accordance with the views of Willey (though without knowing — at least without quoting — his paper on *Ctenoplana*) E. v. Beneden<sup>1)</sup> expresses the opinion that the Ctenophora are ‘des Planariens adaptées à la vie pélagique’. He does not otherwise enter on a discussion of this problem. — Likewise Dawydoff in his description of *Hydroctena Salenskii*<sup>2)</sup> does not enter on a discussion of the relations between Planarians and Ctenophores, stating only that they are “indubitables”, resting on fundamental embryological characters; but he gives the following graphic representation of the Ctenophoran affinities:



In 1902 James Fr. Abbott gave a preliminary note<sup>3)</sup> on *Coeloplana*, but it was not before 1907 that the full report was published<sup>4)</sup>, in which we get at length some very much wanted information about the morphology of this highly important form. Unfortunately the specimens found by Abbott (at Japan) were altogether immature, so that the morphology of the genital organs and the development still remain unknown. The main result of Abbott's researches is that *Coeloplana* can by no means be regarded as a primitive form (— and according to Willey it should be the most primitive of all —). “The weight of morphological evidence bears out the conclusion that *Coeloplana* is a very highly specialized Ctenophore, derived from the Cydippida”. (Op. cit. p. 62). As “vestigial structures reminiscent of a previous pelagic habit” are especially pointed out: the otolith and the rosettes (the latter being apparently superfluous structures on account of the ramifying gastrovascular canals and of the very small amount of parenchyma, the nutritious fluid being thus directly transported to all parts of the body, while in typical Ctenophores the rosettes are thought to serve as carriers of the nutritious fluid into the thick layer of parenchyma). In view of the assertion of Lang, quoted above (p. 41), that it is “ein unabweisbares physiologisches Postulat ... dass bei *Coeloplana* die Anpassung an die kriechende Lebensweise eine grosse Veränderung in der Anordnung der Muskulatur und damit des motorischen Nervensystems nach sich gezogen habe”, it is interesting to note that Abbott states the muscular system to be much more developed than in typical Ctenophores; unfortunately he does not give a more detailed description of the musculature, so that it cannot be seen in which features it differs from that of other Ctenophores. The fact that a basement membrane is developed as a sort of skeletal support for the muscles as in the Polyclads — and as is also found in

<sup>1)</sup> Les Anthozoaires de la “Plankton-Expedition”. *Ergebn. d. Plankton-Exped. d. Humboldt-Stiftung.* II. K. e. 1898. p. 182.

<sup>2)</sup> *Mém. Acad. imp. St. Pétersbourg.* 8. Sér. 14. 1904.

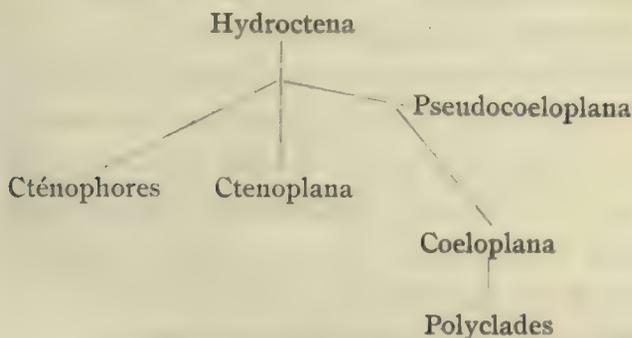
<sup>3)</sup> James Francis Abbott. Preliminary Notes on *Coeloplana*. *Annot. Zoolog. Japonenses.* IV. p. 103—108.

<sup>4)</sup> James Francis Abbott. The Morphology of *Coeloplana*. *Zool. Jahrb. Abt. f. Anat.* Bd. 24. 1907. p. 41—70. Taf. 8—10.

*Ctenoplana* — is in good accordance herewith; such a membrane is not developed in typical Ctenophores. Also the nervous system appears to be specially developed, as expected by Lang; indeed Abbott has found four distinct ganglia developed round the otolith (Op. cit. p. 61. Fig. B); also in *Ctenoplana* similar ganglia are described by Korotneff.

While Abbott is thus opposed to the view of Willey that *Coeloplana* and *Ctenoplana* are primitive forms, he does not, however, accept Lang's theory either. Besides the erroneous homologizing of the axes pointed out by Willey, he finds another important error in Lang's theory, viz. the homologizing of the excretory tubes of *Coeloplana* with the anterior branch of the gastrovascular system in Polyclads (Op. cit. p. 62). Otherwise he does not express any definite opinion regarding the phylogenetic questions, stating only that until the development of *Coeloplana* has been worked out "the true position of *Coeloplana* and its relationship with other groups cannot be certainly decided". (p. 66).

A series of papers discussing the systematic position of the Ctenophora, their relation to the Polyclads a. o., by Kemna, Lameere and Schouteden<sup>1)</sup> may briefly be mentioned here. They are mainly speculative, adducing no new facts. Kemna is inclined to adopt Lang's theory, though laying stress on the Polyclad-larvæ, the processes of the "Müller's larva" being compared with the lobes and auricles of the Lobatae. — Lameere in his first paper maintains the opinion, also held by v. Beneden, that the Ctenophores are Polyclads which have adopted a pelagic mode of life; in the second paper he is of opinion that the discovery of *Hydroctena* has fixed the position of Ctenophores as "Hydrozoaires", not as pelagic Turbellarians; they are "le dernier terme de l'évolution des Narcoméduses", and the Polyclads have nothing to do with them. — Schouteden, who is equally convinced of *Hydroctena* representing the ancestral form of Ctenophores, gives the present diagram of the relations of the Ctenophores (— that *Pseudocoeloplana* rests on a misunderstanding has been pointed out above, p. 31 —).



Finally, in 1911 B. Hatschek in his pamphlet "Das neue zoologische System" (p. 8—9) gives the important statement that Metschnikoff's description of the formation of the mesoderm in Ctenophores is "durchaus irrig". The whole mesoderm "entsteht nur von der Umgebung des Mundes durch Absonderung einzelner Ectodermzellgruppen", in accordance with the observations of Kowalevsky<sup>2)</sup>. He does not enter specially on the theory of the derivation of the Polyclads from the Ctenophora; judging, however, from the genealogical tree which he gives (p. 18), he evidently accepts the theory, (as he did previously in his "Lehrbuch d. Zoologie"), the "Ectero-coelia" (among which the Proscolecida, including the Platodes, rank as the lowest group) being derived from the "Ctenozoa".

<sup>1)</sup> A. d. Kemna. Sur les rapports entre Cténaires et Polyclades. Ann. Soc. R. Zool. et Malacol. de Belgique. 38. 1903. p. LXXIX—LXXXVII.

Aug. Lameere. L'Origine des Cténophores. Ibid. p. LXXXVII—XCVI. — Cténophores et Polyclades. Ibid. 40. 1905. p. CXXVIII—CXXX.

H. Schouteden. Les affinités des Cténophores et Polyclades. Ibid. 40. 1905. p. CXVIII—CXXVII.

<sup>2)</sup> A. Kowalevsky. Entwicklungsgeschichte der Rippenquallen. Mém. Acad. St. Pétersbourg. 7. Sér. X. 1866.

In concluding this historical review of the theory the position adopted towards it in the greater hand-books may still be mentioned. Korschelt & Heider (Lehrbuch d. vergl. Entwicklungsgesch. d. wirbellosen Thiere. I. 1890) regard the Ctenophores as representing "einen nach einseitiger Richtung selbständig ausgebildeten Seitenast des Stammbaumes, der wohl kaum zu einer directen Weiterbildung höherer Thierformen die Grundlage abgab" (p. 101). *Ctenoplana* and *Coeloplana* are not regarded as transitional forms between Ctenophores and Polyclads, their accordances with the latter resting "auf blosser Analogie"; they may show "wie sich der Uebergang freischwimmender Radiärthiere in kriechende bilaterale Formen vollzogen haben könnte" (p. 115). It is conceded that the development of Ctenophores and Polyclads agrees in several important points; also the peculiar movements of the cilia on the processes of Polyclad-larvæ is thought of importance. But "die vielfach vorgenommene Vergleichung der Organsysteme von Ctenophoren und Turbellarien, zumal diejenige des Gastrovascularapparats... ist wenig befriedigend"... "Selbst wenn sie aus einer einheitlichen Wurzel hervorgehen, haben (sie) sich so stark verändert, dass die Vergleiche nur allgemeinerer Natur sein können (p. 115).

Hatschek (Lehrbuch d. Zoologie. Lief. III. 1891. p. 319—332), while acknowledging "den Grundgedanken dieser Hypothese in seiner grossen Tragweite", objects to several of the homologies maintained by Lang, and specially to the derivation of the dorsoventral axis from the primary axis of Ctenophores. *Coeloplana* and *Ctenoplana* are regarded as aberrant Ctenophores, not as transitional forms to the Polyclads.

G. C. Bourne (in Ray Lankester's "Treatise on Zoology"; II. 1900; Ctenophora) maintains that "in point of fact we have no evidence as to whether *Ctenoplana* or *Coeloplana* are primitive or derived forms; such evidence can only be furnished by their development and larval history". "In the present state of our knowledge it cannot be said that the existence of *Ctenoplana* and *Coeloplana* gives any satisfactory evidence of the relationship of Platyhelminthes to Ctenophora, still less of the descent of the former group from the latter. The most that can be said is that *Ctenoplana* and *Coeloplana* afford an interesting suggestion as to how the Polyclada might conceivably have been derived from a Ctenophore-like ancestor". More weight is ascribed to the embryological points of resemblances between the two groups. "The conclusion is that the Turbellaria, the Nemertines, and the Ctenophora are descended from a common ancestor which is most nearly represented by the larva of *Stylochus*". (p. 19). — W. B. Benham, who has treated the Platyhelminths in Ray Lankester's "Treatise on Zoology" IV. 1901, does not enter on a discussion of the relations between Polyclads and Ctenophores, referring to Bourne in this connection. He only states (p. 3) that "no doubt the ancestral form was more or less closely connected with the Coelentera by means of animals of which we know nothing". It thus appears evident that he is not in favour of Lang's theory. It is worth mentioning in this connection that the Rhabdozoa are regarded as the most primitive of Turbellaria, though the nervous system is "much more highly differentiated than in the Polycladida" (p. 12); the Acoela, regarded by v. Graff as the most primitive, are stated to "present every evidence, anatomically as well as embryologically, of degeneration". — F. W. Gamble, in his record of the Flatworms and Mesozoa in "The Cambridge Natural History" II. 1901, p. 28, states that "the work of the last decade has neither proved nor disproved Lang's suggestion that the Ctenophores and Polyclads have been derived from common ancestors".

Finally Delage & Hérouard (Traité de Zoologie concrète. II. 2. Les Coelentérés. 1901. p. 760—765) regard the problem as “une question phylogénétique sans doute insoluble”. “Les ressemblances de *Ctenoplana* et de *Coeloplana* avec les Turbellariés semblent surtout adaptatives et sont probablement secondaires”. They are Ctenophorans adapted to a creeping mode of life, which have acquired structural characters in accordance with this mode of life, characters which approach them to the Planarians “uniquement parce que celles-ci sont aussi des animaux rampants... On s'accorde à dire que ces caractères adaptatifs n'ont pas de valeur phylogénétique, en sorte qu'il ne reste guère en faveur des affinités planariennes des Cténaires que les caractères embryogéniques reconnus par Selenka”. (p. 761).

The once so victorious theory of Selenka and Lang is thus far from being generally accepted by the more recent authors. While everybody agrees that there are undoubted affinities between Polyclads and Ctenophores, the direct phylogenetic relation between the two groups is not accepted. As Abbott states (Op. cit. p. 62) “it is not probable that any morphologist accepts Lang's hypothesis nowadays”.

We may now discuss the objections raised against the theory and see whether the researches on *Tjalfiella* may not perhaps throw some light on the question.

Let us regard firstly the assertion of Willey that *Ctenoplana* and *Coeloplana* are very primitive forms, instead of very specialized as otherwise generally assumed, this being of fundamental importance for the whole question about the relations between Ctenophores and Polyclads. — The reason adduced by Willey for this assertion is, indeed, not very convincing. It is taken as granted that the “natural order of events” is, that the pelagic (and abyssal) fauna has originated from the littoral fauna. “*Ctenoplana* approaches more nearly to a condition of bilateral symmetry than the Ctenophores do, in that it possesses very clearly differentiated dorsal and ventral surfaces. And this is exactly what we should expect to find in the littoral or sublittoral ancestors of such purely pelagic forms as the Ctenophora, the pelagic habit, as is well known, often tending to produce a more or less radial symmetry”. This is, in fact, all that is said in favour of the primitive character of *Ctenoplana*. No support of this assertion is sought for in its anatomical characters. The evident difficulty lying in the existence of apparently reduced costæ in *Ctenoplana* is met with the assertion that “the ctenophoral plates must have put in their appearance for the first time in some form or other”, and there is no reason to regard them as reduced structures merely because they are smaller than in other Ctenophores.

Against this rather too light reasoning Abbott's assertion that *Coeloplana* (and *Ctenoplana*) is a very specialized form, resting on real, anatomical, facts (the presence of the otolith and of rosettes comp. above p. 44) weighs very heavily. Also several other facts from the anatomy might be pointed out against Willey; thus, e. g., it seems not very easily understood how the structure of the genital organs in Ctenophores could have developed from those of *Ctenoplana*, as they are described by Willey. The definitive answer to the question of the primitive or specialized character of *Ctenoplana* and *Coeloplana* must be given by the development, which, unfortunately, still remains unknown. However, we may safely draw some conclusions as to this point from the development of *Tjalfiella*. It has been shown rather conclusively, I think, that *Tjalfiella* and *Ctenoplana* are nearly related. The suggestion seems then quite justified that the young of *Ctenoplana* will likewise prove to be a

typical Cydippid, the more so as the costæ of the grown *Ctenoplana* are quite similar to those of the young *Tjalfiella*. — Finally, it should be emphasized that, even if it is the natural order of events that the pelagic fauna has originated from littoral organisms, it is quite possible that some pelagic forms may again have adopted a littoral, non-pelagic habit.

All evidence is thus against the view of Willey that *Ctenoplana* and *Coeloplana* are primitive forms. They, together with *Tjalfiella*, must be regarded as highly specialized forms, derived from typical, free-swimming forms, of the Mertensiid type. Willey's eloquent apology for *Ctenoplana* not being a degenerate form cannot alter this conclusion. It may perhaps be a consolation that the three forms are not maintained as "degenerate", but, on the contrary, as highly specialized forms.

With this it seems definitely settled that the Platyctenida ("Archiplanoidea") are not the ancestors of the pelagic Ctenophores. We may then return to the original theory: the Turbellarians being derived from the Ctenophores. — But here another essential question must be taken into consideration, viz. which group represents the most primitive of the Turbellarians, the Polyclads as maintained by Lang, or the Acoela, as maintained by v. Graff.

In his work on the Turbellaria in "Bronn. Klassen u. Ordnungen d. Thier-Reichs" v. Graff expresses the view that the nervous system of the Acoela (3—6 pairs of equally developed longitudinal stems, arranged radially round the main axis) represents a primitive condition, which disappears more or less completely in the coelate Turbellarians with the adaptation to the creeping habit. "Diese Configuration des Nervensystems weist auf die Abstammung von radiären Formen hin und festigt die Anschauung, dass die Acölen die den Turbellarienahnen nächststehende Gruppe repräsentiren. Sie macht die Annahme einer Knickung der Hauptaxe im Sinne Lang's, sowie einer secundären Verschiebung des Gehirns an das heutige Vorderende der Turbellarien überflüssig und lässt als formbildende Factoren, welche die Herausbildung der streng bilateralen cölaten Turbellarien aus radiären Ahnen erklären sollen, nur eine Verschiebung des Mundes nach der Bauchseite bei der Anpassung an die kriechende Lebensweise nothwendig erscheinen" (p. 1974). "Die heutigen Acölen leite ich (v. Graff) von drehrunden, langgestreckten Formen ab, mit einer nahe dem Vorderende senkrecht zur Hauptaxe stehenden Gehirnplatte, deren Mitte durch die ihr anliegende Statocyste bezeichnet war..." (p. 1975). *Trichoplax* is thus dropped as an ancestor of the Turbellaria, — very appropriately, it being shortly afterwards shown by Krumbach<sup>1)</sup> to be only the planula of *Eleutheria*, probably abnormally altered through aquarium conditions.

But von Graff does not indicate from which kind of Coelenterate he thinks the Acoela have been derived. The ancestor he depicts does not correspond to any type of radiate animals known. It seems evident that he is at a loss to point out any radiate type from which the Acoela could with any probability be derived. — Further, when he sees an advantage in his theory in the fact, that it makes the bending of the main axis superfluous, which according to Lang's theory must have taken place, he appears to have overlooked that this bending has been shown by Lang to take place ontogenetically in the development of the Polyclads; in the same way he seems to have overlooked that the original position of the mouth in the Polyclads is in the middle of the underside, not at the posterior end of the body, no wandering of the mouth being necessary to produce the bilateral

<sup>1)</sup> Th. Krumbach. *Trichoplax*, die umgewandelte Planula einer Meduse. Zool. Anz. 31. 1907. p. 450—454.

type<sup>1</sup>). Regarding the nervous system it does not appear that it is in any way more primitive than in the Polyclads. But, above all, it seems rather impossible to reconcile the peculiar character of the entoderm in the Acoela with their derivation from a radiate type, the Coelenterates being decidedly not characterized by the lacking of a gastral cavity. v. Graff maintains that "die Thatsachen der vergleichenden Anatomie und der Entwicklungsgeschichte bieten... gar keine Handhabe dafür die Acölie als Rückbildungserscheinung oder als Folge einer secundären Erwerbung zu bezeichnen" (p. 1932), and it is maintained that during the development no trace of a gastral cavity appears. The researches of Pereyaslawzewa<sup>2</sup>) are against this statement; comp. the section of a "gastrula" of *Aphanostoma diversicolor* Ørst., represented in Taf. IV, Fig. 32, of Graff's work, where a very distinct cavity is shown between the large entodermal cells. According to v. Graff (p. 1970) these researches are, however, not very trustworthy. But even if there is really no trace of a gastral cavity in the embryonal development of the Acoela, general morphology decidedly supports the view that the acelous condition is a secondary character, as also the derivation from the Coelenterates maintained by v. Graff seems irreconcilable with the view that the acelous condition is a primitive character. I may also recall the fact that in the Polyclads the entoderm generally forms no gastral cavity from the beginning (sterrogastrula).

Upon the whole I must say that I cannot find any real support for v. Graff's theory. I cannot doubt the correctness of Lang's view that the Polyclads are the most primitive of the Turbellarians.

Having disposed of these two main questions, we may proceed to discuss the special objections raised against the theory of the derivation of the Polyclads from the Ctenophora.

The homologies of the axes of the Polyclad and Ctenophoran body as represented by Lang (comp. p. 38—39) are maintained by Willey to be quite erroneous; he thinks, that he has demonstrated conclusively, that the long axis of the Polyclad body corresponds to [the transverse (tentacular) axis of Ctenophores, not to the sagittal axis of the latter, as Lang maintains. Accordingly the nuchal tentacles of Polyclads are not homologous with the tentacles of Ctenophores, — upon which assumption Lang's theory "rests in the first instance", his interpretation of the axial relations being "framed in accordance with this assumption"<sup>3</sup>) — but with the sensory tentacles of *Ctenoplana*, which undoubtedly represent the polar fields. The tentacles of the Ctenophores, on the other hand, "belong to the same category of structures as the proboscis of Nemertines and of certain Rhabdocele Planarians" (Willey Op. cit. p. 335). As argument for this interpretation of the axial relations Willey adduces the peculiar *Thoë paradoxa* of Chun, in which, at first, only one "directive" tentacle is developed, the other appearing later. In *Ctenoplana* the tentacular axis is certainly equipolar, both tentacles being equally developed, so that we cannot from them conclude which side is the anterior; "but if we consider about which axis the paired structures are situated, we are simply forced to acknowledge that the plane of the tentacles corresponds to the sagittal plane — in other words, that the tentacle axis of *Ctenoplana* and Ctenophora corresponds to the longitudinal axis of Bilateralia". (Willey, Op. cit.

<sup>1</sup>) Also Hatschek (Lehrbuch d. Zool. p. 319—320) assumes a wandering of the mouth and pharynx from the lower end of the body to the middle of the ventral side.

<sup>2</sup>) S. Pereyaslawzewa. Monographie des Turbellariés de la mer noire. Schr. d. neuruss. Naturf. Ges. Odessa. XVII. 1892.

<sup>3</sup>) This is scarcely a fair statement. Lang's theory rests on an elaborate comparison of the anatomy and development of Polyclads and Ctenophores, and the tentacles are not even used "in the first instance" for determining the axial homologies. (Comp. Lang's Monograph, p. 646).

p. 334). No other arguments are produced for this interpretation of the axes in the paper quoted, but later on further support of it is found in the shape of *Heteroplana*. (On *Heteroplana*, a new genus of Planarians. Qu. Journ. of Micr. Sc. N. S. 40. 1898. p. 203).

Concerning the remarkable *Thoë paradoxa* (Chun. Monograph. p. 120—122) I would decidedly join the opinion of Claus<sup>1)</sup> that “offenbar handelt es sich in jenem Ausnahmefall lediglich um eine in Folge heterochroner Entwicklung, eventuell Rückbildung und Ausfall eines Tentakels, eingetretene Symmetriestörung, wie sie in ähnlichen Fällen auch an den Randfäden von Medusen nicht selten beobachtet wird. Aus derselben ergibt sich aber keineswegs die Schlussfolgerung, die der Trichterebene zugehörige Achse als ungleichpolig zu betrachten und deshalb die Trichterebene im Gegensatze zur Magenebene als sagittale zu orientiren und noch weniger die Berechtigung, durch diese den Leib in eine rechte und linke Hälfte zu zerlegen”. If it were a general feature in Ctenophorans that the tentacles were unequally developed, or even one of them totally reduced, the more developed tentacle pointing forwards during the locomotion of the animal, being thus really a “directive” tentacle, that would be a valuable argument for regarding the tentacular axis of Ctenophores as homologous with the sagittal axis of bilateral animals. But the *Thoë* is quite an exceptional case, from which such a view, contradictory to the general morphology and physiology of the whole group, cannot get reasonable support. — As for *Heteroplana* it seems to me quite unnecessary to enter on a discussion of it, the more so as it is not quite easy to understand Willey’s exposition of its significance for the question about the axial relations. It may be sufficient to state that *Heteroplana* is evidently only a mutilated Polyclad (Comp. p. 35).

Willey’s other argument, that the paired structures of *Ctenoplana* are arranged about the tentacular axis, I cannot regard as very forcible either — though the same arrangement is also found in *Tjalfiella*. It seems hard to understand, how the organs could be otherwise arranged, given the elongation of the animal in the tentacular axis and the shortening of the sagittal axis. If the elongation had taken place in the sagittal axis, the tentacular axis being shortened, the organs would necessarily be arranged about the sagittal axis. Examples of this are afforded by the Cestidæ and, less markedly, the Lobatæ. Thus this argument for regarding the tentacular axis of Ctenophores as homologous to the sagittal axis of Bilateralia seems rather valueless. That the tentacular axis is originally the longer of the two horizontal axes of the Ctenophores, as appears evident from the fact that in the young of all the tentaculate forms, even of the Cestidæ, this axis is the longer, does not any more lead to the conclusion that this axis is really the sagittal, the length of an axis being in itself of no great morphological value. Especially, it is impossible to regard the greater length of the tentacular axis as a proof for its being really the sagittal axis, when this interpretation is in contradiction with other morphological facts of primary importance, as is the case here.

Abbott (Morphology of *Coeloplana*, p. 62), on accepting Willey’s interpretation of the axes, points out as a supposed further error of Lang “that he homologized the excretory tubes leading upwards from the infundibulum . . . with the anterior branch of the gastric system of the Polyclads”. It seems that Abbott has overlooked the embryological evidence for this homology (Comp. p. 38)<sup>2)</sup>. In

<sup>1)</sup> C. Claus. Über *Deiopea kaloktenota* Chun als Ctenophore der Adria. Arb. a. d. Zool. Inst. Wien VII. 1886. p. 12.

<sup>2)</sup> Hatschek (Lehrbuch d. Zoologie p. 319) states that “die Entwicklungsgeschichte der Polycladen aufs klarste gegen die Lang’sche Auffassung spricht; der äquatoriale Wimperkranz der Polycladenlarven entspricht nicht dem Körperrande,

fact, I think, this evidence rather conclusive, so it will scarcely be necessary to take up this question for discussion here, the more so as Abbott does not give any reason for his assertion. On the other hand, the excretory tubes afford an argument of great value in the discussion of the homologies of the axes. As is well known, the infundibular canal in typical Ctenophores divides below the apical organ into two branches, excretory canals, which again branch before opening outwards. (Only one of these branches opens outwards, the other remaining a closed ampulla). The two first branches always lie in the sagittal ("stomachal") plane; in *Tjalfiella* and *Coeloplana* the two, simple excretory canals proceed directly from the infundibulum, the infundibular canal having been reduced on account of the shortening of the longitudinal (main) axis; they lie in the sagittal plane, in conformity with what obtains in other Ctenophores. That the same will prove to be the case in *Ctenoplana* can scarcely be doubted. — It is then evident that if we can point out a homologue to the excretory vessels of Ctenophores in the Polyclads, we will have a sure argument for which axis is homologous to the sagittal axis of Ctenophores — and this is fortunately the case. Only one tube is developed in the Polyclads, being simple as in *Tjalfiella*, and having only in the early stages an indication of an outward opening; of the other tube slight traces may be distinguished. Now, this excretory tube is situated behind the cerebral ganglion (apical organ); in the later development it prolongs forward together with the moving forwards of the brain, and develops into the unpaired anterior branch of the gastrovascular system, the position of which above the cerebral ganglion is thus naturally explained (Comp. fig. 10, p. 39). This fact (which was justly emphasized by Lang) seems to prove conclusively, that the longitudinal axis of the Polyclads is homologous to the sagittal axis of the Ctenophores, as maintained by Lang. Therefrom naturally follows, that the nuchal tentacles of the primitive Polyclads are homologous to the tentacles of Ctenophores, not to the sensory tentacles, viz. polar fields of *Ctenoplana*, and the tentacles of Ctenophores have nothing to do with the proboscis of Nemerteans, as suggested by Willey.

The homologies of the gastrovascular system are especially pointed out by Korschelt & Heider (Op. cit.) as "wenig befriedigend", and Lang (Monogr. p. 648) also acknowledges that *Coeloplana*, in which, according to the description of Kowalevsky, the mouth opens directly into the infundibulum, without an ectodermal pharynx, "entfernt sich in diesem Punkte ebenso sehr von den Polycladen wie von den Ctenophoren". The researches of Abbott have eliminated this difficulty; but the study of *Tjalfiella* also gives additional support for the homology of the gastrovascular system of Polyclads and Ctenophores.

A detailed homologizing of the ramifying gastrovascular canals of Polyclads with those of the Ctenophores cannot be carried out, at least in the present state of knowledge. In *Tjalfiella* there is first formed a single pair of ramifying canals on each side of the sagittal axis, and from these the genital canals are differentiated later on. *Ctenoplana* is not sufficiently known in this respect. In *Coeloplana* the arrangement of the main gastrovascular canals appears to differ very considerably from that of *Tjalfiella*, especially in the presence of two main canals in the sagittal plane. These

sondern umgürtet den Körper der Quere nach und das Cerebralganglion entsteht am vorderen Körperpol". I fail to see the discrepancy between the developmental facts and the homologies maintained by Lang. That the cerebral ganglion develops at the anterior end of the embryo, is in no way contradictory to the fact that it, together with the whole anterior end, wanders forward in the course of development.

sagittal canals, which also occur in *Ctenoplana*, are otherwise quite unknown in Ctenophores, and the way in which Abbott (Op. cit. p. 62) seeks to explain them, does not appear to me very acceptable; probably the study of their formation in the embryo will give the clue to their homology. But seeing that we cannot thus homologize in a more detailed way the gastrovascular canals of *Coeloplana* with that of other Ctenophores (— and we can also scarcely point out a direct homologue in typical Ctenophores to the branching canals of *Tjalfiella* —), it can certainly not be expected that a more detailed homologizing of the ramifying canals of Polyclads with those of Ctenophores should be possible. A general homology is all that can be expected, and here *Tjalfiella* and *Coeloplana* undoubtedly show the way along which the transformation of the peripheral gastrovascular system from the Ctenophoran to the Polyclad type has taken place. It may perhaps be suggested that *Ctenoplana* in this respect will be more primitive than *Tjalfiella*. — It is worth recalling here the peculiar respiratory tentacles of *Coeloplana*, discovered by Abbott (Op. cit. p. 48. Taf. 8, fig. 1), processes from the branches of the sagittal gastrovascular canals. They are very much like the dorsal cirri of *Thysanozoon*, which likewise are in connection with the gastrovascular canals.

While thus the peripheral canals do not and cannot be expected to afford more than a general homology in the two groups, the case is different with the rest of the gastrovascular system. The stomach ("Hauptdarm") of the Polyclads, of course, corresponds to the infundibulum of the Ctenophores, both giving rise to the peripheral canals and both being of entodermal origin. The important physiological accordance (comp. p. 39) may also be recalled here. Probably nobody would raise any objection to this homology, so that it is unnecessary to say more about that.

The "Pharyngealtasche" of Polyclads is regarded by Lang as homologous to the stomodæum of Ctenophores, both being of ectodermal origin. The "pharynx" of Polyclads, forming a ringwall within the pharyngeal sac, is regarded as homologous to the stomodæal folds of Ctenophores. In both a narrow opening leads from the stomodæum to the stomach. This seems, indeed, highly plausible. There are, however, some differences to be noticed. The epithelium of the pharyngeal sac of Polyclads is not ciliated, while in the Ctenophores it is ciliated. The stomodæal folds of Ctenophores are paired organs (situated in the transverse plane), in Polyclads they (the "pharynx") originate as a continuous ringwall (a mesodermal thickening). The stomodæum of Ctenophores is compressed in the sagittal plane, in the Polyclads it is a wide sac, more or less complicated, but not compressed. — In view of the higher specialization of the Polyclads the existence of these special structures is, however, not more than what should be expected — and, furthermore, they are not unparalleled in the Ctenophores.

In *Mertensia ovum*, which is generally thought to be one of the most primitive of Ctenophores, the stomodæum is only in the lower part compressed in the sagittal plane; in the upper part it is (on account of the strongly developed stomodæal folds) not thus compressed, the transverse diameter being even larger than the sagittal. In *Tjalfiella* it has developed into the large "suboral" cavity, which is no way compressed in the sagittal plane, the transverse axis being much the larger. Also in *Coeloplana* it is stated by Abbott (Op. cit. p. 51) to be "not compressed in either plane but approximately square in shape". In *Ctenoplana* it is evidently as in *Tjalfiella*, as may be concluded rather safely from the figure copied from Korotneff (p. 26). Thus there is no difficulty for the homology in the shape of the stomodæum.

Regarding the stomodæal folds the discrepancy, that they are paired organs in Ctenophores, a continuous ringwall in Polyclads, cannot be removed at present. But the strong development of the folds in *Tjalfiella*, *Ctenoplana* and *Coeloplana* is very suggestive of the "krausenförmiger Pharynx" found in the more primitive Polyclads; especially in *Coeloplana*, where the walls of the pharynx are "thrown into a great number of folds" (Abbott, p. 51) the condition would seem to be nearly as in the primitive Polyclads; unfortunately Abbott does not give any information as to whether they are really paired structures as in *Tjalfiella* or go all round the pharyngeal wall.

Through the observations on *Mertensia ovum* recorded below my attention was called to the fact that the stomodæum of Ctenophores really consists of two divisions, viz. a larger, lower part, comprising the stomodæal folds — the pharynx s. str. — and a small upper part, consisting of a narrow canal, forming the connection between the pharynx and the infundibulum; this latter part, which I designate as the oesophagus, is always strongly compressed in the sagittal plane. In *Mertensia* it is unusually long and conspicuous, while in other typical Ctenophores it is only quite short, which accounts for its not having been distinguished hitherto. In *Tjalfiella*, *Coeloplana* and *Ctenoplana* it is very conspicuous; (it is designated as the "stomodæal canal" by Abbott). (Comp. the note p. 22). The same two parts are also to be distinguished in the Polyclads. Lang does not treat this oesophagus specially, designating it only as the "inner mouth"; he sees therein only the opening in the "diaphragm" through which the pharyngeal cavity is in connection with the stomach. That it is really a canal comparable to the oesophagus of Ctenophores is, however, evident enough; I need only refer to such a figure as Taf. 28, fig 1 of Lang's Monograph. Unfortunately he does not give any information as to whether it is compressed in the one or other plane; it might be expected to be compressed in the sagittal (longitudinal) plane. Wishing very much to have this rather important question settled, I asked for some specimens of a pair of the more primitive forms of Polyclads from the Zoological Station at Naples, viz. *Thysanozoon Brochii* Gr. and *Stylochus neopolitanus* Lang. On removing the dorsal skin over the pharynx in *Thysanozoon* it was very easily seen that the inner opening of the oesophagus is really a longitudinal slit, as it ought to be according to the theory; in *Stylochus* the opening could not be exposed clearly by direct preparation, but horizontal sections showed that it is likewise here a longitudinal slit. — The diaphragm, the wall separating the stomach from the pharyngeal cavity in Polyclads, and through which the oesophagus passes, is, of course, also represented in Ctenophores, though generally quite small on account of the compression of the pharynx. In *Mertensia* it is distinct enough (Comp. fig. 11 d.), on account of the widening of the pharynx, and in *Tjalfiella* it is even more developed than in any Polyclad; in fact the whole wall separating the pharyngeal ("suboral") cavity from the infundibulum and transverse canal must be regarded as the homologue of the diaphragm of Polyclads (comp. Pl. VI, figs. 2 and 9); in *Ctenoplana* it must evidently be very nearly the same condition, and also in *Coeloplana* the diaphragm must doubtless be very distinct, judging from the description of the pharynx.

The new facts brought to light thus all tend to strengthen the homology of the gastrovascular system in Polyclads and Ctenophores; the only differences of any weight to be noted being the histological character of the epithelium in the pharyngeal sac (ciliated in Ctenophores, non-ciliated in Polyclads) and the stomodæal folds, paired organs in Ctenophores, unpaired in Polyclads —

and these two points are in good accordance with the greater specialization of the pharyngeal apparatus in Polyclads. It thus appears that the homologizing of the gastrovascular system in Polyclads and Ctenophores, instead of being "wenig befriedigend", must be declared to be satisfactory, even to an uncommon degree. — It should also be pointed out that the fact of the oesophagus of Polyclads being a longitudinal slit is another important support for the homology of the longitudinal axis of Polyclads with the sagittal axis of Ctenophores.

The homologies of the nervous system are somewhat more questionable, the main difficulty lying in the rather disputable character of the nervous system of the Ctenophores. But also here the more recent researches have brought to light facts which are in favour of the theory of the derivation of the Polyclads from the Ctenophores. Lang has maintained as "ein unabweisbares physiologisches Postulat" that the adaptation to the creeping mode of life in *Coeloplana* must have modified to a considerable degree both its musculature and its nervous system. The researches of Abbott have shown that this is really the case; while he does not enter on a more detailed description of its muscular system, he gives the important information that four distinct ganglia have developed round the apical organ (Op. cit. p. 61). Also in *Ctenoplana* ganglia appear to have developed (cf. Korotneff. Op. cit. p. 248). On the other hand the sessile *Tjalfiella* does not show any indication of ganglia. These facts would seem to show that the change of habits from pelagic to creeping has been of primary importance for the development of the nervous system. (— It would be of unusual interest to study *Mertensia ovum* in regard to its nervous system; on account of its strongly developed muscular system it should be expected that also the nervous system has been considerably more developed than in other pelagic Ctenophores —). Adding to these facts that Samassa (*Zur Histologie d. Ctenoph.* p. 229—231) upon histological and physiological grounds comes to the result, that the development of the Polyclad nervous system from the apical organ and ciliated ridges of Ctenophores is highly probable, it must certainly be agreed that this point of the theory has been strengthened by the recent researches.

The otolith itself, being doubtless an adaptation to the pelagic life, should be expected to have become rudimentary in the creeping forms. This is also decidedly the case in *Tjalfiella*, whereas it is still typically developed in *Coeloplana* and *Ctenoplana*, deviating from that of pelagic Ctenophores only in minor points. The polar fields, which have totally disappeared in the grown *Tjalfiella*, have been somewhat specially developed in *Ctenoplana* ("sensory tentacles" of Willey); their condition in *Coeloplana* is unknown, being not mentioned by Abbott. (It may be suggested that the two vertical tracks from the otolith in Fig. 6, Taf. 8, of Abbott's memoir may represent the polar fields). In the Polyclads both otolith and polar fields have disappeared completely. The presence of otoliths in the Acoela I would regard as a new formation, being of quite another structure than in the Ctenophores.

No homologue of the eyes of Polyclads has hitherto been found in Ctenophores. It is, however, quite possible that the whitish-yellow spots occurring along the periphery of *Coeloplana* represent the first rudiments of organs sensitive to light, as suggested by Abbott. Also in *Ctenoplana* a series of (red) spots occur along the margin of the body, which even more than those of *Coeloplana* are suggestive of eyes. The fact that in the more primitive Polyclads eyes occur along the margin all round the body is in full accordance herewith, so that it seems highly probable that the origin of

the eyes of Polyclads is indicated here. (If *Heteroplana* were really a Ctenophore, related to *Ctenoplana*, as maintained by Willey, it would afford the direct connection between Polyclads and Ctenophores in this point, having undoubted eyes along the margin. But, as stated above, it can scarcely be doubted that it is a true Polyclad).

The presence of a general ciliation of the epidermis in Polyclads and its absence in Ctenophores would in itself not mean a difference of so much importance as to imply a difficulty to the theory. Lang rightly points out that there are, in any case, traces of ciliation in Ctenophores, both in the grown and the embryonic stages. However, it is by no means without importance to notice that *Tjalfiella*, *Ctenoplana* and *Coeloplana* also in this regard appear to represent a transitional condition. In *Tjalfiella* the basal surface, the suboral cavity and the "chimneys" are ciliated. In *Ctenoplana* and *Coeloplana* the whole underside is ciliated; according to the first descriptions (by Kowalevsky and Korotneff) they are ciliated over the whole body, but this is denied by the later researches of Abbott and Willey, who maintain that only the ventral surface is ciliated.

This leads to a couple of questions of very great morphological importance: to what corresponds the flat underside of *Ctenoplana* and *Coeloplana*, and how has the conspicuous flattening of the body in these two forms originated? The most obvious explanation of the transformation of the high body of typical pelagic Ctenophores into the flat body of the creeping Ctenophores would be, that it has been brought about through a simple shortening of the main axis of the body. This is, however, scarcely the right explanation; the facts revealed by the study of the development of *Tjalfiella* decidedly point in another direction. In the young Cydippid of *Tjalfiella* the lower part of the body is divided through the deep transverse furrow into two large lobes, which may be folded out, so that the animal becomes quite flat (Pl. III, fig. 6); it is doubtless with the inside of these lobes that the animal attaches itself to the Umbellula, the furrow thus becoming converted partly into the basal surface, partly into the "suboral" cavity and the chimneys—allowing that there is no distinct limit between the widened pharyngeal cavity and the furrow<sup>1</sup>). The epithelium of the furrow is ciliated and remains so in the grown animal in the parts derived from the furrow. *Ctenoplana* completely corresponds with the Cydippid of *Tjalfiella*; the two lobes of the body can be opened or folded up; the inside of the lobes (lower side of the body) being ciliated. The only difference from *Tjalfiella* is, besides the absence of the "chimneys", that the pharyngeal cavity appears to be more distinctly limited from the furrow (comp. fig. 3, p. 26). The conclusion seems then inevitable that also in *Coeloplana* the whole ciliated underside corresponds to the transverse furrow of *Tjalfiella* and *Ctenoplana*. The definite proof of this can, of course, only be given by the study of the development of *Coeloplana*; but the facts available do not seem to leave any doubt that this is the explanation of the ciliated underside of *Coeloplana*, the ciliation being thus in itself not a special adaptation to the creeping habit. — The flattening of the body in the creeping Ctenophores thus appears to be due, not to a direct shortening of the whole main axis of the body, but mainly to a splitting up of the lower part of the body. That also some shortening of the

<sup>1</sup>) In the grown specimens it would seem that the whole of the "suboral" cavity and the chimneys represent the pharyngeal cavity, the flattened basal surface alone corresponding to the transverse furrow of the young (comp. Pl. III, figs. 5, 11). This interpretation, however, is not directly supported by the facts of the development. But further material may perhaps give the proof of it.

main axis has taken place, is evident from the reduction of the infundibular canal in these forms, the excretory canals proceeding directly from the infundibulum. The dorsal side of *Coeloplana* thus corresponds to the whole of the body surface of a *Pleurobrachia*. Another question here arises, viz. whether in the Polyclads there is anything corresponding to the transverse furrow of the creeping Ctenophores. It seems that such is really the case. Among the processes of the pelagic Polyclad-larva there is a rather broad, præoral, ventral process, which would appear to correspond to the one lobe; the paired posterior processes accordingly would correspond to the other lobe, having only become secondarily divided. Whether the unpaired dorsal process morphologically also belongs to this lobe seems more questionable; it may perhaps represent a new formation. It is worth recalling in this connection that Lang (Monograph p. 380) seems somewhat in doubt, whether the ciliated band connecting the paired processes is really in connection with that of the anterior ventral process. That the processes are in the transverse plane, is in accordance with the suggestion of their being homologous to the transverse lobes of *Tjalffiella* and *Ctenoplana*. That they are quite resorbed during the metamorphosis of the Polyclad would not seem to make such an homology impossible. A consequence of this suggested homology would be, that only the middle part of the ventral side of Polyclads corresponds to the whole of the ventral side of *Coeloplana* and *Ctenoplana*, the Polyclads thus representing a further stage of development in the transformation from pelagic to creeping organisms.

This question about the homology of the ventral side of the Polyclads has been answered in another way by those of the previous authors, who have paid attention to it. 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, Hatschek (Lehrbuch d. 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<sup>1)</sup> 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 panczerina* Chun, which even uses the inverted pharynx for creeping, being taken as the proof of this homology. — The morphology of *Tjalffiella* 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 suggested homology of the larval processes of the Polyclads with the transverse lobes of *Tjalffiella* and *Ctenoplana*<sup>2)</sup> would also seem to throw light on the homologies of the ciliated band encircling the margin of the processes of the Polyclad-larvæ. In *Tjalffiella* and *Ctenoplana* the whole

<sup>1)</sup> Lehrbuch d. Histologie. p. 184. — Systematische Stellung von *Hydroctena salenskii*. Zool. Anz. XXVII. 1904. p. 570.

<sup>2)</sup> As mentioned above (p. 45) Kemna suggested that the larval processes of the Polyclads were homologous to the lobes and auricles of Lobatæ. This was evidently a happy thought, representing an important step in the right direction. That the auricles have nothing to do with the larval processes is clear enough now. But at that time it might not seem so improbable — though it is, of course, always dangerous to seek for the origin of some little specialized structure in a very differentiated organ of some highly specialized forms, as the Lobatæ undoubtedly are.

inside of the lobes is clad with a thick, ciliated epithelium (comp. the sections, Pl. X); in the Polyclad-larvæ the processes are likewise originally clad with a uniform ciliation, which in the course of development becomes specialized so as to form a ciliated band. (Lang, Monograph, p. 377). Hatschek (Op. cit. p. 320) thinks the "präorale Wimperkranz" of the Polyclad-larvæ to have originated from the costæ of Ctenophores through such a form as *Charistephane*. "Man könnte den Wimperkranz von acht einander genäherten Plättchengruppen ableiten, aber umgekehrt auch den geschlossenen Wimperkranz für das primäre halten; vielleicht ist es richtiger beide Bildungen von einem gemeinsamen Grundtypus abzuleiten". Without entering on a detailed discussion of this theory I would only point out, that it does not seem very appropriate to derive an evidently little differentiated structure as the ciliated band of the Polyclad-larvæ from such a highly differentiated structure as the combs of Ctenophores, and even to adduce one of the most specialized forms, like *Charistephane* (with only two rows of exceedingly broad combs) for the comparison. Further I would suggest that it is scarcely correct to designate the ciliated band of the Polyclad-larvæ as a preoral band (as is also done by Lang, comp. his diagram, fig. 34. B.; Monogr. p. 404). As mentioned above, Lang was sometimes in doubt whether the band of the anterior, unpaired process was really in connection with that of the other processes (Monogr. p. 380). This fact is in good accordance with the explanation here set forth of the origin and homology of the processes and the ciliated bands of the Polyclad-larvæ, viz. that the processes correspond to the transversal lobes of *Tjalfiella* and *Ctenoplana*, (and accordingly also to the lobes of the Lobatae), the bands being only a specialization of the general ciliation covering the lobes; accordingly it is only the band of the anterior ventral, unpaired lobe, which corresponds to the preoral ciliated band of the *Trochophora*, the band of the paired, posterior processes corresponding to the postoral band. Thus the existence of both a preoral and a postoral ciliated band, and of a non-specialized ciliated part between these bands, in the *Trochophora* is very naturally explained.

Regarding the musculature it has already been mentioned that in *Coeloplana* it has been specially developed in accordance with the creeping habit of the animal. That it is also more developed than usual in *Ctenoplana* is quite probable — though the enormous muscular system ascribed to it by Korotneff and partly by Willey has proved to rest on a misapprehension (comp. above, p. 28). Lang points out the existence of a basal membrane in Polyclads, serving as a sort of skeletal support for the muscles, as an adaptation to their creeping life habit. It is very interesting to notice that also in the creeping *Coeloplana* and *Ctenoplana* a basal membrane has developed, while in the sessile *Tjalfiella* and the pelagic Ctenophores no such membrane occurs. The musculature is thus in very beautiful accordance with the theory.

The homology of the genital organs is supported by the fact that both Ctenophores and Polyclads are hermaphrodites, the genital organs being in close relation to the gastrovascular system. On the other hand there would seem to be a considerable difference as to how they originate. In Ctenophores they are stated to originate from the entoderm (Chun) or the ectoderm (Hertwig), in Polyclads they originate probably from the entoderm; but this is not beyond doubt, — it is possible that they are derived from the mesoderm. In the memoir on *Gunda segmentata* Lang was not in doubt

as to the entodermic origin of the genital cells, but in the Monograph on the Polyclads he has some doubt about this. Since, however, in the Coelenterates the genital cells may arise either from the ectoderm or the entoderm in nearly related forms, Lang is of opinion that such a discrepancy would not imply any considerable difficulty to the theory. This may perhaps be true; but it would certainly be more satisfactory to the theory, if it could be proved that the origin is the same in both groups — and the new facts acquired are decidedly in favour thereof. As has been shown above, all evidence is decidedly for the entodermal origin of the genital cells in Ctenophores (— and *Tjalfiella* is not the least important support for this —); regarding the Polyclads the observations of Lang are equally in favour of the entodermic origin. So long then as there is no proof of the contrary, it may be held that there is accordance in this point between the two groups. — A difference not to be removed, at present at least, is this, that while in the Ctenophores the genital products are ejected through the gastrovascular system, no genital ducts existing, in the Polyclads there are special genital ducts, the genital organs being lined with a tunica propria which continues directly into the genital ducts. According to the statements of Willey *Ctenoplana* would afford a very important transitional stage in this regard, the genital organs being lined with a tunica propria continuing into genital ducts opening outwards, on the dorsal side. But, as pointed out above (p. 29—30), these statements very much need to be verified. On the other hand it is by no means improbable that *Coeloplana*, the most specialized of the creeping Ctenophores, will prove to be intermediate between Ctenophores and Polyclads in regard to the genital organs; it would even not seem very surprising if copulatory organs were developed in *Coeloplana*, as is suggested by Lang. In any case it will be of the greatest interest to have the genital organs (and development) of *Coeloplana* examined.

The greatest difficulty to the theory lies in the excretory organs, as is duly pointed out by Lang. It has been suggested by Chun that possibly the rosettes of the Ctenophores are the homologues of the excretory organs; but there is, in any case, no proof of this. But even if nothing can be found in Ctenophores corresponding to the excretory organs, it may be said of these as of the copulatory organs, that they must have originated once, and then it is only what should be expected, that they have originated in the most primitive of the Bilateralia. The suggestion that *Coeloplana* might possess an excretory system (Lang, p. 655) seems disproved by Abbott's discovery that it has typical ctenophoran rosettes.

Finally the question of the mesoderm must be mentioned. Through the researches of Metschnikoff a complete accordance appeared to be established between Ctenophores and Polyclads in this respect, and, as Samassa states (Op. cit. p. 235) "dieselben waren sogar allein im Stande die von den übrigen Bilateralthieren so sehr abweichenden Mesodermverhältnisse der Polycladen aufzuklären". The very definite assertion of Hatschek ("Das neue zoologische System", p. 8) "dass die Angaben Metschnikoff's über die Bildung des Mesoderms dieser Tiere durchaus irrig sind" would seem to raise new difficulties here. Hatschek's researches being as yet unpublished, it is impossible to enter on a discussion of this question. But the fact pointed to above (p. 45) that Hatschek also derives the Turbellarians from a point on the stem of the "Ctenozoa", seems to show that the development of the mesoderm in the Ctenophores is not opposed to the theory of Lang.

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 researches 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. It seems to be an established fact that we can here really follow the transformation of the radiate into the bilateral type. The main point in this transformation lies in the relations of the main axis. After having been shortened through the flattening of the aboral side of the body it becomes bent through the wandering forwards of the apical pole, while the oral pole still remains in the middle of the under side. At the same time it becomes considerably shortened through the splitting up, along the transverse plane, of the oral half of the body. By the folding out of the lobes the flat underside is formed. The sagittal and transversal planes of the radiate body pass directly into the sagittal (vertical, longitudinal) and transversal planes of the bilateral body; the latter, of course, must be bent parallel to the main axis. Secondary changes of the axial relations are then introduced by the wandering forwards (or backwards) of the oral pole. But there is no reason to enter on the further development of the bilateral type. It may be sufficient to have demonstrated how the transformation from the radiate to the primitive bilateral type has been brought about.

A necessary conclusion from the close affinity between Ctenophores and Polyclads would seem to be, that the Ctenophores ought to be classified with the Platyhelminths 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. I must, however, refrain from discussing this question on the present occasion, the more so as it cannot be done with due weight, before *Coeloplana* has been studied more fully in regard to both its anatomy and its development.

## II.

### The pelagic Ctenophora of the Northern Atlantic.

The species mentioned in this part of the report have, most of them, been the object of repeated descriptions, a very extensive literature existing about them. There is no reason to enter in a more detailed manner upon these forms in general; however, I am able to give some additional information, which may be found not without value. As for the literature it has been thought unnecessary to quote all the references; they have been very carefully collected by Römer and Moser, to whose works I may refer. Only the more important references are given.

The species dealt with in this part are:

- Mertensia ovum* (Fabricius).
- Pleurobrachia pileus* (O. Fr. Müller).
- *crinita* Moser.
- Bolina infundibulum* (O. Fr. Müller).
- Beroë cucumis* Fabricius.

Besides, notes are given on some few other species, which have been recorded as occurring in the Northern Atlantic, viz. *Hormiphora plumosa* (Sars), *Lesueuria hyboptera* A. Ag., *Cestus veneris* Les. and *Beroë Forskålii* Chun.

The species hitherto recorded only from the Atlantic Coasts of North America are not dealt with, unless there are synonymical reasons for mentioning them.

#### 1. *Mertensia ovum* (Fabricius).

- Beroë ovum*. O. Fabricius. Fauna Groenlandica. 1780. p. 362.
- *compressa*. H. Mertens. Beobach. u. Unters. über die beroeartigen Akalephen. Mém. Acad. Imp. St. Pétersbourg. 6. Ser. II. 1833. p. 525. Taf. 9.
- *octoptera*. — Ibid. p. 528. Taf. 10.
- Mertensia ovum* Mörch. A. Agassiz. North American Acalephæ. Ill. Catal. Mus. Comp. Zool. II. 1865. p. 26.
- — Fabr. E. Vanhöffen. Die grönländischen Ctenophoren. Bibl. zool. VIII. 1895. p. 17.
- — — — Ctenophoren. Nordisches Plankton. XI. 1903. p. 2.

*Mertensia ovum* (Fabr.) F. Römer. Die Ctenophoren. Fauna Arctica. III. 1903. p. 70, 72.

— — Fabr. F. Moser. Die Ctenophoren der Deutschen Südpolar-Expedition. Deutsche Südpolar Exp. 1901—1903. Bd. XI. Zoologie Bd. III. 1909. p. 123.

*Callianira compressa* Mertens. F. Moser. Ibid. p. 138.

**Non:** *Mertensia ovum*. H. B. Torrey. The Ctenophores of the San Diego Region. Univ. Calif. Publ. Zool. 2. II. 1904. Pl. I. 1.

Our knowledge of this species is very incomplete, in spite of its having been mentioned often enough in literature and likewise repeatedly figured. This insufficiency, which is the more unfortunate as *Mertensia ovum* is supposed to represent one of the most primitive of all Ctenophores, is mainly due to the great difficulty of preservation, so great that Römer even states that it is upon the whole impossible to preserve it. This is certainly exaggerated; since it has proved to be possible to preserve satisfactorily so delicate a form as *Bolina infundibulum*, it will doubtless also be possible to do so with *M. ovum*; only experiments are needed in order to find out the right method to be applied. Another reason of the incomplete knowledge of this form is the fact, that it occurs only in the purely arctic waters, thus being not very accessible for study, except at the Coasts of North America, where it has, however, not been made the object of study since A. Agassiz (Op. cit.) published his observations on its postembryonal development.

In some Plankton-samples from the "Ingolf" I have found several specimens, which can with certainty be referred to *M. ovum*. The samples having been simply preserved in alcohol, these specimens are, of course, not in a fine state of preservation; of most of them only the main parts of the gastrovascular system and the tentacle bases are preserved, but a few small specimens are nearly complete, though evidently much shrunk and having lost their transparency. This material, poor enough, it is true, has however enabled me to give some additional information of its anatomy and to correct some errors in the previous descriptions.

Agassiz (Op. cit. p. 26) points out as a feature characteristic of this species (and genus) "the great distance at which the lateral chymiferous tubes (the pharyngeal vessels) are placed from the digestive cavity, and the close connection which is shown there to exist between the tentacular apparatus and the lateral tubes, the base of the tentacular apparatus seeming to give rise to this long, slender tube, enclosing the digestive cavity in its two wide arches, when seen from the broad side" — this description being also given by Moser (Op. cit. p. 124). Further the tentacular apparatus "differs from that of *Pleurobrachia* in being limited to the abactinal part of the spherosome, and not extending towards the actinostome, as in *Pleurobrachia*" (p. 28). The figures which accompany Agassiz' description are mere sketches, which do not give much support to the description; it is true that the figures 36—37 show a quite short tentacle-basis, but these figures differ so much from the fig. 29, which represents a grown specimen, that it seems not very convincing that they really represent the same species — though Agassiz states that in this stage "the development of the actinal part of the spherosome has become so striking, that we cannot fail to recognize in the young *Acaleph* a *Mertensia*". In reality no arguments are given for the referring of the young stages figured to *M. ovum*. It is, in any case, very unfortunate that the size of the specimens figured is not

indicated. But even if these young stages really belong to *M. ovum*<sup>1)</sup>, they cannot prove that the short tentacle-basis is characteristic of the grown *Mertensia*. On the contrary the tentacle-basis is unusually long, as I can show.

In fig. 11 is represented the tentacle bases and the central part of the gastrovascular system of *Mertensia ovum*, drawn from one of the specimens in the "Ingolf" material. It shows the tentacle

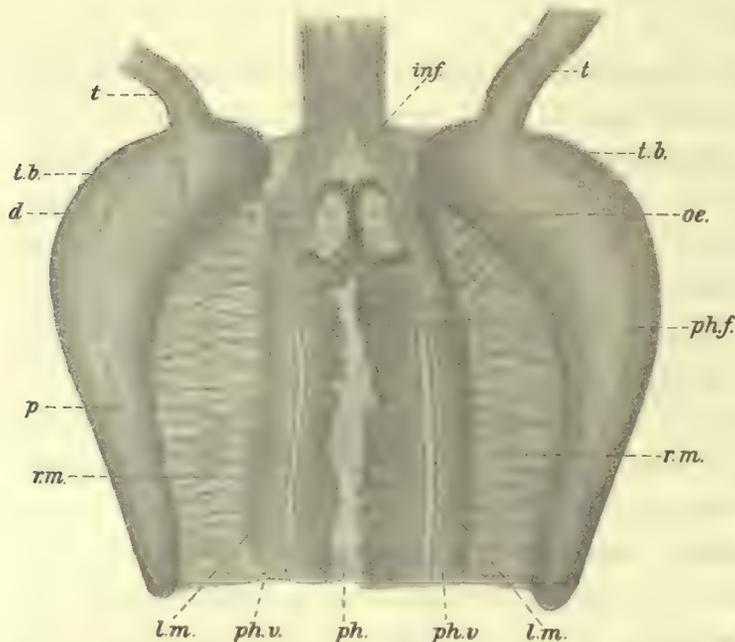


Fig. 11. Pharynx and tentacle-bases of *Mertensia ovum*. d. diaphragm; inf. infundibulum; l. m. longitudinal muscles; oe. oesophagus; p. series of pigment spots; ph. pharynx; ph. f. pharyngeal (stomodæal) folds; ph. v. pharyngeal vessel; r. m. radial muscles; t. tentacle; t. b. tentacle-basis.

bases as rather long<sup>2)</sup>, characteristically curved bodies, from the upper end of which the tentacle proceeds; this shape the tentacle bases have in all the specimens available, and it is likewise seen in the sketch made from a living specimen by Vanhöffen (Nordisches Plankton, fig. 1); also in *Beroë compressa* of Mertens, which is, in my opinion, undoubtedly a synonym of *M. ovum*, they have the same shape and size. It may then possibly be right that the tentacle bases are short in the very young specimens, as shown in the two figures of A. Agassiz — but in the larger specimens, from a size of ca. 3<sup>mm</sup>, they are not "limited to the abactinal part of the spherosome", as maintained by Agassiz. His fig. 29 is too little detailed for showing anything clearly of the shape and size of the tentacle-bases.

The peculiar feature of the pharyngeal vessels following close along the tentacle bases rests on a misunderstanding. The pharyngeal vessels join the pharynx as in other Ctenophores, as I have been able to see clearly both on sections and on the not sectioned material. What Agassiz has taken to be the pharyngeal ("lateral") vessel is evidently the tentacular vessel.

Moser (Op. cit.) states that the tentacle bases, judging from the figures of Agassiz, are not longitudinally divided as in other Cydippids. This would appear to be really so, also on the preserved material; in sections it is seen, however, that the structure is in accordance with the usual type, only the two halves of the basis lie so close together, partly even overlapping one another, that it can only be seen in sections that there are really two parts as usual. It may be remarked that along each side of the tentacle basis is seen a rather conspicuous series of pigment spots (fig. 11); this would appear to be what Mertens mistook for the ovaries.

<sup>1)</sup> It is peculiar that Fewkes does not mention Agassiz' description of the young *Mertensia* in his short note on *Mertensia ovum* (On certain Medusæ from New England. Studies from the Newport Marine Zoological Laboratory. Bull. Mus. Comp. Zool. Vol. XIII. 1887. p. 212), where he records that he has traced the development of some Ctenophoran eggs "into young *Mertensia*, (which) are possibly of this species".

<sup>2)</sup> The oral end of the pharynx being destroyed in the specimens preserved it cannot be seen there how far down towards the mouth the tentacle basis reaches; from Vanhöffen's sketch (fig. 1) of a living specimen they are seen to reach nearly to the mouth. It is worth mentioning that in a specimen, which can scarcely have been more than 3<sup>mm</sup> long, the tentacle bases have already the same shape and relative length as in the grown specimens.

The stomodæum is seen in a very marked way to consist of two distinct parts. The upper part is strongly compressed in the sagittal plane; its rather thick walls curve outwards above at the opening into the infundibulum, as a pair of inner lips. This part is distinguished as the oesophagus. Between the oesophagus and the pharyngeal vessel is a conspicuous clear space, without muscles, which may be distinguished as the diaphragm, as it is doubtless the homologue of the diaphragm in the Polyclads. Below the oesophagus the stomodæum is not compressed in the sagittal plane. It is nearly square, a little larger in the transverse plane. This, evidently, depends on the strong development of the pharyngeal folds. There is a distinct keel on each side in the sagittal plane, but it is only farther down that the sagittal compression of the stomodæum becomes apparent. This lower, larger part of the stomodæum, comprising the stomodæal folds, is distinguished as the pharynx. — This differentiation of the stomodæum, which has hitherto been overlooked, as it appears, is a general feature in the Ctenophores. I have found it quite easily observable also in *Pleurobrachia*, (comp. fig. 13, p. 70) *Euchlora* and *Bolina*, besides in *Tjalfiella* and upon the whole in the Platyctenida; also in *Beroë* it exists. Likewise the same feature is found in the Polyclads. (Comp. above, p. 53). It is especially distinct, where the pharyngeal folds are much developed, causing thus a widening of the pharynx in the transverse plane; where the folds are only small, the pharynx is compressed in the sagittal plane also in the upper part, so that the transition from the pharynx to the oesophagus becomes quite even, no distinct limit being seen.

The pharyngeal folds are, as seen in fig. 11, strongly developed, in the shape of the usual folded bands. In Mertens' figure 1, Taf. 9, they are very well shown; he describes them (designating them as "Gallengefässe") as "ganz drüsigte gewundene Organe, die bis an die Mundspitze reichen, und dort noch nach aussen gegen sich selbst eingeschlagen sind". Moser's statement (p. 124) that "über Form und Länge der Magenwülsten fehlen bisher Angaben" thus does not hold good — and even in case the *Beroë compressa* of Mertens were really different from *M. ovum*, that statement is not correct. Fabricius says in his description of "*Beroë ovum*" (Fauna groenlandica, p. 362): "Intra illos cirros (the tentacles), et paulo antierius, 2 cirri minores rubicundi conspiciuntur, quos extra corpus extendere non vidi, nec credo illam posse". It appears evident that these two short "cirri" can only be the pharyngeal folds; this is put beyond doubt by the following notes found (on p. 288) in a handwritten work of O. Fabricius: "Zoologiske Samlinger eller Dyrebeskrivelser" (1809), preserved in the Zoological Museum of Copenhagen; they are given here in translation. "The two shorter cirri, which have their place between the long ones in the middle of the worm (as it appears, in the cavity itself), were pink brown, and must be regarded as a pair of mouth-tentacles. . . . When it has got the Crustacean ("Marfluen", "*Oniscus cicada*") agglutinated with its cirri and carried to the mouth, the Crustacean appears to become powerless, and the mouth tentacles then catch it there and carry it further to the stomach". — Fabricius thus has not only observed and described the pharyngeal folds of *M. ovum* long before Mertens, but he is, upon the whole, the first, who has seen this structure of the Ctenophores.

Regarding the gastrovascular system I cannot give any information beyond that given above of the position of the pharyngeal vessels. I would only recall the remarkable statement of Mertens (Op. cit. p. 526), that from the part of the subtransversal vessels continuing towards the apical pole

from the point of the aboral processes of the body he "deutlich beobachtete, dass von hier sich baumartig verzweigte Gefäße gegen den Darmkanal erstrecken". If this proves to be correct, it is indeed a most interesting feature, probably homologous to the proliferations from the meridional vessels of *Bathycytena Chuni* (Moser). (Comp. p. 36, note).

A very surprising feature of *M. ovum* is the strong development of its muscular system, as is easily observed in the preserved specimens. (Comp. fig. 11). The infundibular canal is quite surrounded by a thick layer of longitudinal muscles; at the level of the infundibulum they divide so as to pass outside the diaphragm, continuing down along the outer side of the pharyngeal vessels (the inner side of these vessels is close to the pharyngeal wall, not separated therefrom by a muscle layer). At the level of the transverse, perradial vessels the longitudinal muscles must, evidently, be divided into four groups, uniting again, two on each side, below the transverse vessel. It is only on sections, however, that one can realize how exceptionally these muscles are developed. As seen in fig. 12, representing a transverse section of the infundibular canal, the muscles form a thick layer round the canal, the single threads being arranged more or less distinctly in a feather-like way, as it is known e. g. in the earth-

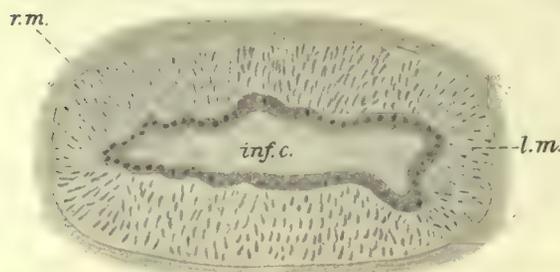


Fig. 12. Transverse section of the infundibular canal of *Mertensia ovum*. inf. c. infundibular canal; l. m. longitudinal muscles; r. m. radial muscles.  $\frac{90}{1}$ .

worm. The single threads are rather thick, comma-shaped in cross-section. The whole muscle-bundle appears to be limited outwards by a fine membrane. The longitudinal muscles along the outer side of the pharyngeal vessels are arranged in a similar way, but the muscle threads are less numerous here. Between the pharynx and the tentacle-bases there is a conspicuous network of anastomosing muscle-strands. Also these smaller bundles appear in sections to be surrounded by a thin membrane. The same reticulum of muscle-bundles is also seen in the

aboral part of the animal, taking almost the appearance of ring-muscles over the muscle-bundle round the infundibular canal; in fact, I am not quite sure whether there are not real ring-muscles here.

This strong development of the musculature is quite astonishing and, as far as hitherto known, quite unique in the Ctenophores. It would, indeed, be very interesting to have this species made the object of a close histological and anatomical study. It may be supposed that its nervous system will prove to be considerably more developed than usual among Ctenophores, judging from its muscular system.

The very interesting observation of Mertens, that it uses its tentacles for attaching itself to stones etc. on the bottom, when the sea is in motion through stormy weather, in order to avoid being thrown ashore and crushed, may be recalled here. Likewise Mertens (p. 527) records it to possess strong regenerative power. (Comp. below, sub. *Bolina infundibulum*).

Several specimens were taken by the "Ingolf" at the stations 29 (65° 34' N. 54° 31' W.), 33 (67° 57' N. 55° 30' W.) and 34 (65° 17' N. 54° 17' W.); in the Journal of the Expedition it is mentioned from station 32 (66° 35' N. 56° 38' W.), all these stations being in the Davis Strait. — On the "Danmark" Expedition it was observed by Mr. Fr. Johansen in considerable numbers in the months of August and September 1907 at "Danmarks Havn" (North-East Greenland, 76° 47' N. 18° 45' W.), the

size varying from ca. 2 to ca. 25<sup>mm</sup> in diameter. It is stated to occur mainly on the ice-foot, stretching its long tentacles horizontally over the ice. (A coloured sketch of the animal leaves no doubt that it was really *M. ovum*).

This species doubtless occurs all along the Greenland Coast, both the West and East Coast. With the cold polar stream it is carried down along the North American East Coast, probably as far south as the influence of this stream prevails here, viz. to Cape Cod. From Iceland it is recorded by Faber<sup>1)</sup>, who states to have found it especially at the North Coast, and also once at the Westmann-Islands. The latter statement is scarcely correct. Its occurrence at the North Coast of Iceland is certainly due to the Polar Stream, which must evidently also carry the species down along the East Coast; but the Polar Stream does not reach to the Westmann Islands. Faber has then here most probably mistaken a *Pleurobrachia pileus* for *M. ovum*. It is further known to occur also at Spitzbergen and in the Bering Sea, so that it is doubtless circumpolar, as maintained by Chun (Ctenophoren d. Plankton-Expedition, p. 10), Römer and Vanhöffen. It is a very decided cold-water form, limited to the polar waters, as pointed out by Römer. It is not in accordance herewith that it is also recorded from the coast of California and further from some Norwegian fjords and Skagerak. The statement of its occurrence at California is due to Torrey. In his paper "The Ctenophores of the San Diego Region" he figures (Pl. I. 1) a Ctenophore which is designated as *Mertensia ovum* — but only in the explanation of the plate; in the text it is not mentioned with a word. I quite agree with Moser (Op. cit. p. 126) that it is not *Mertensia ovum*, as is at once seen from the rounded apical side of the body and from the shape and position of the tentacle-bases. Whether it is a *Hormiphora*, as suggested by Moser, I do not feel convinced; but here the fact only concerns us that it is not *Mertensia ovum*, this species being thus not known from the Californian coast.

The statement of its occurrence in Norwegian fjords is due to D. Damas & E. Koefoed<sup>2)</sup>: "Nous ne l'avons observée dans les régions septentrionales que dans les fiords profonds de la Norvège et elle est signalée dans le Skagerak. Mais elle se trouve là exclusivement dans les couches profondes, tandis qu'au Spitzbergen c'est une forme de surface". I have been unable to find in the literature the statement of its occurrence in the deep waters of the Skagerak to which Damas & Koefoed refer; but even if *M. ovum* has really been recorded from there, I must doubt the correctness. And also for the alleged observation of *M. ovum* in the deep fjords of Norway it is not seen, how the correctness of the observation has been ascertained — nor is it stated in which fjords it was observed; I therefore think that the occurrence of this species in the Norwegian fjords cannot be taken as an established fact.

The occurrence of *M. ovum* in the Bering Sea rests on the supposition that Merten's *Beroë compressa* and *octoptera* are identical with *M. ovum*, it having not later been recorded from there<sup>3)</sup>. But the identity of these species of Mertens with *M. ovum* has recently been decidedly objected to

<sup>1</sup> Fr. Faber. Naturgeschichte der Fische Islands. Mit einem Anhang von den isländischen Medusen und Strahlthieren. 1829. p. 202.

<sup>2</sup> Le Plankton de la Mer du Grönland. Duc d'Orleans. Croisière océanographique dans la mer du Grönland en 1905. (p. 416).

<sup>3</sup> In the Report of the International Polar Expedition to Point Barrow, Alaska (Washington, 1885) the species is recorded as observed near Point Barrow, the identification being made by I. W. Fewkes after sketches made on the expedition.

by Moser, who thinks them to represent a species of the genus *Callianira*, *C. compressa*; (Moser. Op. cit. p. 138). It will be necessary to enter a little into this question.

The reasons adduced by Moser against the identity of *Beroë compressa* Mertens with *M. ovum* Fabr. are these. "*Beroë compressa* hat eine ausgesprochene Herzform, infolge von zwei wohlausgebildeten, flügel förmigen Fortsätzen am Sinnespol, die in der Grösse ungefähr denen von *Callianira antarctica* Chun entsprechen, während *Mertensia ovum* allerdings schwach herzförmig ist, aber der Fortsätze durchaus entbehrt". Each of these processes "weist ferner eine ziemlich tiefe, trichter förmige Einbuchtung auf, die an dessen Spitze beginnt und bis zu dessen Ursprungsstelle, in der Höhe des Sinnespols, verläuft, wo sie sich in die Scheidenöffnung fortsetzt ... Ferner sind auch die flügel förmigen Kanten, auf denen die Rippen verlaufen, bei *Beroë compressa* viel auffallender und stärker ausgebildet als bei *Mertensia ovum*" (p. 124). — It may first be stated that according to Mertens (Op. cit. p. 525) "die vier Flügel sind wieder mehr oder weniger tief eingeschnitten", so that it is evident already therefrom, that too much weight ought not to be laid on the prominence of these ridges as a specific character. This becomes much more evident, if we compare the figs. 3 and 4 of Mertens with the fig. 2 of Vanhöffen (Nordisches Plankton), the latter showing that the ridges in Greenland specimens may be as prominent as in those of the Bering Sea. Concerning the height of the aboral processes it is true that the figures of Mertens differ very much from those of Agassiz; but in a sketch of a specimen of *M. ovum* from West Greenland (Holstensborg) made by Traustedt, (which is preserved in the Copenhagen Museum) these processes are as high as in the specimens of Mertens. Also in fig. 29 of Agassiz there is a distinct indication of an apical process on the left side (while nothing corresponding is seen on the right side), bearing witness that the animal figured had the usual processes, though perhaps less developed than usual. Likewise in Vanhöffen's fig. 1 they are very little developed. It appears then that the development of these processes is very variable (dependent on age?) — if there are not two separate species, one with high, the other with low apical processes. This latter alternative I would think very improbable. But here also renewed studies of the living specimens must bring the decision. In any case it is certain, that both forms occur at the West Coast of Greenland, as is proved by the sketches of Traustedt and Vanhöffen.

The *Beroë octoptera* of Mertens is regarded by Moser (and, in my opinion, with full right) as the young of *B. compressa*. "Naturgemäss muss ein Jugendstadium von *Beroë compressa*, bei dem die flügel förmigen Fortsätze am Sinnespol und die vorspringenden Kanten noch gar nicht oder nur wenig entwickelt sind, *Mertensia ovum* sehr ähnlich sein, welches letzteres ja auch Chun auffiel. Aber das gerade spricht gegen die Zusammengehörigkeit dieser beiden. Eine junge *Mertensia ovum* von der Grösse der *Beroë octoptera* gleicht nur wenig dem ausgewachsenen Tier, nach den Angaben von Agassiz über deren Entwicklung. Auch die Farbe von *Beroë octoptera* spricht nicht für die Identität beider, denn es fehlen ihr die auffallenden, orange Pigmentflecken der jungen *Mertensia ovum*, die Agassiz beschreibt, und es ist ausgeschlossen, dass Mertens sie übersehen hätte. Somit ist die Zusammengehörigkeit von *Beroë octoptera* mit *Mertensia ovum* ganz unwahrscheinlich, während die Behauptung, dass es sich um ein Jugendstadium von *Beroë compressa* handelt, sehr viel für sich hat. Die Identifikation von *Beroë compressa* mit *Mertensia ovum* ist aber erst recht unmöglich, und füge ich (Moser) beide den Callianiren, unter dem Namen *Callianira compressa*, als eine einstweilen noch zweifelhafte Art bei". (Op. cit. p. 125).

I would remark to this whole reasoning, that it is scarcely justifiable to lay so much stress on the description of the young stages of *M. ovum* given by Agassiz. As pointed out above, there is no statement about the size of the specimens figured, so that a direct comparison with the figures of Mertens' *Beroë octoptera* cannot be duly carried out — and upon the whole, it can scarcely be taken as a sure fact that all the figures given by Agassiz are really the same species. I would not find it justifiable either to lay so much stress on the presence or absence of some pigment spots, at least in these old and imperfect descriptions and figures. Further, as I think it has been proved beyond doubt that *B. compressa* is really identical with *M. ovum*, the same must, of course, be the case with *B. octoptera*, which is almost certainly the young of it.

While I am thus decidedly of opinion that the *Beroë compressa* and *octoptera* of Mertens are only synonyms of *Mertensia ovum*, against the view held by Moser, I willingly agree that especially the large aboral processes indicate a relation to the genus *Callianira*, as was formerly thought by Chun (Monograph, p. 279; in the "Ctenophoren der Plankton-Expedition" this view is dropped), and recently maintained by Moser. In fact, I think it very probable that the two genera *Mertensia* and *Callianira* will prove to be nearly related, belonging to one and the same family, the Mertensiidæ. The character upon which Chun established the two families, *Mertensiidæ* and *Callianiridæ*, is the presence or absence of the apical processes, it being evidently due to the unsatisfactory description and figures of Agassiz that they are taken to be absent in *Mertensia ovum*. Since, however, they are really present in *Mertensia* as well as in *Callianira* it can scarcely be doubted that these two genera must really belong to the same family, which must, of course, keep the name *Mertensiidæ*, the diagnosis having to be altered accordingly into "apical processes present". Whether there are other features of the rank of family characters must be left undecided, until the much needed closer study of the anatomy of *Mertensia ovum* has been undertaken.

To the family Mertensiidæ Chun (Monograph) also referred the genera *Euchlora* and *Charistephane* and later on (Ctenophoren d. Plankton-Expedition) the genus *Tinerfe* Chun. That this latter form really belongs to this family seems evident enough. As for *Charistephane*, which is very probably only a larval form (with dissogony) of a Lobate or Cestid, as suggested by Chun (Monograph, p. 278), it must be left undecided to which family it really belongs. For *Euchlora*, characterized especially by the opening of the tentacle sheath at the oral pole of the body and, perhaps, by the unbranched tentacles (it is not quite certain that they are so in *Euchlora filigera* Chun), it seems necessary to establish a separate family, **Euchloridæ** n. fam. To give the full diagnosis of this family is also impossible at the present stage of our knowledge; a closer study of *Euchl. filigera* and especially of the structure of the tentacles of both species is needed. That there are no cnidoblasts, as is stated by Chun, may be taken as certain, but it is as yet unknown whether the tentacles are provided with colloblasts of the usual ctenophoran structure. To the family Euchloridæ the genus *Dryodora* Ag. would also seem to belong. (It is referred by Moser to the Mertensiidæ, together with *Euchlora*). Especially its simple tentacles and the lacking of the pharyngeal folds indicate a closer relation to *Euchlora*. It is, however, too little known, our knowledge resting alone on the description and figures given by Mertens, so that its true position must remain somewhat uncertain as yet.

## 2. *Pleurobrachia pileus* (O. F. Müll.).

- ? *Beroë pileus*. O. Fr. Müller. Prodrömus zoologiæ danicæ. 1776. p. 232. No. 2817.  
 ? — — O. Fabricius. Fauna grönlandica. 1780. p. 361.  
*Cydippe bicolor*. M. Sars. Beskrivelser og Iagttagelser over nogle mærkelige eller nye i Havet ved den bergenske Kyst levende Dyr. 1835. p. 35. Tab. 7, fig. 17.  
*Pleurobrachia rhododactyla*. L. Agassiz. Contributions to the Natural History of the Acalephæ of North America. II. The Beroid Medusæ of the Shores of Massachusetts. (Mem. Amer. Acad. N. Ser. IV. 1849).  
 — — Agass. A. Agassiz. North American Acalephæ. 1865. p. 30—33.  
 — *rhodopsis*. Chun. Ctenophoren d. Golfes v. Neapel. 1880. p. 282. Taf. II. Fig. 5—6.  
 — *pileus* Fabr. Vanhöffen. Die grönländischen Ctenophoren. 1895. p. 21.  
 — — — Chun. Ctenophoren d. Plankton-Exped. 1898. p. 15.  
 — — aut. Römer. Die Ctenophoren. Fauna arctica. III. 1903. p. 70, 75.  
 — — Fabr. Vanhöffen. Ctenophoren. Nordisches Plankton 1903. p. 3.  
 — — — Moser. Ctenophoren d. Siboga-Expedition. 1903. p. 5.  
 — *rhodopsis* Chun. Moser. Ibid. p. 6.  
 — *pileus* Fabr. — Ctenophoren d. deutschen Südpolar-Exped. 1909. p. 141—146.  
 — — (F.) A. Ghigi. Ctenofori. Raccolte planctoniche fatte della R. Nave "Liguria" nel viaggio di circumnavigazione del 1903—05. Vol. II. Fasc. I. 1909. p. 9.  
 — *rhodopsis* Chun. A. Ghigi. Ibid. p. 9.

While it is generally agreed that the *Pl. rhododactyla* of the American coasts is identical with the *Pl. pileus* of the European Coasts, nobody has hitherto doubted that the species *Pl. rhodopsis* established by Chun for the Mediterranean form was really distinct, and judging from the literature there should be no difficulty in distinguishing it from *Pl. pileus*. After the diagnosis given by Chun (loc. cit.) it is seen to differ from *Pl. pileus* among other characters in the meridional vessels being voluminous and "nicht scharf von den adradialen Stämmen abgesetzt". Moser (Siboga-Ctenophoren, p. 30) gives the following differential diagnoses of the two species:

<i>Pl. pileus.</i>	<i>Pl. rhodopsis.</i>
"Eiförmig, Rippen lang. Scheide und Tentakelbasis ziemlich lang. Eintritt der adradialen Gefässe steil über dem Trichter im aboralen drittel der Rippe. Darüber die Scheidenöffnung.	Eiförmig, Rippen ziemlich kurz. Scheide kurz. Tentakelbasis nicht lang. Eintritt der adradialen Gefässe auf gleicher Höhe mit dem Trichter, in der Mitte der Rippe, auf gleicher Höhe die Scheidenöffnung.

The colour is thus given by Chun: "Durchsichtig, Tentakelbasis und Fangfäden rosa pigmentiert". In Moser; Ctenophoren d. deutschen Südpolar-Expedition (p. 148) the species is mentioned

as "die eiförmige, rosenrotgefärbte *Pleurobrachia rhodopis* ...", this somewhat increased colouring being evidently due to a lapsus memoriæ of Dr. Moser.

These distinguishing characters certainly seem quite excellent. Finding, however, that the young specimens of *Pl. pileus* were not easily distinguished from *Pl. rhodopis* after the diagnosis given, I asked for some material of *rhodopis* from the Zoological Station at Naples. I was then rather surprised in finding that these specimens did not correspond very well with the diagnosis of *rhodopis*; especially the opening of the tentacle-basis was not at the level of the infundibulum, but placed as in *Pl. pileus* of a corresponding size. After a careful comparison with specimens of *pileus* from the North Sea I became convinced that it is impossible to distinguish the two forms. The characters pointed out as distinguishing *Pl. rhodopis* from *pileus* are only characters of the young, found exactly alike in specimens from the Mediterranean and the North Sea. It is in correspondence herewith that the specimens examined by Chun were only 5—7 mm. In the preserved specimens I find the opening of the tentacle sheath lying at the level of the infundibulum at a size of 3—4 mm, while in specimens of 5—7 mm it is already somewhat more apically placed. This difference evidently is due to the preservation, the size of the animals being more or less reduced thereby.

Another fact is decidedly in favour of the identity of *Pl. rhodopis* and *pileus*, viz. that while *Pl. pileus* has otherwise an almost cosmopolitan distribution, it is not known from the Mediterranean<sup>1)</sup>, doubtless because the specimens found there are eo ipso taken to be *rhodopis*, which latter has, on the other hand, not been recorded from outside the Mediterranean. The improbability of such a world-wide pelagic form not occurring in the Mediterranean is evidently as great as that of another similar pelagic form not occurring outside the Mediterranean.

The identity of *rhodopis* and *pileus*, on the other hand, would seem to be disproved by the observations of Garbe<sup>2)</sup>, who has found very considerable anatomical differences between the young of the two forms. In the youngest specimens of *Pl. rhodopis* examined, 0.5 mm in diameter (collected at Trieste), the gastrovascular system was as yet very little differentiated, being represented only by a large, undivided sac in each side half of the body; in young specimens of *Pl. pileus* from Helgoland, of only 0.4 mm diameter the gastrovascular system was found almost completely formed as in the grown specimens. Also in regard to the development of the genital organs very considerable differences were found to exist between the two species, which need not be recorded in a more detailed way here. — It is, of course, beyond doubt that such two forms could not be identical — on the contrary, the differences found by Garbe are so considerable, that it seems really astonishing that such could obtain in two species of the same genus. — The explanation of the remarkable discrepancy between Garbe's and my own

<sup>1)</sup> Moser (Op. cit. p. 145) doubts the correctness of a statement of Sovinsky, according to which *Pl. pileus* occurs in the Black Sea. As I have not seen Sovinsky's work ("Einführung in das Studium der Fauna des Ponte Caspo, aral. Meeres-Bassin". 1902), I can form no judgment of the case, but it would beforehand seem very probable that the Mediterranean *Pleurobrachia*, which is really *Pl. pileus*, also occurs in the Black Sea, corresponding to the fact that it occurs also in the Baltic. — When Moser further says that "es wäre wertvoll, zu erfahren ... welche Art unter dem Namen *Pleurobrachia rhododactyla* gemeint ist, die nach Graeffes kurzer Mitteilung (1884) im Golf von Triest häufiger ist; dass es sich hier um unsere nordische *Pleurobrachia pileus* handeln sollte, lässt sich kaum annehmen bei dem Fehlen anderer nordischer Arten wie z. B. *Beroë cucumis*", it must be stated, firstly, that Graeffe ("Übersicht der Seethierfauna d. Golfes v. Triest. III. Coelenteraten. 1884. p. 30) mentions *Pl. rhodopis*, not *Pl. rhododactyla*, and next that the Mediterranean *Beroë ovata* is doubtless identical with *Beroë cucumis*, which generally occurs together with *Pl. pileus*. (Comp. below, sub *Beroë cucumis*).

<sup>2)</sup> Aug. Garbe. Untersuchungen über die Entstehung der Geschlechtsorgane bei den Ctenophoren. Z. wiss. Zool. Bd. LXIX. 1901.

observations is doubtless this, that his supposed specimens of *Pl. rhodopis* are not this form at all, but most probably belong to some species of Lobatae. This suggestion is supported by the fact, that in Garbe's material of young Pleurobrachiae from Helgoland were found a pair of specimens showing essentially the same structure of the gastrovascular system as his "*Pl. rhodopis*" from Triest. Now it can be said with rather great certainty, that these latter young Ctenophores from Helgoland can only be young *Bolina infundibulum*, the only other tentaculate Ctenophore occurring here besides *Pl. pileus*. It is in good accordance herewith, that the costae are placed very close together, as is characteristic of the young *Bolina* (which was even named *Cydidippe quadricostata* by Sars on account of this peculiarity). — I think then that there can be no doubt that Garbe's *Pleurobrachia rhodopis* is really the young of some species of Lobatae (evidently not *Bolina*, since the specimens from Triest differ in some points from those from Helgoland). The mistake is not to be wondered at very much, it being in fact a very difficult matter to distinguish such very young specimens of Lobatae from true Cydippids. Garbe's observations thus cannot disprove the identity of *Pl. rhodopis* with *Pl. pileus*, which I think has been conclusively established.

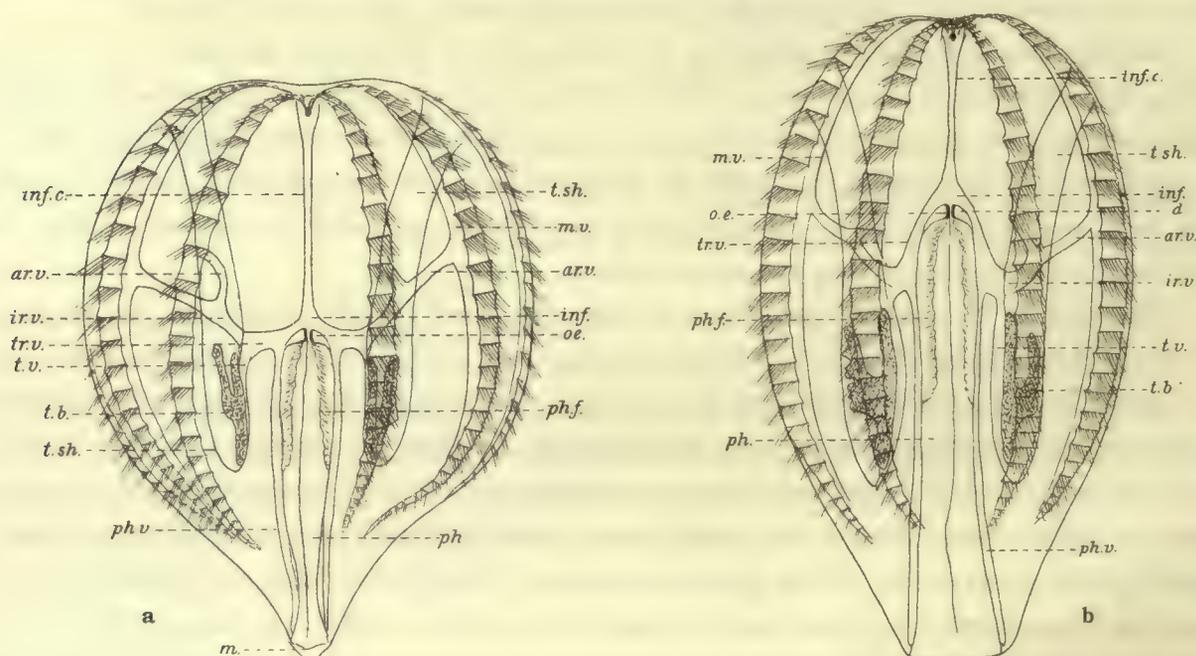


Fig. 13. a. b. *Pleurobrachia pileus*, showing different relations of the gastrovascular system and tentacle bases, due to different stages of contraction. ar. v. adradial vessel; d. diaphragm; inf. infundibulum; inf. c. infundibular canal; ir. v. interradial vessel; m. mouth; m. v. meridional vessel; oe. oesophagus; ph. pharynx; ph. f. pharyngeal (stomodæal) folds; ph. v. pharyngeal vessel; t. b. tentacle base; tr. v. transverse (perradial) vessel; t. sh. tentacle sheath; t. v. tentacle vessel.

In the work quoted, on the Ctenophores of the German South-Polar Expedition, Dr. Moser points out the great variability found in this species in regard to the shape, size and position of the different parts of the body. All transitional forms occurring together at the same locality, these differences must be referred to "individuelle Schwankungen und Kontraktionszustände, ... Altersunterschiede und ... die verschiedenen Konservierungsmethoden" . . . . . "Die Untersuchung deutet darauf hin, dass mit dem Alter die Form vielfach mehr zylindrisch wird, der Magen sich im Verhältniss zum Trichter sehr verlängert und die Tentakelbasen grösser werden und sich ersteren nähern. Berücksichtigt muss

auch noch werden, dass sich das Tier so kontrahieren kann, dass aus der kugeligen Form eine zylindrische wird, wobei die inneren Organe sich in die Länge strecken und teilweise zusammenrücken, z. B. die Tentakelbasen sich dem Magen nähern" (p. 144). My observations are in full accordance herewith. In fig. 13 a—b are figured a pair of specimens showing such great differences in the arrangement of the radial canals of the gastrovascular system, that one would scarcely think it possible that they could belong to the same species. Especially the direction of the main transverse canals is different, in one (a) horizontal, in the other (b) nearly vertical; similarly the position of the tentacle base is at the level of the upper end of the pharynx in one, nearly at the middle of the pharynx in the other specimen. Also the shape is very different, the one nearly spherical, the other subcylindrical. But all transitions between these two extremes occur among the specimens from one and the same locality, so that there cannot be any doubt that these differences are due either to individual variations or to the different stages of contraction on preservation (or to both). I have not had occasion to examine any large number of specimens of this species in a living state, so I cannot say definitely whether such differences really occur in the living specimens; but for my own part I do not doubt that these differences are mainly due to the contraction on preservation. Likewise I suppose that the more cylindrical shape, which Dr. Moser suggests to represent a growth change, is due to the preservation. — Observations on living specimens are necessary to decide these questions.

A peculiar variation was found in a few specimens, viz. the infundibular canal being split up in a greater part of its length (Fig. 14); in one case it was even divided in the whole length.

Regarding the colour of the tentacles it should be mentioned that there are two laterally placed, close series of pigment spots; these series continue upwards, along the sides of the upper part of the tentacle basis, receding somewhat on passing over from the tentacle to the basis. This arrangement I have found in all the specimens examined, so that it very probably is a constant feature of this species. In Pl. 3, fig. 5 of L. Agassiz' memoir, quoted above, these series of pigment spots are indicated, their receding at the basis of the tentacle being well shown, while otherwise the arrangement in two distinct series along the tentacle is not given.

Chun (Monogr. p. 242) states, as an instance showing "wie die relativen Grössenverhältnisse derselben Art an den verschiedenen Küstenpunkten, je nach der Häufigkeit von heftigen Winden, ausgiebigen Schwankungen unterworfen sind" that "im Allgemeinen die amerikanische *Pleurobrachia rhododactyla* doppelt so gross (ist), als die offenbar mit ihr identische *Cydippe* (*Pleurobrachia*) *pileus* der stürmischen Nordsee". This is doubtless not correct. The *Pleurobr. pileus* abounds in the North Sea in sizes by no means smaller than

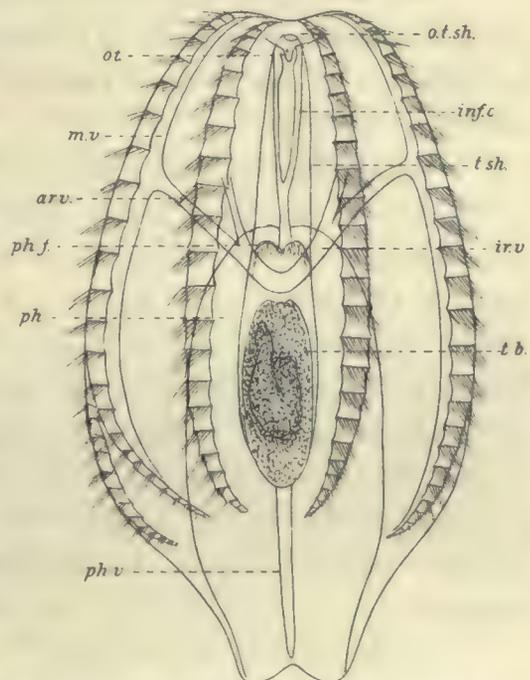


Fig. 14. *Pleurobrachia pileus*, seen from the tentacular plane; showing forking of infundibular canal. Letters as in Fig. 13, besides: ot. otolith; o. t. sh. opening of the tentacle sheath.

those represented, evidently in natural size, on the Pl. I of L. Agassiz' memoir. According to Vanhöffen they may reach a size of 25<sup>mm</sup> in diameter, and Evans and Ashworth<sup>1)</sup> even record a length of 30<sup>mm</sup>; so large I have not observed them myself.

In a few specimens I have observed a parasitic Nematod, lying within the jelly; in one case the parasite had wound itself round the tentacle basis. All the specimens of the worm being immature, it seems evident that it does not reach its full development in the *Pleurobrachia*, but in some other animal, which preys upon the latter. I can give some information hereof. In the collection of the Copenhagen Museum there is a specimen of a *Pleurobrachia* found in the stomach of *Cyclopterus lumpus* (from the North Sea, Capt. Sølling); this fact, combined with the observations of O. Fabricius (Fauna groenlandica, p. 363) that at Greenland *Mertensia ovum* is eaten by the same fish, seems to leave no doubt that *Cyclopterus lumpus* really preys upon the *Pleurobrachia*; it may then not seem improbable that the Nematod occurring in the *Pleurobrachia* is the young of one of those Nematods found as parasites in the *Cyclopterus*, viz. *Ascaris succisa* Rud. and *Agamonema capsularia* Dies., and of these two it would evidently be the latter, the diagnosis (Diesing, Systema Helminthum II, p. 116) "extremitate caudali obtuse cum acumine" being quite in accordance with the specimens observed in the *Pleurobrachia*. Also the size is in accordance, the specimens found being ca. 1.5<sup>cm</sup>, while the size of *Agamonema* is stated by Diesing to be  $\frac{1}{2}$ —1".

The occurrence of this Nematod in *Pleurobrachia* was already observed by Forbes, who in his paper "On two British Species of Cydippe"<sup>2)</sup> (Ann. Nat. Hist. III. 1839 p. 148) says that "imbedded in the substance of one of these animals, near the stomach, is a remarkable parasitic worm, in shape resembling a *Filaria*".

Besides the Nematod, I have found a small Trematod in the *Pleurobrachia*, in the pharynx or in the jelly of the body; it may occur in considerable numbers in the same specimen and is much more common than the Nematod. It may be suggested that it is the young of one of the distomes living in *Cyclopterus*, which of them I do not venture to say — the more so, as there is also the possibility, that the final host of these Trematods is another animal. I have been informed by Dr. C. G. Joh. Petersen, director of the Danish Biological Station, that he has sometimes found specimens of *Acanthias vulgaris* having the stomach full of *Pleurobrachia*. It is then, of course, also possible that *Acanthias* is the final host of the Nematod found in *Pleurobrachia*. — It is worth pointing out that also in *Acanthias* the Nematod *Agamonema capsularia* occurs. On the other hand the same Nematod occurs in a considerable number of fishes (e. g. the cod, salmon) so that it must be supposed that the *Pleurobrachia* is not the only first host of this parasite.

In the material of the "Ingolf" Expedition there are no specimens which can with any certainty be referred to this species.

The distribution of *Pleurobrachia pileus* appears to be very wide, perhaps cosmopolitan. It is common over the whole of the North Atlantic, both at the European and American Coasts. In the Danish seas it is common everywhere, in the North Sea, Skagerak and Kattegat. In the Baltic it may

<sup>1)</sup> Wm. Evans and I. H. Ashworth: Some Medusæ and Ctenophores from the Firth of Forth. Proc. R. Phys. Soc. Edinburgh. XVII. 1909. p. 308.

<sup>2)</sup> The paper appears to have been overlooked by the recent authors on Ctenophora. The two species described, but not named, by Forbes are evidently both *Pleurobrachia pileus*.

occur even so far as the Åland Sea, according to Levander<sup>1)</sup>, the species being thus evidently very euryhaline, even if it is found there only in the deeper water. It is in good accordance therewith that it is also stated to occur in the Black Sea (Comp. above, p. 69). By the German South Polar Expedition it was found in considerable numbers in the Antarctic Sea, Moser (Ctenoph. d. deutschen Südpolar-Exp. p. 144) pointing out "dass hier ein Fall von Bipolarität vorliegt, wie er bis jetzt nur bei ganz wenig Arten nachgewiesen ist". The fact recorded by Dr. Moser herself (Op. cit. p. 143) that it also occurs at the Seychelles and at Ascension is, however, not in favour of regarding this as a case of bipolarity; it shows that the species is also found in the warm regions, so that it will probably prove to occur all over the oceans, not only in the Northern and Southern seas, its distribution thus being not discontinuous, as it ought to be, if it were really a case of bipolarity. — From the Pacific this species is not known with certainty. Ghigi (Op. cit. p. 9) states that it occurs at the West Coast of North America down to the Californian peninsula. This statement, however, evidently rests on the supposition that the *Pleurobrachia bachei* figured by Torrey (The Ctenophores of the San Diego Region, Pl. I, Fig. 3) is identical with *Pl. pileus*, a supposition which is also made by Moser (Op. cit. p. 145). While I quite agree that Torrey's *Pl. bachei* differs from the true *Pl. bachei* Agass. in what appears to be the main character of this species, viz. the opening of the adradial vessels into the meridian vessels above (aborally to) the opening of the tentacle sheath, so that it can scarcely be identical with this species<sup>2)</sup>, I cannot, on the other hand, accept its identity with *Pl. pileus*, the shape and oblique direction of the tentacle bases and the position of the opening of the tentacle sheath rather far from the apical pole being essential differences from the latter species; also the prominent red colour of the pharyngeal folds is a difference from *Pl. pileus*, in which these folds are generally much less conspicuously coloured, faint violet or yellowish. Anything definite cannot, however, be said about this question, because Torrey gives no information at all [about the specimen figured. If it is a grown specimen, it may represent a new species; if it is a young specimen magnified, it may not be impossible that it will prove to be identical with *Pl. pileus*.

Damas & Koefoed in "Le Plankton de la Mer du Grönland"<sup>3)</sup> (p. 414), state that *Pl. pileus* "manque tout à fait en plein océan". I do not think this statement quite justified. In the collection of the Copenhagen Museum there are some specimens taken at 50° 20' N. 30° 10' W. (4. VI. 1889, by Lieutenant Ulrich, on the Corvette "Dagmar"), which I think are undoubtedly *Pl. pileus*. By the German South Polar Expedition a specimen was taken between Ascension and the Cap Verde Islands (Moser, Op. cit. p. 143). These facts show that the species can, in any case occasionally, be found in the open sea and is not wholly bound to the coastal waters.

From the Greenland seas *Pl. pileus* is generally recorded in literature, e. g. by Lütken<sup>4)</sup>,

1) K. M. Levander. Förekomsten af Ctenophorer i Östersjön. Medd. af Soc. pro Fauna et Flora Fennica. H. 25. 1900. p. 104.

2) Moser (Op. cit. p. 145) regards *Pleurobrachia bachei* Agass. as synonymous with *Pl. pileus*, suggesting the characters by which it is stated by Agassiz to differ from *pileus* (*rhododactyla*) to be due to "Unterschiede in der Kontraktion . . . oder aber auf einem zufälligen Unterschied beruht". It does not appear very probable that the main character, the position of the opening of the tentacle sheath adorally to the opening of the adradial into the meridional vessels, could be due to contraction. But this form very much needs to be more carefully studied than has hitherto been the case.

3) Duc d'Orleans. Croisière océanographique dans la mer du Grönland en 1905.

4) C. F. Lütken. A revised list of the Acalephæ and Hydrozoa of Greenland. Arctic Manual. 1875. p. 187. (*Pleurobrachia rhododactyla* Agass.).

Mörch<sup>1)</sup>, Levinsen<sup>2)</sup>, Römer<sup>3)</sup> and Vanhöffen<sup>4)</sup>. These statements all rest on Fabricius' old description, and it is a mistake when Vanhöffen (Op. cit. p. 16) thinks its occurrence at Greenland "durch die Arbeiten von Lütken und Levinsen genügend beglaubigt". There are no specimens of *Pl. pileus* from Greenland in the collection of the Copenhagen-Museum and as *Pl. pileus* is not so very difficult to preserve in a tolerable condition, this means something. Further Vanhöffen did not observe the species at Greenland during his stay there, and neither was it observed by the Danish expeditions to East Greenland or by the "Tjalfe" Expedition. It may be concluded from this that *Pleurobrachia pileus* does not occur at the Coasts of Greenland. Having reached this conclusion I was very pleased in finding later, in the work quoted of Damas & Koefoed (p. 414), that they did not observe the species at Greenland either, stating that *Pl. pileus* "n'existait certainement pas dans la partie occidentale de l'itinéraire" (viz. at the East Coast of Greenland).

From this then it follows that the *Beroe pileus* of Fabricius (Fauna grönlandica, p. 361) is not the species now generally designated as *Pleurobrachia pileus* Fabr. The diagnosis given by Fabricius: "*Beroe globosa*, costis octo, cirrisque duobus ciliatis" (which is a quotation from O. Fr. Müller (Op. cit.)) cannot give any clue to what species it really is, and neither do the accompanying remarks: "hanc sæpissime vidi tempore autumnali in sinibus natantem, eleganter in aqua coloribus suis nitentem; nunquam tamen ob debilitatem eius sufficienter contemplari contigit" give the clue. That it might possibly be the same as his *Beroe ovum*, as is suggested by Römer (Op. cit. p. 77), I would not think very probable, judging from Fabricius' excellent observations on the latter species. The solution of this question perhaps is given by the fact that recently a new species of Ctenophore, *Pleurobrachia crinata* Moser has been discovered at Greenland, collected by Vanhöffen. I would suggest that this is perhaps the real *Beroe pileus* of Fabricius. The common North Atlantic species, however, may well keep the name *pileus* O. F. Müll. (nec Fabr.). Nobody can tell definitely which species is really meant with Martens' "Mützener Rotzfisch". But it is certain that it is either *Mertensia ovum* or *Pleurobrachia pileus*, which both occur at Spitzbergen. There being no doubt about which species has the claim of the former name, the name *pileus* Müll., (non Fabr.) with good right belongs to the northern *Pleurobrachia*, in accordance with the almost universal use, and in spite of the fact that Fabricius most probably used it in another sense. (It may be remembered that the author of the name *pileus* is not Fabricius, but O. Fr. Müller to whose Prodrömus Fabricius refers under his *Beroe pileus*.) I agree that it is probable that Martens' "Mützener Rotzfisch", to which the name *pileus* was given by O. Fr. Müller, is the species now called *Mertensia ovum*, but as it cannot be put beyond doubt, there is, in my opinion, no reason to alter the species-name of our most common Ctenophore; and even if it could be proved definitely that the "Mützener Rotzfisch" is really *Mertensia ovum* I would think this case one of those, where an exception from the priority rule should take place.

<sup>1)</sup> Naturhistoriske Bidrag til en Beskrivelse af Grönland af J. Reinhardt, J. C. Schiødte, O. A. L. Mörch, C. F. Lütken, J. Lange, H. Rink. (Særskilt Aftryk af Tillægene til "Grönland, geografisk og statistisk beskrevet af H. Rink). 1857. p. 97.

<sup>2)</sup> G. M. R. Levinsen. Meduser, Ctenophorer og Hydroider fra Grönlands Vestkyst. Vid. Medd. Nat. Foren. København 1892. (p. 7, *Pl. rhododactyla* Agass.).

<sup>3)</sup> F. Römer. Ctenophoren. Fauna Arctica. III. 1903. p. 77.

<sup>4)</sup> E. Vanhöffen. Die grönländischen Ctenophoren. Bibl. Zool. VIII. 1895. p. 21.

### 3. *Pleurobrachia crinita* (Moser).

*Pleurobrachia crinita*. F. Moser. Die Ctenophoren d. deutschen Südpolar-Exped. p. 147. Taf. XX.  
Fig. 7—10.

This peculiar species, which is hitherto known only from Greenland (the Karajak-Fjord, Vanhöffen), has not been brought home by any of the Danish Expeditions. That it must be distributed along the whole of the West Coast of Greenland can scarcely be doubtful, and likewise it can scarcely be doubted that it has a much wider distribution, the existence of very local forms of pelagic animals being upon the whole not very probable. — Whether it is a specially cold-water form, like *Mertensia ovum*, cannot be decided from the little information hitherto given of it.

It may perhaps be doubted that this species should really be referred to the genus *Pleurobrachia*. Ghigi (Op. cit.) has established a separate genus, *Moseria*, for those species with the mouth-edge bent outwards so as to form a funnel-shaped collar (viz. *Pleurobr. pigmentata* Moser, *Pl. striata* Moser and *Euplokamis australis* Benham). It is not impossible that the *Pl. crinita* ought also to be referred to this group (to the genus *Tinerfe* Chun it also bears some resemblance). I would, however, remark that the main character of the genus *Moseria* as diagnosed by Ghigi very much needs to be verified by study of the living forms. The mouth opening can greatly alter its shape in *Pl. pileus* e. g., and in some preserved specimens it may be quite funnel-shaped. It would then not be unreasonable to suppose, that the natural shape of the mouth in these forms is perhaps not as in the preserved specimens, after which these species have been described. I would be inclined to think the character of the costæ of more importance. In any case I agree that the two species, *pigmentata* and *striata* apparently stand apart from the other species. Whether *Euplokamis australis* ought really be grouped with them seems to me less convincing.

### 4. *Bolina infundibulum* (O. Fr. Müller).

*Beroë infundibulum*. O. Fr. Müller. Prodrömus Zoologiæ Danicæ. 1776. p. 232. No. 2816.

— — O. Fabricius. Fauna grönlandica. 1780. p. 360.

*Bolina septentrionalis*. H. Mertens. Die beroëartigen Acalephen. 1833. p. 515. Taf. 7.

*Mnemia norvegia*. M. Sars. Beskrivelser og Iagttagelser... 1835. p. 32. Tab. 7. Fig. 16.

*Cydippe quadricostata*. M. Sars. Ibid. p. 36. Tab. 8. Fig. 18.

*Bolina alata*. L. Agassiz. On the Beroid Medusæ of the Shores of Massachusetts. Contrib. to the Nat. Hist. of the Acalephæ of North America. II. Mem. Amer. Ac. IV. 1850. p. 349. Pl. VI—VIII.

— — A. Agassiz. North American Acalephæ. Ill. Cat. Mus. Comp. Zool. II. 1865. p. 15—18.

— *microptera*. A. Agassiz. Ibidem. p. 19.

— *infundibulum*. Chun. Ctenophoren d. Golfes v. Neapel. 1880. p. 294.

— *norvegica* (Sars). C. Vogt u. E. Yung. Lehrbuch d. praktischen vergleichenden Anatomie. 1888. I. p. 170—195.

*Lesucuria vitrea* M. Edwards. M'Intosh. Notes from the St. Andrews Marine Laboratory. Annals Mag. Nat. Hist. 6. Ser. II. 1888, p. 464; 6. Ser. V. 1890, p. 46.

- Bolina infundibulum* Martens. Chun. Ctenophoren d. Plankton-Exped. 1898. p. 22.  
 — — (O. F. Müller). F. Römer. Ctenophoren. Fauna arctica. III. 1903. p. 78.  
 — — (Fabricius). Vanhöffen. Ctenophoren. Nordisches Plankton. 1903. p. 5.  
 — *septentrionalis* Mertens. Vanhöffen. Die grönländischen Ctenophoren. Bibl. Zool. VIII. 1895. p. 19.  
 — *infundibulum* Martens. F. Moser. Japanische Ctenophoren. (Beitr. z. Naturg. Ostasiens, herausg. v. Doflein). 1908. p. 48.

Regarding the synonymy of this species I would first point out that the author of the name *infundibulum* is O. Fr. Müller, as rightly stated by Römer (Op. cit.), but not Fabricius, and still less Martens, who did not mention this form by any other name than the "Springbrunner Rotzfisch". This was translated by O. Fr. Müller, in his "Prodromus Zoologiæ Danicæ", into "*Beroë infundibulum*"; this is correctly given by Chun in his Monograph (p. 294), but in his "Ctenophoren d. Plankton-Expedition" (p. 13) he says that "Fabricius übersetzte diese Bezeichnung mit *Beroë infundibulum*", and this latter incorrect statement is repeated by Moser (Japanische Ctenophoren, p. 52).

The *Cydippe quadricostata* of Sars is ranged by Moser (Ctenophoren d. deutschen Südpolar-Exped. p. 163) among the quite uncertain species. It was pointed out already by Mc. Crady<sup>1)</sup> that it probably represents only the young of *Bolina infundibulum* (*Mnemia norvegica* M. Sars), which interpretation was adopted by A. Agassiz (North American Acalephæ; p. 13) and by Chun (Monograph. p. 125). No arguments are given by Moser against this interpretation of *Cydippe quadricostata*, and it seems, indeed, indisputable. No other Ctenophores occur in Norwegian seas, or upon the whole in the North Atlantic, to which it could be referred. It is true, Aurivillius<sup>2)</sup> regards it as identical with *Hormiphora plumosa*; but it is by no means a sure fact that *Hormiphora plumosa* occurs in the North European Seas (comp. below). There are also no morphological reasons for referring it to any other form than *Bolina infundibulum*.

That the species mentioned by M'Intosh (Op. cit.) as *Lesueuria vitrea* is really *Bolina infundibulum* cannot be doubted, as was rightly pointed out by Vanhöffen (Grönländische Ctenophoren, p. 19). Also Evans & Ashworth (Op. cit. p. 310) appear to be of this opinion.

Concerning *Bolina alata* Agass. I quite agree with Moser that it cannot be distinguished from *B. infundibulum*. The same is, I think, the case with *Bolina microptera* A. Ag. In the description of this form (loc. cit.) Agassiz points out as one of its specific characters that "the lateral lobes are very short, with complicated windings of the long ambulacral tubes". This might perhaps seem to indicate that it is really a separate species; but as I have found a rather considerable variation in this regard in the specimens of *Bolina infundibulum* observed by me during a stay at the Biological station of Trondhjem last summer (1911), I do not think this a feature of sufficient importance for maintaining *B. microptera* as a separate species — the more so as no figures are given of it. The question can perhaps not be regarded as definitely settled at present; in any case careful studies of living material of this as well as of the other American species, *Bolina vitrea* L. Agass., are very desirable. The beautiful

<sup>1)</sup> John Mc. Crady. On the development of two Species of Ctenophora, found in Charleston Harbor. (Proc. Elliot Soc. Nat. History. Charleston S. C. 1857. p. 8).

<sup>2)</sup> C. W. S. Aurivillius. Vergleichende thiergeographische Untersuchungen über die Plankton-Fauna des Skageraks in den Jahren 1893—1897. Kgl. Svenska Vet. Akad. Handlingar. Bd. 30. No. 3. 1898. p. 27.

figure given of the latter by A. G. Mayer<sup>1</sup>) is, as regards the colour, not in accordance with the description of Agassiz.

The Mediterranean species, *Bolina hydatina* Chun, is stated to differ from *B. infundibulum*, besides in the less developed windings of the lobe-vessels and some other minor characters, in the remarkable fact that the subventral vessels precede the subtentacular ones in the course of the development from the young to the adult form, while in *B. infundibulum (alata)* it is exactly the reverse according to Agassiz. With full reason Chun points out (Dissogonie, p. 93) that "es ist im hohen Maasse auffällig, dass bei nahe verwandten Arten so bemerkenswerthe Differenzen in dem Gange der postembryonalen Entwicklung obwalten". Though the figures given by Agassiz show this very clearly, I think we may desire to see this statement verified by renewed researches. The fig. 8 especially does not appear to me very convincing, and I may call attention to the fact that in the much more advanced stage represented in his fig. 12 the subtentacular vessels are represented as ending at the sides of the lobes, not uniting in the middle, and not distinctly in advance of the subventral vessels. Also the facts pointed out above in regard to his figures of young *Mertensia ovum* make me hesitate in accepting as beyond doubt the statements and figures of the development of *Bolina*.

There would, however, appear to exist another very conspicuous difference between the young of *B. infundibulum* and *hydatina*. In the young specimen of ca. 1<sup>mm</sup> diameter represented by Vogt & Yung (Op. cit. p. 175—176) in figs. 75—76 the tentacular vessel is represented issuing from one of the interradial vessels, not occupying the middle between the two interradial vessels. I have had occasion to convince myself of the correctness of this observation (on a specimen of 1.5<sup>mm</sup> diameter). Judging from Taf. IX, fig. 3 of Chun's memoir "Die Dissogonie", this would not appear to be the case in *B. hydatina*; but no quite corresponding stage being figured by Chun, the existence of this difference cannot be regarded as beyond doubt.

If these differences in the development of *B. hydatina* and *infundibulum* prove to be sure facts, there will, of course, be no doubt possible that they are really two different species. But until then I cannot feel very convinced of the specific difference between the two forms. The length of the auricles and of the costæ are not reliable characters; I have observed a rather considerable variation therein in *B. infundibulum*. The only difference of somewhat more value, which I can find between *hydatina* and *infundibulum* is in the windings of the lobe-vessels. Judging from the fig. 1, p. 82 of Chun's memoir "Die Dissogonie", which represents a specimen of ca. 9<sup>cm</sup> height, these windings are decidedly less developed than in *infundibulum*; even though a not inconsiderable variation obtains in regard to the development of the windings in *B. infundibulum*, I have never observed them so little developed in the latter.

The question about the specific value of *Bolina hydatina* must then be left undecided for the present. Judging, however, from the fact shown above that the Mediterranean *Pleurobrachia rhodopis* cannot be distinguished from *Pl. pileus*, and from the fact shown below, that the Mediterranean *Beroë ovata* can, at most, be regarded as a variety of *Beroë cucumis*, it will probably be conceded that the conclusion lies near at hand that also *Bolina hydatina*, only found in the Mediterranean, is only a

<sup>1</sup> A. G. Mayer. Some Medusæ from the Tortugas, Florida. Bull. Mus. Comp. Zool. Vol. 37. 1900. Pl. 27. Figs. 91—92. Moser (Japanische Ctenophoren, p. 53) supposes that the rosy colour of the specimen figured by Mayer "mit der natürlichen Farbe nichts zu tun hat, da Agassiz ausdrücklich die Farblosigkeit hervorhebt und Mayer sonst wohl von einer Identifikation beider Abstand genommen hätte". This point might well deserve an authentic explanation.

local(?) variety of *Bolina infundibulum*, (which is not recorded from the Mediterranean), these three forms being almost invariably found together.

A detailed account of the anatomy of this species is given by Vogt & Yung (Op. cit.). I have found it, upon the whole, very careful and exact; some few remarks should, however, be made to it. In the figs. 71—72 (p. 172) the long (subventral costæ) are shown to continue to about the middle of the lobes, and from there to the lower end they are represented as being set with rather coarse hairs, somewhat similar to those of the auricles. These hairs I have never been able to observe, and I think I can maintain that they do not exist, in any case in the younger specimens. Likewise I have never seen the costæ proceed so far down on the lobes. Seeing, however, that the specimen figured by Vogt & Yung must have had a height of ca. 15<sup>cm</sup>, while the largest specimens observed by me were only ca. 5<sup>cm</sup> high, I do not venture to maintain that it cannot be in these large specimens as represented in the figures quoted. The large folds at the base of the closed lobes represented in these figures I have not observed either.

In the description of the gastrovascular system we find the remarkable statement, that the subtentacular vessels bend downwards at their upper end continuing into the excretory vessels; thus a closed circle is made here, as shown by the fig. 85, p. 193. Such a connection between the excretory and the subtentacular meridional vessels being otherwise unknown in Ctenophores, I was beforehand inclined to think that this was a misrepresentation. However, I am not able to disprove this statement, on the contrary, my observations would seem to support the statement of Vogt & Yung. In the young specimens I found that the subtentacular vessel has a little adapical prolongation above

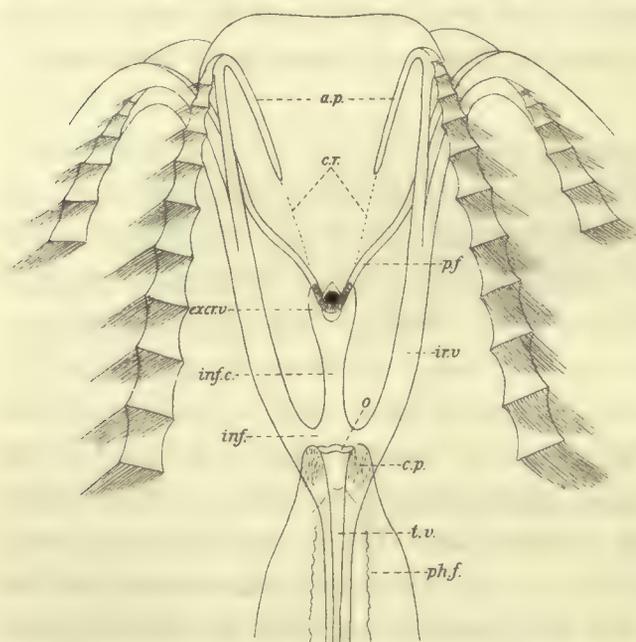


Fig. 15. Aboral portion of *Bolina infundibulum* (Fabr.) from the transversal plane, a. p. apical prolongation of the sub-transversal meridional vessel; c. p. ciliated pouch of pharynx; c. r. ciliated ridge ("nerve"); excr. v. excretory vessel; inf. infundibulum; inf. c. infundibular canal; ir. v. interrarial vessel; o. opening of the oesophagus into the infundibulum; ph. f. pharyngeal (stomodæal) folds; p. f. polar field; t. v. tentacle vessel.

the place, where the adradial vessel joins it. In the largest specimens observed (ca. 5<sup>cm</sup> high) this prolongation had increased very considerably, as shown in fig. 15. Considering the much larger size of the specimens studied by Vogt & Yung, it seems quite possible that in such large specimens the prolongation of the subtentacular meridional vessels has increased so much as to join the excretory vessel. — Also L. Agassiz (Op. cit. p. 364) appears to have observed such a connection of the vessels (— he believes that all eight meridional vessels are in connection with the "ring"-vessel below the the apical organ —). — It may be remarked that I did not observe any cilia along the adapical continuation of these vessels, such as are shown in the quoted figure of Vogt & Yung.

Regarding the windings of the subventral vessels in the lobes Vogt & Yung state to have failed to see "die reizenden Arabesken, in welche jene Linien, die nur durch das Vorhandensein des

Gefäßes angedeutet waren, auf der Oberfläche der Lappen anderer Arten auslaufen" (Op. cit. p. 182). It may then not be superfluous to say, that I have found no particular difficulty in observing these windings, and that I have found them in general corresponding with the representation given thereof by L. Agassiz (Op. cit.), especially in his Fig. 4, Pl. 7 and fig. 7, Pl. 8. The median fold is always simple, while the two lateral folds have generally two smaller, secondary folds, which may again be subdivided. That the windings will prove to be more complicated in such large specimens as those observed by Vogt & Yung, is very probable. It is worth remarking that the windings in the two lobes may be somewhat different, as was also observed by Vanhöffen (Grönländische Ctenoph. p. 19).

The description of the muscular system given by Vogt & Yung is not very satisfactory; though I have not studied the arrangement of the muscles in all details, I can give some additional information thereof. The "mighty" retractor muscles of the apical organ, also described by Chun (Monogr. p. 292; Dissogonie, p. 82, fig. 1), who states them to go from the apical organ to the basis of the lobes — I have certainly observed; but I cannot agree that they are so very strong, and I have found the fibres to be attached to the subventral vessels, not reaching to the lobes. Inside the peculiar netshaped musculature on the adoral side of the lobes are found some longitudinal muscles, converging towards the mouth. These, of course, serve to open the lobes, being the antagonists of the netshaped muscles. From the meridional vessels radial muscles run inwards; on the contraction of these muscles the costæ are retracted, the skin folding over them. Other muscular threads serve to draw aside the folds of the skin so as to expose again the costæ. But I shall not enter here on the details of this delicate muscular system. — It may be observed that even when the costæ are fully exposed there is seen a distinct line along each side of them, the margin of the folds which cover them when retracted; the costæ thus lie in concave ridges. Also the intercostal areas are slightly concave on the sides of the animal, while at the apical pole they are distinctly convex.

The wonderful researches of Chun on the dissogony having been made on the Mediterranean *Bolina*, which would appear to be only a local form of *B. infundibulum*, the question naturally arises, whether dissogony occurs also in the form from the North European coasts; this question becomes the more interesting, as Chun has found that the dissogony "nur unter dem Einfluss einer erhöhten Oberflächentemperatur des Seewassers eintritt" (Dissogonie, p. 103). Though I have not had occasion to study myself the newly hatched young of *Bolina*, I think it can be said with rather great certainty that dissogony obtains also in the specimens of our seas. As stated above (p. 70) it can scarcely be doubted that the young Ctenophore from Helgoland, thought by Garbe (Op. cit.) to be the young of *Pleurobrachia rhodopis*, is really a young *Bolina*. In Taf. XXXVII, fig. 18 he figures a section of a specimen 0.5<sup>mm</sup> in diameter, in which the genital organs are already in full activity, producing eggs and spermatozoa. As in the specimens studied by Chun only 4 genital organs are developed. They lie close to the tentacle bases, so that there would appear to be a difference here between this specimen and those studied by Chun, the latter having the genital organs developed along the subventral vessels, not along the subtentacular. This difference, however, is only apparent. In the figure quoted of Garbe the testes are represented as lying close to the tentacle, the ovaries on the other side. This is a proof that the vessels in which the genital organs have developed are really the subventral; if it were the subtentacular the arrangement of the ovary and testis would have been the reverse.

There is thus no disagreement with the results obtained by Chun from the study of specimens from the Mediterranean. The slight development of the meridional vessels in the specimen figured by Garbe would seem to indicate that it has been the young, not of a grown specimen, but of a young in dissogony. (Comp. Taf. IX, figs. 10—11 of Chun's memoir "Die Dissogonie").

It is well known that this delicate species offers the greatest difficulties to preservation; in most preserving fluids, and specially in alcohol and formaline, it completely dissolves, almost in an explosive manner, scarcely some small pieces of skin remaining of it — strangely enough, since the consistence of the jelly is rather firm, though I would not agree with Vogt & Yung (Op. cit. p. 176) that it is "sehr hart und der Körper bietet fast denselben Widerstand wie Knorpel". The reason of this difficulty in the preservation appears to lie in a quite remarkable impermeability of the jelly. I have watched the penetration of the different preserving fluids under the microscope and found that, while the skin of the animal is, of course, at once fixated, the ciliation of the pharynx and the circulation within the gastrovascular canals continue as if nothing had happened. When then the preserving fluid begins to penetrate into the jelly, the muscle fibres contract so violently that all the inner organs break to pieces, like an explosion. On applying the mixture of Chrom-Osmic acid used by Lo Bianco<sup>1)</sup> for Ctenophores, one may succeed in preserving the skin and accordingly the shape of the animal rather intact, at least in small specimens, but the inner organs are, generally, destroyed in the usual way. Having made this observation I thought that, if it might be possible to narcotize the animal before killing it, preservation in a satisfactory state might succeed. My experiments as to this gave the surprising result that the animal appeared to be nearly insensible to the different narcotizing reagents, such as ether, cocaïn, chloral, epsomsalt, tobacco; thus a specimen remained alive for two days in a solution of tobacco so strong that the water was quite brown and strongly smelling. When at last the animals could not stand the reagents any longer, they dissolved, no narcotizing being obtained. When nearly giving the matter up in despair I tried to add alcohol in drops to the water in which the animals were kept — and this time with excellent result. Complete narcotizing was easily obtained in this way, and then the inner organs remained complete, when the fixating fluid (Chrom-Osmic acid) was added. Thus I succeeded in getting some specimens excellently preserved — until a new difficulty arose. During the time when the experiments described were carried out (at the Biological Station in Trondhjem, in the month of July 1911) the weather was very cold; then the temperature rose very considerably, and now in the warm weather the preservation did not succeed. The narcotizing and fixation succeeded as usual, but soon after the Chrom-osmic acid had been applied, the lobes of the animal swelled to deformity, the upper part of the body contemporaneously shrinking to almost nothing. I cannot doubt that the reason of this must be sought for in the high temperature. But, in any case, I have found, how the *Bolina* can be preserved very satisfactorily — in cold weather.

It naturally follows from the great delicacy of *Bolina* that it must be very liable to be damaged, when the sea is rough. In fact, I have often observed specimens which were more or less lacerated. The same observation is made by Chun for the *Lobatae* upon the whole. "Sie sind vollauf den Gefahren ausgesetzt, welche Wind und Wellenschlag in Gefolge haben. Bei jedem Sturme werden

<sup>1)</sup> Salvatore Lo Bianco. The methods employed at the Naples Zoological Station for the preservation of marine Animals. Bull. U. S. National Museum. 39. 1899. p. 26.

sie zerfetzt und massenhaft vernichtet; es dauert nach stürmischen Zeiten oft eine Woche bis man unter dem überreichen Material von Bruchstücken wieder völlig intakte Exemplare entdeckt". Chun then thinks that "ein recht erheblicher Bruchtheil aller Lobaten allein schon durch Wellenschlag der Vernichtung preisgegeben werden, da den Ctenophoren nach den übereinstimmenden Berichten aller Beobachter ein Regenerationsvermögen abgetrennter Theile durchaus abgeht" (Dissogonie, p. 103). The dissogony is then thought to be a specially acquired means, through which these forms, which are thus far so badly adapted to the life in the surface waters that they are constantly destroyed by the physical environment, secure their survival in this strange struggle for life.

This supposed inability of regenerating even smaller parts of the body in such fragile and comparatively low organisms appeared to me very strange and not very convincing; I therefore paid special attention to the matter during my stay at the Trondhjem station. I very soon observed specimens which had all appearance of the lobes being in regeneration. Wishing, however, to have the matter put beyond doubt I undertook some experiments in order to have the question solved definitely. Having taken one day a good deal of specimens in a large plankton-net, these specimens, all more or less lacerated through the capture, were put in a large jar, full of water. On examining them two days afterwards I found the wounds closed, and the lost parts (lobes, auricles, tentacles and combs) were very evidently about to regenerate, the vessels of the lobes having already begun to form anew. In the course of a week the specimens had completely regenerated the lost parts, these being only as yet slightly smaller than the corresponding normal parts. Also the windings of the lobe vessels had been formed again as normal.

Having thus ascertained that the *Bolina* has a very considerable regenerating power, I determined to carry out some more exact experiments and try to decide how far the regenerating power goes. Some specimens were cut in different ways. In one the apical organ was extirpated, another was divided in two halves after the sagittal plane, a third after the transversal plane and a fourth was divided horizontally in two parts. The experiments succeeded completely. In the course of a week the two halves of each of the vertically divided animals each regenerated the lacking part, likewise the lower part of the horizontally divided specimen regenerated the lacking upper part; only the upper part of this specimen succumbed before it had regenerated the mouth. In one of the halves of the specimen divided after the sagittal plane the two half lobes coalesced in the wrong way so as to form one sagittal lobe; but it afterwards amended it so as to get normal lobes again. That the extirpated apical organ very soon regenerated, need scarcely be emphasized, this being indeed a small thing in comparison with what the other specimens performed. But this had the special interest of proving that the apical organ has no influence on the regeneration, (as was, of course, also shown by the complete regeneration in the lower part of the horizontally divided specimen).

The experiments were carried out in the time from the 18th to the 28th of July, when my sojourn in Trondhjem ended. The regenerating halves of the specimens had then not yet fully reached the size of the original halves, but it seemed evident that in the course of a few days more they would have reached quite the normal condition again. — It is worth noticing that the regenerating specimens became considerably reduced in size during the regenerating process.

It may still be noticed that the above mentioned specimens, which were captured in the

plankton-net (on the 13th July), were still alive on the 28th, after having been kept all this time in the same jar, without the water having been changed or aërated. They were certainly in a somewhat poor condition at last, but this was evidently due to the high temperature during the last days; so long as the weather remained cool they were in a perfectly healthy state, and I have not the least doubt that they would have kept so for a long time, had the temperature remained low. My experience thus differs considerably from that of Evans & Ashworth, who state that "of a dozen (specimens of *Bolina*) brought home alive none survived the night" (Op. cit. p. 310). — The high temperature, of course, also influenced the regenerating specimens; otherwise I suppose the regeneration would have been complete during the ten days. — The food of the animals in the jar, where the water was not changed, appeared to be small Peridinians, which developed in great numbers therein. These specimens were often observed standing on their lobes on the bottom of the jar, but that did not seem to have any inconvenience to them, and they easily rose to the surface again.

Through these experiments it is definitely shown that the *Bolina* is in possession of quite a marvellous regenerating power, and it may not seem unreasonable to suggest that the same will prove to hold good also for other Lobatae — and upon the whole for the Ctenophora. (Also in *Beroë cucumis* I have seen distinct traces of regeneration; but experiments were not undertaken with that species). Chun's suggestion that the dissogony serves to counteract the destruction caused by a rough sea accordingly does not hold good.

It may still be mentioned that Chun's statement of the "übereinstimmenden Berichten aller Beobachter" that Ctenophores cannot regenerate is not quite correct either. Mertens (Op. cit. p. 494, 527—528) describes the regeneration of *Mertensia ovum* and also of *Cestus*. While the suggested regeneration of *Cestus* is doubtless a mistake of the wellknown fact that small isolated pieces may keep alive for a rather long time, it is not quite sure that it is likewise a mistake with the "*Beroë compressa*", since he states expressly to have observed the development of new combs. But in any case the literature is thus not without statements that a regenerating power exists in Ctenophorans. And this is, indeed, not the only statement of that kind. There is found another, much more important and quite unquestionable statement of extensive regeneration occurring in Ctenophorans, viz. in Chun's own, often quoted work on the dissogony. It is there shown that, when the egg of *Bolina* has undergone the first cleavage, the two halves of the egg, when isolated, each develop to a half larva, which is fully capable of living and even develops mature sexual products just as the normal larvæ do. These half larvæ are stated by Chun (Op. cit. p. 105) to regenerate later the lacking half of the body, so as to become, in all probability, quite normal. This observation is, certainly, in much better accordance with my observations of the excessive regenerating power of the grown *Bolina* than with the assertion of its total inability of regeneration.

By the "Ingolf"-Expedition *Bolina infundibulum* was observed on the 6th of July 1895, when at anchor on the "Great Hellefiske Bank" in the Davis Strait, off Holstensborg. Specimens were not preserved, but that it was really *Bolina infundibulum* can not be doubted. In the plankton-samples there are several pieces of skin of Ctenophores, which I feel rather convinced are of this species; but, of course, this cannot be fully ascertained, so it seems preferable not to give the stations. From Iceland (Skutliffjörd, 15. VI. 1892) there are some specimens, rather well preserved (with dilute osmic acid) by Mr.

Will. Lundbeck. — On the "Danmark" Expedition it was observed in September 1907 at the "Skibshavn" (76° 47' N., 18° 26' W.) in considerable numbers and in different sizes.

This species is distributed over the whole of the Northern Atlantic, from Spitzbergen and Greenland down along the American Coast to the Gulf of Georgia, at least, and on the European side to the Danish and British Seas, and most probably to the Mediterranean. From the Bering-Strait it is known through Mertens, so that it is evidently circumpolar. Regarding its vertical distribution Damas & Koefoed (Op. cit. p. 415) state that it goes beyond a depth of 200<sup>m</sup>.

### 5. *Beroë cucumis* Fabricius.

- Beroë cucumis*. O. Fabricius. Fauna groenlandica. 1780. p. 361.  
 — — ? O. Fabr. M. Sars. Beskrivelser og Iagttagelser... 1835. p. 30. Pl. 6. Fig. 15 a—d.  
*Idyia roseola*. L. Agassiz. Contributions Nat. Hist. U. S. America. II. 1860. p. 270—288. Pl. I—II.  
 — — Agass. A. Agassiz. North American Acalephæ. Ill. Cat. Mus. Comp. Zool. II. 1865. p. 36.  
 ?— *cyathina* A. Agass. — Ibidem. p. 38.  
 ? *Idyopsis Clarkii* Agass. — Ibidem. p. 39.  
*Beroë ovata* Eschsch. Chun. Ctenophoren d. Golfes v. Neapel. 1880. p. 308. Taf. XIV. Figs. 1—2.  
 — *cucumis* Fabr. — Ctenophoren d. Plankton-Expedition. 1898. p. 26.  
 — *ovata* Bosc. — Ibid. p. 26.  
 — *cucumis* Fabr. Vanhöffen. Die grönländischen Ctenophoren. Bibl. Zool. VIII. H. 20. 1895. p. 20.  
 — — — — Ctenophoren. Nordisches Plankton. 1903. XI. p. 7.  
 — — — Römer. Die Ctenophoren. Fauna Arctica. III. 1903. p. 81.  
 — *ovata* Bosc. — Ibidem. p. 84.  
 — — Eschsch. Moser. Die Ctenophoren d. Siboga-Expedition. 1903. p. 20.  
 — *cucumis* Fabr. — Ibidem. p. 21.  
 — *ovata* Bosc. — Japanische Ctenophoren. 1908. p. 22.  
 — *cucumis* Fabr. — Ibidem. p. 23.  
 — — — — Cténophores de la Baie d'Amboine. Rev. Suisse de Zool. 16. 1908. p. 10.  
 — — — — Ctenophoren d. deutschen Südpolar-Exped. 1909. p. 154.  
 ?— *Clarkii* L. Agass. — Ibidem. p. 157. Taf. XXI. Fig. 16—17.

The question about the possible identity of *Beroë cucumis* Fabr. and the Mediterranean *B. ovata* Bosc. was raised by Vanhöffen. In his paper "Die grönländischen Ctenophoren" (p. 20) he says: "Die kräftigere *Beroë ovata* der wärmeren Meere mag, bis weitere Untersuchungen vorliegen, als eigene Art gelten, da ich kein genügendes Vergleichsmaterial habe, diese Frage zu entscheiden, obwohl ich mir nicht verhehlen kann, dass der von Chun (Ctenoph. Golfes Neapel, p. 305) zwischen *B. ovata* und *B. roseola* (= *cucumis*) angegebene Unterschied, das Fehlen eines Gefässnetzes auf der Magenwand von *B. roseola* nicht stichhaltig ist. Sowohl bei der grönländischen *Beroë* wie auch bei den Exemplaren von Kiel habe ich die die Magenwand umspannenden Äste der von den Meridionalgefässen ausgehenden Prolifikationen nachweisen können".

Objecting to this cautious suggestion of the possible identity of the two species Chun (Die

Ctenophoren d. Plankton-Exped. p. 27) points out more precisely as the difference between the arctic *B. cucumis* and the Mediterranean-Atlantic *B. ovata* that "bei *Beroë cucumis* enden die auf die Magenwand übertretenden Prolifikationen der Meridionalgefäßen blind, ohne ein anastomosirendes Netzwerk von Gefäßmaschen zu bilden, welches mit dem Magengefäß kommuniziert; bei *B. ovata* anastomosiert ein Teil der Gefäßprolifikationen, indem sie nicht nur unter sich, sondern auch mit dem Magengefäße Verbindungen eingehen".

This is accepted by Vanhöffen in his "Ctenophoren" in "Nordisches Plankton" and especially by Moser (Japanische Ctenophoren, p. 19), who gives the difference between the two species more precisely thus: "Bei *Beroë cucumis* sind, im Gegensatz zu den Meridionalgefäßen, die Magengefäße unverzweigt; die auf die Magenwand übertretenden Prolifikationen der Meridionalgefäße enden blind. — Bei *Beroë ovata* sind auch die Magengefäße verzweigt; ihre Äste bilden mit jenen der Meridionalgefäße ein anastomosierendes Netzwerk auf der Magenwand". It is further maintained (p. 21) that *Beroë ovata* "eine ausschliesslich mediterrane Form ist, währen aus den Funden von Ambon und von der japanischen Küste hervorgeht, dass *Beroë cucumis* nicht eine exklusiv nordische und atlantische Form ist, sondern auch in den warmen Meeren vorkommt und ein Kosmopolit im weitesten Sinne des Wortes ist".

After this definition it seems easy enough to distinguish the two species, and the alleged occurrence exclusively in the Mediterranean<sup>1)</sup> of *B. ovata*, while *B. cucumis* is not known to occur there, would alone seem to make it impossible to confuse the two species. But nature does not agree with this; the sharp distinction between the two forms does not really exist. From a careful study of a large material of *Beroë* from the Danish and Norwegian Seas, from Greenland, from the Atlantic and the Mediterranean I have found all transitional stages to exist in regard to the development of proliferations from the pharyngeal vessels, from the highly branched condition characterizing the "species" *ovata* to the unbranched condition characterizing the "species" *cucumis*. My attention was first called to this fact by the examination of a number of specimens from the Godthaab Fjord, Greenland, brought home by Mr. Ad. S. Jensen from the "Tjalfe"-Expedition. Some of these specimens had the pharyngeal vessels quite unbranched, while others had them more or less richly provided with alternating proliferations. That the differences in this respect were not due to growth-changes, was evident from the fact that the proliferations were developed in a specimen of 10<sup>mm</sup> length, while in other specimens of 15<sup>mm</sup> length no proliferations at all were developed. All these specimens were in all other regards so decidedly alike that it would be quite unreasonable to separate them into two species. The same differences were found in specimens from another Greenland locality (Holstensborg). Among a considerable number of specimens from the Skagerak, which I collected in June 1911 on the "Thor",

<sup>1)</sup> R. T. Günther (Report on the Coelenterata from the intermediate waters of the N. Atlantic obtained by Mr. George Murray during the Cruise of the "Oceana" in 1898. Ann. Nat. Hist. 6. Ser. XI. 1903. p. 429) certainly mentions *Beroë ovata*; but there is no guarantee at all that this was really another species than *B. cucumis*. That the *B. ovata* mentioned by Hartlaub (Beiträge zur Meeresfauna von Helgoland. IV. Die Coelenteraten Helgolands. Wiss. Meeresuntersuchungen. N. F. II. 1894. p. 204) is really *B. cucumis*, has been shown by Moser (Japanische Ctenophoren, p. 20). M. & C. Delap (Notes on the Plankton of Valencia Harbour. 1899—1901. Ann. Rep. Fish. Ireland. 1902—3. Pt. II. App. I. 1905. p. 5) record *Beroë ovata* Esch. as the only Beroid occurring at this locality. That it is the same as *B. cucumis* can scarcely be doubted. Also Evans & Ashworth (Some Medusæ and Ctenophores from the Firth of Forth. Proc. R. Phys. Soc. XVII. 1909. p. 311) state that "in this area the specific names *ovata* and *cucumis* have doubtless been applied to the same form". Römer (Op. cit. p. 85), gives several other instances, where *B. ovata* has been recorded from the North European Seas. The *Beroë ovata* mentioned by Fewkes and Hargitt (see below, p. 86) may perhaps be something different (*Beroë Clarkii*).

there were also found some specimens with proliferations from the pharyngeal vessels, though none had them very richly developed. Being, of course, very anxious to examine specimens from the Mediterranean, I got a couple of large, beautiful specimens from the Zoological Station at Naples; one of them had the proliferations from the pharyngeal vessels very richly developed, the other had only very few proliferations. Later on I got a considerable number of specimens from the Mediterranean from the "Thor", and likewise found a very considerable variation in regard to the proliferations from the pharyngeal vessels; most of them had the proliferations richly developed, but in some of them, among which some of the largest specimens, there were quite few or only a single pair of them. Finally I have found the same variations to exist in specimens from the Atlantic.

The result is then that it is impossible to maintain *B. ovata* as a separate species, the only character thought to distinguish it from *B. cucumis*, the proliferations from the pharyngeal vessels, being quite unreliable on account of its great variability. All transitional stages may be found together in the same locality, in Greenland as well as in the Mediterranean. It is, however, evident that in the specimens from the North European Seas, and probably of the whole North Atlantic the general condition is that the pharyngeal vessels have no proliferations, while in the Mediterranean form there is generally a rich development of these proliferations. There may then perhaps be reason to separate the latter as a special form or variety of *B. cucumis*. Also in the specimens from the warm regions of the Atlantic at my disposal I have found the proliferations generally more developed than in the northern form.

Regarding the synonymy of *B. cucumis* I would further point out that it is perhaps not quite certain that *Idyia cyathina* A. Agass. is identical with it and perhaps it is not certain either that *Idyiopsis Clarkii* L. Agass. is a distinct species as maintained by Moser. As to the first of these, it is true that L. Agassiz states (Op. cit. p. 287) that "there is not the slightest structural difference between the two" (viz. *cyathina* and *roseola*); but A. Agassiz (North American Acalephæ, p. 39) states that "the ovaries and spermaries are much longer sacs than in *I. roseola*, and not so numerous". This character together with the differences in shape (— "it is widest at two thirds the distance from the mouth; it then tapers as suddenly for another third of the distance to the mouth, and then very gradually" —) and habits (— "instead of the sluggish movements which characterize *Idyia roseola*, *Idyia cyathina* is very active, and seems to retain the embryonic features of the genus, — short rows of flappers, and great activity in its adult condition" —) would perhaps seem to indicate that it is not identical with *B. cucumis*.

In the "Japanische Ctenophoren" (p. 20—21) Moser reaches the conclusion, after a careful revision of the literature on that subject, that *Idyiopsis Clarkii* L. Agass. (together with *Idyiopsis affinis* L. Agass.) should be regarded as a doubtful species; in the "Ctenophoren d. deutschen Südpolar-Expedition" (p. 157—159) the author maintains it as a distinct species after having examined some well preserved specimens brought home from the Tortugas by Dr. R. Hartmeyer. The characters upon which the species is maintained are: the shape of the body and the position of the costæ. Judging from the figures given by Moser the shape is certainly more rounded at the apical pole than is generally the case in *B. cucumis* — but how much of that is due to contraction on preservation? The polar plates having been withdrawn, it is evident that no small amount of contraction has taken

place. Further I must state, concerning the arrangement of the costæ, that it may be found quite alike in *B. cucumis*; thus e.g. a large specimen from Naples shows exactly the same arrangement as that seen in fig. 17 of Moser. The characters pointed out by Moser as distinguishing *B. Clarkii* from *cucumis* thus appear to me of rather slight value. Some more weight I would ascribe to the different coloration; L. Agassiz (Op. cit. p. 288) states "from notes made years ago... that the rows of locomotive flappers have on each side a band of yellow and brown stellate dots, and that the edge of the mouth, as well as the fringes around the circumscribed area, were dotted in the same manner". This coloration differs rather much from that of *B. cucumis*, so that it seems quite probable that *B. Clarkii* is really different from *B. cucumis*. But the descriptions hitherto given are by no means sufficient. Renewed careful observations on living material are needed for deciding the question about the specific value of both *B. Clarkii* and *cyathina* (— which may perhaps prove to be identical —), as well as of the other Ctenophores of the North American Coasts<sup>1</sup>.

While it is quite probable that there will prove really to exist two different species of *Beroë* at the North American Atlantic Coasts, it may be said with rather great certainty that only one species normally occurs in the North European Seas. It is true that Hartlaub<sup>2</sup>) mentions a small *Beroë* from Helgoland, which he regards as specifically distinct from *B. cucumis*, without giving, however, the characters by which it should be distinguished. Though I have been unable to obtain specimens of this form for study, as it has not been observed more recently there, I cannot regard it as doubtful that it is really only *B. cucumis*<sup>3</sup>). — Another thing is, that perhaps *Beroë Forskålii* may sometimes occur in the North European Seas (Comp. below, p. 92); but there can, of course, be no question of Hartlaubs' small Beroid being this species, the more so as it was found nearly the whole year round, which could not have been the case with *B. Forskålii*.

Having the opportunity last summer (1911) of studying a fair number of living specimens of *Beroë cucumis* at the Biological Station of Trondhjem I paid attention to the possible existence of other characters by which to distinguish *B. cucumis* from *B. ovata*, instead of the character of the pharyngeal vessels, which I had then already found to be without the value of a certain distinguishing character. I thought especially that some difference might possibly exist in the distribution of the peculiar sabre-shaped cilia of the mouth-edge. In *Beroë Forskålii* they are shown by Chun (Monograph, p. 185, Taf. XIV, a. fig. 8) to radiate inwards in attenuating bands from a continuous band at the mouth-edge; Chun does not describe their arrangement in *B. ovata*, but on the specimens at my disposal I found them to be arranged only in a simple band along the edge. The same was found to

<sup>1</sup>) The *Beroë ovata* mentioned by I. W. Fewkes (Notes on Acalephs from the Tortugas, with a Description of New Genera and Species. Bull. Mus. Comp. Zool. IX. 1882. p. 251) is probably the same as *B. Clarkii*. Whether this is also the case with the *Beroë ovata* mentioned by Ch. W. Hargitt (The Medusæ of the Woods Hole Region. Bull. Bureau of Fisheries. XXIV. 1904, p. 73) as being found commonly at Woods Hole (in 1901), seems very doubtful. Judging from the few notes which are found under the two species "ovata" and "cucumis" it appears rather evident that both are really *B. cucumis*; it is only the large specimens ("40–70 mm in polar diameter") which are distinguished as *B. ovata*, while the smaller specimens ("15–20 mm in polar diameter") are designated as *B. cucumis*.

<sup>2</sup>) Cf. Hartlaub. Beiträge zur Meeresfauna von Helgoland. IV. Die Coelenteraten Helgolands. Wiss. Meeresuntersuchungen. Abth. Helgoland. N. F. II. 1894. p. 204.

<sup>3</sup>) Also Römer (Op. cit. p. 83) is inclined to regard it as identical with *B. cucumis*, suggesting "dass sie in dem wärmeren Wasser der Nordsee nicht die Grösse erreicht, wie die Exemplare der kälteren Strömungen, sondern hier schon bei der geringen Höhe von 1 cm geschlechtsreif wird". This suggestion, of course, must be dropped on the demonstration of the *B. ovata* of the Mediterranean and the warm Atlantic regions being identical with the *B. cucumis* of the North Atlantic. — A question to be yet examined is, however, at what size *B. cucumis* becomes sexually mature in the different regions in which it occurs.

be the case in the typical *B. cucumis* from the Trondhjem Fjord, as I have upon the whole found the same arrangement in all the specimens examined, so far as they were in a condition allowing the examination of this feature. — I would recall, on this occasion, the observation of L. Agassiz that these cilia are arranged in longitudinal lines, giving the mouth-edge a finely striated appearance (Op. cit. p. 281, Pl. I. fig. 2. a, Pl. II, fig. 19), as I have also found to be the case. The latter figure also shows the red pigment spots of the mouth-edge to have the shape of fine longitudinal striæ, a condition which I find to hold good also for those pigment spots occurring inside the band of the sabre-shaped cilia along the wall of the pharyngeal cavity.

On adopting Chun's suggestion that the sabre-shaped cilia serve the purpose of retaining the prey, in a similar way as the teeth of snakes, Samassa (Histologie d. Ctenophoren, p. 165) concludes that "demnach dürfte ihnen beim erwachsenen Thier active Beweglichkeit kaum zukommen". This suggestion is certainly not right. Chun (loc. cit.) has observed that when the *Beroë* catches a prey these cilia are very actively moving and "in die Gallerte des Opfers eingeschlagen werden", and I have observed them (under the microscope) to be in a constant, very lively movement, also when they are not about to catch a prey.

This species most probably possesses the same great power of regeneration as *Bolina infundibulum*. Though I have made no direct experiments in order to ascertain this, I think the conclusion quite justified by the observation of several specimens (in the Trondhjem Fjord) which had all appearance of having regenerated different parts of their body. Numerous more or less mutilated specimens were often observed, it being sometimes even difficult to find a complete specimen. Such mutilation being evidently not due to the smooth waters of the fjord, the explanation of this phenomenon is most probably this, that these specimens were damaged by the rough sea outside the fjord, afterwards being carried into the fjord by the tidal current. That all these specimens would regenerate completely I have not the slightest doubt. — Already M. Sars (Op. cit. p. 31) noticed a great percentage of damaged specimens; he observed rightly that the mutilated specimens are as active in their movements as the undamaged; but when he suggests that they might continue to live in this condition — "so little is the mutual connection of the single parts and organs of these low animals" — he is evidently not right, having overlooked the important fact of the regeneration. The same holds good of L. Agassiz (Op. cit. p. 273), who has observed that the large specimens are broken to pieces by the heavy September storms of the American Coasts, from which fact it is concluded that "the adult *Idyias*, having performed their part in life, break up under the influence of the waning summer; while, during the whole winter, the young....subside into deep waters, to reappear only with the more genial season, when they complete their growth, reproduce their kind, and die in their turn". This certainly looks very plain; but in our seas at least the large specimens do not disappear with the fall. I have observed large specimens in the Gullmar Fjord (at the Zoological Station of Kristineberg, Sweden) in the month of January. The question of the duration of life in these forms is an unsolved problem, as are so many other points in their biology.

M. Sars records to have observed a specimen in which the whole aboral portion was lost, so that it resembled a broad ring; however, the specimen appeared to be quite well and comfortable. I have also found such a specimen; on keeping this specimen in a jar together with a *Bolina* I had

the pleasure of seeing it catching the latter in the usual way. Of course, the Bolina glided out again the opposite way; — it reminded me of the horse of Münchhausen! — It being on one of the last days of my stay at the Trondhjem Station I could not substantiate, whether the specimen thus mutilated was able to regenerate the lost main part of its body.

In a pair of the larger specimens caught in the Skagerak I have found *Hyperia*, one specimen in each. It would seem to be the same parasite, which was observed by Sars (Op. cit. p. 32), though he states that they were always found attached to the combs.

Specimens of *Beroë cucumis* were taken by the "Ingolf"-Expedition on the following stations:

Station 11.	(64° 34' N. 31° 12' W.)	1	small specimen.		
—	52. (63° 57' - 13° 32' - )	1	—	—	—
—	80. (61° 02' - 29° 32' - )	1	—	—	—
—	96. (65° 24' - 29° 00' - )	1	—	—	—
—	140. (63° 29' - 6° 57' - )	1	large	—	—

Further a small specimen was taken at 61° 32' N. 10° 47' W. (between stations 45 and 46). Besides, the occurrence of Beroids is noted in the Journal of the Expedition at a number of other stations; as, however, it cannot be said with full certainty that these must have been *Beroë cucumis*, it has been thought better not to name these stations. Also on the "Danmark" Expedition it was observed at North East Greenland (75° 7' N. 9° 23' W.) in August 1906, numerous specimens, in all sizes. In March 1907 some large specimens were observed in an opening in the ice, an interesting observation, showing the occurrence of the species under the ice.

This species has quite a cosmopolitan distribution, occurring in the arctic and antarctic, as well as in the tropical seas. Regarding its bathymetrical distribution very little is known. Only Damas & Koefoed (Op. cit. p. 415) state that it extends beyond the depth of 200<sup>m</sup> 1).

The following species have been recorded from the North European Seas, but there is no definite proof as yet, that they really occur there. As set forth below (p. 95) it is, however, by no means improbable that they — and perhaps some other southern forms — will prove to occur there under certain hydrographical conditions. A few notes may be given on these forms.

**Hormiphora plumosa** (M. Sars). Edw. J. Bles in his "Notes on the Plankton observed at Plymouth during June, July, August and September 1892" (Journ. Mar. Biol. Assoc. II. N.S. 1892. p. 340) mentions *Hormiphora plumosa* as "the Ctenophore common at Plymouth". That this is simply a wrong identification of *Pleurobrachia pileus* is beyond doubt, as might be concluded from the fact that he does not mention the latter as occurring there. Dr. E. J. Allen has also kindly informed me that Bles was mistaken herein; *Pleurobrachia pileus* is common at Plymouth, together with

<sup>1)</sup> The differential catches recorded by R. T. Günther (Op. cit.) afford no certainty of the depth at which *Beroë cucumis* (*ovata*) and other unidentified Ctenophores were taken. The statement that a specimen of *Beroë ovata* was taken "between 1510 fathoms and the surface" is certainly not of much value. Closing nets alone can give fully reliable results in regard to the bathymetrical distribution.

*Bolina infundibulum* and *Beroë cucumis*, no other Ctenophores than these three being known from this locality. (Cf. "Plymouth marine Invertebrate Fauna". Journ. Mar. Biol. Assoc. VIII. 1906. p. 206).

The species is further stated by C. W. S. Aurivillius in his "Vergleichende thiergeographische Untersuchungen über die Plankton-Fauna des Skageraks in den Jahren 1893—1897 (Kgl. Svenska Vet. Akad. Handl. Bd. 30. 1898) to occur in the Skagerak in the months of July—November, and likewise Hj. Théel in his paper "Om Utvecklingen af Sveriges zoologiska Hafsstation, Kristineberg, och om Djurlifvet i angränsande Haf och Fjordar" (Arkiv för Zoologi. Bd. 4. No. 5. 1907, p. 61) records it to occur in the Gullmar Fjord (at the Swedish Coast of the Skagerak) in the month of August. It is impossible to say at present whether these statements are correct or not. No material of the supposed *Hormiphora* is found preserved either in the Stockholm Museum or at the Zoological Station at Kristineberg, as I am informed by Professor Théel and Dr. Östergren, so I have been unable to reexamine any of the specimens thus identified. Since, however, both authors mention both *Pleurobrachia pileus* and *Hormiphora plumosa*, their statements can not be disposed of as simple cases of erroneous identification. That Aurivillius (Op. cit. p. 27) takes *Cydidippe quadricostata* M. Sars (the young of *Bolina infundibulum*, cf. p. 76) to be synonymous with *Hormiphora plumosa* does not support the correctness of his identification of this species; but, on the other hand, it is not a sufficient proof either, that the identification was incorrect. In the Report on the Plankton of the Danish Seas in 1898—1901<sup>1)</sup> it is stated that no specimens of *Hormiphora plumosa* were found in the Plankton-samples.

With certainty *Hormiphora plumosa* is as yet known only from the Mediterranean. The fragments of *Hormiphora* observed by A. G. Mayer<sup>2)</sup> at the Tortugas, Florida, may as well belong to one of the Atlantic species described by Chun (Ctenophoren d. Plankton-Expedition), *H. spatulata* Chun<sup>3)</sup> and *H. palmata* Chun.

**Lesueuria vitrea** M. Edw.<sup>4)</sup> This form, known otherwise only from the Mediterranean — where it has been observed only a few times (in 1852 by M. Sars and in 1870 by Spagnolini) since it was described in 1841 by Milne Edwards<sup>5)</sup> — is recorded from the Coast of Scotland by M'Intosh<sup>6)</sup> in 1888—1890, but has not been met with anywhere since then. This remarkably irregular occurrence may be explained in different ways. It might be supposed that the *Lesueuria* is a

<sup>1)</sup> De danske Farvandes Plankton i Aarene 1898—1901, II., af Søren Jensen, A. C. Johansen og I. Chr. L. Levensen. K. Danske Vidensk. Selsk. Skr. 6. R. Bd. XII. 1903. p. 283.

<sup>2)</sup> A. G. Mayer. Some Medusæ from the Tortugas, Florida. Bull. Mus. Comp. Zool. XXXVII. 1900. p. 82.

<sup>3)</sup> It may be suggested that the specimen figured in Taf. III. Fig. 4 by Chun (Op. cit.) as a large specimen of *Hormiphora spatulata* is perhaps only a *Pleurobrachia pileus*, the unusual place of the tentacle-bases being due to contraction on preservation (Comp. Fig. 13. b. p. 70). That the tentacles have only simple branches is certainly not in contradiction with this suggestion, and there are no facts to support the assumption of Chun (Op. cit. p. 17) that the eolidia-shaped branches of the tentacles disappear with age. The level at which the opening of the tentacle sheath lies is also more in accordance with *Pl. pileus* than with the specimen of *Horm. spatulata* of 8 mm length in Taf. III, Fig. 3.

<sup>4)</sup> On p. 60 is wrongly named *Lesueuria hyboptera* A. Ag.

<sup>5)</sup> H. Milne Edwards. Observations sur la structure et les fonctions de quelques Zoophytes, Mollusques et Crustacés des Côtes de France. Ann. d. Sci. nat. Zoologie. 2. Sér. XVI. 1841. p. 199. Pl. 2—4.

<sup>6)</sup> M'Intosh. Notes from the St. Andrews Marine Laboratory. IX—X. Ann. Mag. Nat. Hist. 6. Ser. 2, 1880. p. 464, 6. Ser. V. 1890. p. 46.

deep-water form, which only now and then is carried to the surface under certain hydrographic conditions, or that it is no separate form at all, but only a *Bolina* in a heteromorph condition, as suggested by Vanhöffen (Grönländische Ctenophoren, p. 18—19). (That the *Lesueurina vitrea* recorded from Scotland by M'Intosh is really *Bolina infundibulum*, as pointed out by Vanhöffen (Grönland. Ctenoph. p. 19) and Evans & Ashworth (Op. cit. p. 309) is another thing, not implying eo ipso that the true *Lesueurina* is the same). Finally Moser (Ctenophoren d. deutschen Südpolar-Expedition, p. 178), thinking that there is no support for the suggestion of Vanhöffen, expresses the view that the *Lesueurina* "allerdings wahrscheinlich jetzt ganz ausgestorben ist", which would certainly also account for its not having been observed for more than 25 years. While there is no real support for the first suggestion — and still less for the last one —, all evidence is for the assumption that the *Lesueurina* is no separate form at all. On the other hand, I would not simply adopt the suggestion of Vanhöffen that it is a heteromorph condition of *Bolina*, perhaps due to the dissogony<sup>1</sup>), and thus really a normal condition. In my opinion the *Lesueurina vitrea* is only a *Bolina infundibulum* (or perhaps some other Lobate) which has lost its lobes through mutilation, and the same I think will prove to hold good of *Lesueurina hyboptera* A. Agass. I have myself observed such mutilated specimens of *Bolina infundibulum*, which were exactly like *Lesueurina* and which I would have regarded as such without the knowledge of the regenerative power of the *Bolina*. It is true that A. Agassiz (North American Acalephæ, p. 24) has noticed that mutilated specimens of *Bolina* are very like the *Lesueurina*, and it should then be taken as an argument in favour of the distinctness of the *Lesueurina* that, in spite of its likeness with the mutilated specimens of *Bolina*, it is maintained as a separate form, the characters distinguishing it from the *Bolina* being the great length of the auricles and the position of the mouth. But the length of the auricles (which I have found to be rather variable) may be as great in *Bolina*, and the position of the mouth does not differ either in the two forms, if specimens of the same size are compared. If in the specimen of *Bolina* copied from Vogt & Yung in the fig. 11 of Vanhöffen's Ctenophoren (Nordisches Plankton) we imagine the lobes removed, the result will be a *Lesueurina* not to be distinguished from the *L. hyboptera* of Agassiz, as copied in the fig. 10 of the same work. Concerning the *Lesueurina vitrea* of Milne Edwards there is only one thing which makes me hesitate a little in regarding it likewise as belonging to *Bolina infundibulum*, viz. the patches of yellowish and greenish colour shown on the costæ in his figure 1, Pl. 2, the *Bolina* being otherwise not thus coloured. This might perhaps indicate that the *L. vitrea* of Milne Edwards really belongs to another Lobate; among the other Lobates known from the Mediterranean *Deiopea kaloktenota* Chun would alone have to be taken into consideration here. But the narrow costæ in the quoted figure of Milne Edwards do not recall the broad costæ of *Deiopea*, which, moreover, is described as "vollkommen durchsichtig".

Leaving the question undecided, to which species the *Lesueurina vitrea* should be referred, it

<sup>1</sup>) "Die von Agassiz (an der Ostküste Nordamerikas) beobachteten Arten *Bolina alata*, *Mnemiopsis Gardeni*, *Mnemiopsis Leidy* und *Lesueurina hyboptera* scheinen sich nur von *Bolina septentrionalis* durch das wechselnde Verhältnis der einzelnen Organe zu einander, der Randlappen mit den Kanälen zu den Aurikeln und dem mehr oder weniger tief herabhängenden Mundrohr zu unterscheiden, Verhältnisse, die teils durch Kontraktionszustände erzeugt sein können, teils auch vielleicht auf verschiedene Altersstufen oder durch heteromorphe Stadien derselben Art, bedingt durch die von Chun bei Ctenophoren entdeckte Dissogonie, oder endlich auf wirklicher Artverschiedenheit beruhen können". (Grönländische Ctenophoren; p. 19).

may be regarded as fairly certain that the genus *Lesueuria* cannot be maintained. It represents only mutilated specimens of *Bolina* (and perhaps also other Lobatæ), which have lost their lobes. Still less, of course, can the family *Lesueuridae*, established by Chun, be maintained. As a character of this family Chun regards the slight development of the lobe vessels, necessarily following from the rudimentary condition of the lobes. It may not be superfluous to point out that the otherwise excellent fig. 1, Pl. 3, of Milne Edwards does not show the course of the vessels in the lobes. The small vessels proceeding from the base of the auricle a little way along an "appendice tentaculaire" and ending blindly a short way from the auricle, I would suggest to represent the beginning of the marginal vessel of the lobe. The upwards directed continuation of the subventral vessel may be said with certainty not to be in connection with the other vessels at the base of the auricles, as stated by Milne Edwards; it is the vessel which forms the windings within the lobe; I have found the development of the vessels within the regenerating lobes of *Bolina* to begin in exactly the same way with the formation of the upward directed branch of the subventral vessels. — For *L. hyboptera* Agassiz certainly gives a figure (28) showing "the connection between the lateral and longitudinal ambulacra, forming a circular tube round the actinostome"; but the figure is a mere sketch, which can decidedly not be regarded as a valid proof of such a condition of the lobe vessels really existing here, contrary to what obtains in all other Lobatæ, — the more so as Agassiz himself states (Op. cit. p. 25) that "it differs in no essential way in its mode of formation from what we observe in *Bolina*".

The definite proof of the view of the *Lesueuria* here set forth must be given along the experimental way; if it is right, as I cannot doubt, the "*Lesueuriae*" will, if kept under favourable conditions, regenerate their lobes. Meanwhile, till the contrary has been proved, the *Lesueuria* must be regarded only as a mutilated *Bolina* or other Lobate. — It is also worth recalling that Agassiz states the *L. hyboptera* to be abundant in September, viz. the time when the *Beroë* is recorded to be broken to pieces by heavy storms.

**Cestus Veneris** Lesueur. This species, which is otherwise not known to occur North of 40°—50° lat. N. in the Atlantic, is recorded by N. Wagner<sup>1)</sup> to have been found in the White Sea (Solowetski Bay), in the middle of the summer, and even rather commonly. Chun (Ctenophoren d. Plankton-Exp. p. 20), Vanhöffen (Ctenophoren, Nordisches Plankton, p. 6), Römer (Ctenophoren, Fauna Arctica, p. 86) and Moser (Japanische Ctenophoren, p. 12, 14) suggest that it is probably another, undescribed, arctic species of *Cestus* which Wagner has observed here. I would not be inclined to adopt this suggestion. That the influence of the Gulf Stream is felt as far northwards as both the White Sea and Spitzbergen, is certain, and then it would not seem impossible that the *Cestus* might be carried northwards under certain especially favorable conditions — in spite of Römer's definite assertion that "an einem Transport durch die Ausläufer des Golfstromes auf so weite Entfernungen kann bei einer so zarten und typischen Warmwasserform nicht gedacht werden". That an otherwise unknown arctic species of this genus should exist, does not appear very probable, as it could then scarcely have avoided being detected by some of the numerous observers of arctic Ctenophores; on the other hand, it seems hardly possible that Wagner could have mistaken any other animal for a *Cestus*. The correctness of Wagner's observation can then scarcely be doubted.

<sup>1)</sup> N. Wagner. Die Wirbellosen des Weissen Meeres. I. 1885. p. 54.

**Beroë Forskålii** Chun. This species Wagner likewise records to have observed (together with *B. cucumis*) in the White Sea. His remark that it "hat eine so grosse Verbreitung, dass man sie in allen europäischen Meeren antreffen kann" (Op. cit. p. 54), does certainly not support the belief that his identification of this species was correct, there being no other statements of its occurring in the Atlantic or the European Seas, except the Mediterranean. A support of his statement is, however, found in the fact that Walter<sup>1)</sup> records to have observed two species of *Beroë* at Spitzbergen, one of which must also have been *B. Forskålii*, if the observation is correct.

That *B. Forskålii* really occurs in the Atlantic I cannot doubt. This is also supported by the fact that the collection of the Copenhagen Museum contains a pair of specimens taken at 5° N. 21° W. (Hygom, 1856) and at 47° N 7° 30' W (in the Bay of Biscay, 29/8. 1861), which I think must be referred to this species. Accordingly I must believe that it will prove to be widely distributed in the warm regions of the Atlantic, and it might then well be carried with the Gulf Stream both to Spitzbergen and the White Sea, like *Cestus Veneris*. — Its occurrence in the Atlantic is in good accordance with the fact that it is distributed over nearly the whole Indo-Pacific (Moser. Japanische Ctenophoren, p. 26), while its occurrence alone in the Mediterranean, besides the Indo-Pacific, as hitherto supposed, was a zoogeographic riddle.

### Zoogeographical Remarks.

The geographical distribution of the Ctenophores of the Northern Atlantic has been made the object of a more or less detailed study especially by Chun, Römer, Moser and Damas & Koefoed. The views expressed above of the synonymy of such species as *Pleurobrachia pileus*, *Bolina infundibulum* and *Beroë cucumis* having a rather important bearing upon the value of these forms in the study of zoogeography, it may not be superfluous to give here some remarks on this matter.

The Ctenophores being absolutely dependent on the currents for their distribution, they are, of course, of no small value for the determination of the extension of the different currents — provided that they occur only in the cold or the warm water, and not in both. In case they are so little affected by temperature that they may live both in the arctic and the warm regions of the sea, their occurrence at some place or other can, of course, not be taken as a proof of the extension thither of one or the other stream. This appears exactly to be the case with the species *Pleurobrachia pileus*, *Bolina infundibulum* and *Beroë cucumis*. Especially the latter, which is decidedly cosmopolitan in its distribution, cannot be regarded as an especially arctic species, characteristic of the arctic regions (Chun), or as "hocharktisch und arktisch mit eurythermer Tendenz" (Römer). This species is, in fact, without value for the discussion of such problems. It cannot even be termed a "boreal" form, as suggested by Damas & Koefoed. The same appears to hold good of *Bolina*, even if it is not cosmopolitan in its distribution, being hitherto known only from the Atlantic, but from the warm region (probably including the Mediterranean) to the most arctic regions of the Polar Sea. Perhaps the case will prove to be somewhat different with *Pleurobrachia pileus*. As stated above it

<sup>1)</sup> A. Walter. Biologische und tiergeographische Züge aus dem ostspitzbergischen Eismeere. I. Die Quallen als Stromweiser. Deutsche geographische Blätter. Bremen. 1890. p. 92.

appears not to occur in the Greenland Seas, as also Römer (Op. cit. p. 76) and Damas & Koefoed (Op. cit. p. 413) state that it does not occur under high-arctic conditions. The more remarkable is the fact that it occurs in the antarctic regions under conditions corresponding to the most arctic (Moser. Ctenoph. d. deutsch. Südpolar-Exp.) — so remarkable, indeed, that one can scarcely help thinking that it may, perhaps, not be really this species.

While these three species are thus of little or no value for judging of the currents, the case is quite different with *Mertensia ovum*. This is a true arctic form, not occurring outside the polar water, and if it is found in some place, where it does not occur usually, it affords the proof that arctic water has intruded — and I would even be inclined to reverse the statement, viz. that where *Mertensia ovum* does not occur, there is no polar water.

This has an important bearing upon the question, whether the polar water reaches the North European Seas, as is maintained by Aurivillius<sup>1)</sup> and Chun<sup>2)</sup>. “Im Laufe des Winters kann das Plankton der kalten Stromgebiete sich so weit nach Süden vorschieben, dass von den vereisten Fjorden West-Grönlands in dem Smith-Sund und in der Baffinsbai bis nach Helgoland und in die westliche Ostsee eine einheitliche arktische Fauna die Oberfläche bevölkert”. (Chun. Op. cit. p. 8). The proof of this Chun finds in the occurrence in these waters of such forms as *Pleurobrachia pileus*, *Bolina infundibulum* and *Beroë cucumis*, the Siphonophore *Diphyes arctica*, and the Appendicularians *Oikopleura labradoriensis* and *Fritillaria borealis*, while Aurivillius mentions as “arktisch im engen Sinne”: *Sagitta arctica*, the Crustaceans *Calanus hyperboreus*, *Euchæta norvegica*, *Metridia longa*, *Euphausia inermis* and the Pteropod *Clione limacina* (Op. cit. p. 87—91). That the Ctenophores named are really without value as a proof of the presence of arctic water, is already sufficiently explained, and the same appears to hold good of all the other forms. Of *Diphyes arctica* Damas & Koefoed (Op. cit. p. 414) state that “sa distribution est indépendante de la température, de la salinité et de l'origine des eaux dans lesquelles il se trouve”; *Fritillaria borealis* is known also from the Mediterranean and the Bismarck Archipelago. Without entering on a more detailed discussion of the geographical distribution of all the forms mentioned above — (most of them are given in “Nordisches Plankton” as distributed over the North Atlantic down to ca. 50°—60° N.) — I must express my conviction, in perfect accordance with Damas & Koefoed (Op. cit.), that not one of them is really and exclusively arctic and thus cannot be taken as a proof of the intrusion of arctic water into the North-Sea and Skagerak. — *Mertensia ovum*, if definitely proved to occur there, would give the indubitable proof of the intrusion of arctic waters here; but there is no proof that this species really occurs in these Seas (Comp. above, p. 65). I quite agree with Moser (Ctenoph. d. deutsch. Südpolar-Exp. p. 180) that the fact of *Mertensia ovum* not occurring here is a proof that the arctic waters do not reach so far South in the North European Seas, “denn andernfalls wäre nicht einzusehen, warum *Mertensia ovum* nicht zeitweise auch hier, wie an der amerikanischen Küste, weiter südlich vordringen sollte”. — This result is in accordance with the view of the hydrography of these seas set forth by Martin Knudsen<sup>3)</sup> where the polar stream is stated not to reach the North European Coasts.

<sup>1)</sup> Carl W. S. Aurivillius. Vergleichende thiergeographische Untersuchungen über die Plankton-Fauna der Skageraks in den Jahren 1893—1897. Kgl. Svenska Vetensk. Akad. Handl. Bd. 30. 1898. (p. 133—135).

<sup>2)</sup> C. Chun. Die Beziehungen zwischen dem arktischen und antarktischen Plankton. 1897.

<sup>3)</sup> Martin Knudsen. Havets Naturlære. Hydrographi, med særligt Hensyn til de danske Farvande. Skrifter udg. af Kommissionen for Havundersøgelser. Nr. 2. København 1905.

*Pleurobrachia crinita* is regarded by Moser as a local form. Though it is as yet known only from the Karajak-Fjord at West Greenland, I do not doubt that it will prove to be widely distributed — whether in the arctic or Atlantic waters nobody can say in the present state of our knowledge. It may have been simply overlooked or confused with other species (*Pl. pileus*?), or it may perhaps be a form which generally occurs in greater depths, only occasionally rising to the surface (— as would appear to be the case with several species of Ctenophores, which are met with only occasionally —). Upon the whole I am not inclined to believe in the existence of very local species of such eminently planktonic organisms as the pelagic Ctenophores. — With the non-pelagic forms the case is, of course, different; thus it is quite possible that *Tjalfiella* is a very local form, though I would be more inclined to suppose that it will prove to be more widely distributed, probably in the warm region of the Atlantic. But as regards the pelagic Ctenophores it is not obvious, how they could avoid being carried along with the currents, getting thus a wide distribution in the waters otherwise affording suitable conditions in regard to temperature and salinity.

These considerations also apply to the Mediterranean fauna of Ctenophores. Moser (Op. cit. p. 178) regards as peculiar to this sea no less than 10 species of Ctenophores, viz. *Euchlora rubra*, *Euchl. filigera*, *Lesueuria vitrea*, *Pleurobrachia rhodopis*, *Hormiphora plumosa*, *Lampetia pancerina*, *Euplokamis stationis*, *Beroë ovata*, *Bolina hydatina* and *Deiopea kaloktenota*. Of these I think *Pleurobr. rhodopis* and *Beroë ovata* have been proved above conclusively to be identical with the common Atlantic species, *Pl. pileus* and *Beroë cucumis*, and very probably *Bolina hydatina* is identical with *B. infundibulum*, while *Lesueuria vitrea* is evidently only a damaged *Bolina* (or some other Lobate). The remaining six species have certainly not yet been recorded from the Atlantic; but it can scarcely be doubted that they must be carried out (or in) by the strong current in the Gibraltar strait, so that they will prove to occur at least in the neighbouring regions of the Atlantic, as is the case with the other species found in the Mediterranean, e. g. *Vexillum parallelum*, *Eurhampæa vexilligera*, not to mention the nearly cosmopolitan *Cestus veneris* and *Beroë Forskålii*.

Another thing would be, if there are perhaps true deep-sea Ctenophores in the Mediterranean. Such would, probably, be incapable of passing the Gibraltar Strait and thus might represent true local forms. The same would perhaps be the case, if such deep-sea forms should prove to occur in the Polar-Sea. But the existence of deep-sea Ctenophores in these seas remains as yet an unsolved problem. — An almost equally interesting problem, viz. the bathymetrical distribution of the pelagic Ctenophores has scarcely been touched as yet. Differential hauls, taken from different depths to the surface, have certainly been made by several expeditions; but reliable results will scarcely ever be reached in that way. The use of closing nets will be needed for the study of this problem.

As *Mertensia ovum* must be regarded as a characteristic form of the arctic water, bearing evidence of the distribution of the polar stream, other forms again are unquestionably bound to the warm waters and can afford proof of the intrusion of warm currents, as e. g. the Gulf Stream. The question whether such forms are known from the North Atlantic is answered in the negative by Moser (Op. cit. p. 180). "Der Golfstrom verschleppt offenbar keine einzige Warmwasser-Ctenophore dorthin (viz. the Ice Sea) oder auch nur an die nordeuropäischen Küsten....; wenigstens ist bisher kein einziger Fund bekannt, der im Sinn einer solchen Verschleppung gedeutet werden könnte".

Against this assertion I would recall the statement of Wagner, that he has found *Cestus veneris* and *Beroë Forskålii* in the White Sea; this occurrence of these two forms can only be explained in this way, that they have been carried thither by the Gulf Stream<sup>1</sup>). — Though it must be agreed that the statement of Wagner cannot be regarded as beyond doubt (— and the same applies to Walter's record of two species of *Beroë*, one of which would evidently be *B. Forskålii*, at Spitzbergen —), I must regard it as very probable that such warm-water Ctenophores will prove to occur in the North European Seas, from the Skagerak along the Coasts of Norway, and probably sometimes so far North as both Spitzbergen and the White Sea, it being a well known fact that the Gulf Stream makes its influence felt so far North.

It is a well known fact, first recorded by M. Sars (Fauna littoralis Norvegiæ I. 1846.), that both Salps and large Siphonophores are sometimes carried in great numbers to the coasts of Norway; and this is a phenomenon occurring, generally in September—November, most years. That these forms are carried to the Norwegian Coasts with the Gulf Stream, nobody can doubt. But it seems very improbable that such Ctenophores, which otherwise occur together with these animals in the Gulf Stream, should not also be carried along together with them to the North European Coast — viz. such forms as *Cestus Veneris* and *Beroë Forskålii*. Besides these also other forms might be expected — I would name e. g. *Eucharis*, *Tinerfe*, *Hormiphora*. I had hoped to be able to give the definite proof of the correctness of this suggestion, but, unfortunately, last year (1911) proved to be exceptional, in that the Salps did not appear at the Norwegian Coast, either during my stay at Bergen and Trondhjem or later in the fall of that year. That careful observations of the pelagic organisms accompanying the Salps will prove at least some of the Ctenophores named to be among them I cannot doubt.

As mentioned above (p. 73) Moser regards the occurrence of *Pleurobrachia pileus* in both the arctic and antarctic Seas as "ein Fall von Bipolarität..., wie er bis jetzt nur bei ganz wenig Arten nachgewiesen ist" (Op. cit. p. 144). Later on in the same work (p. 182) the author states that the arctic and antarctic fauna have only the two species *Pleurobrachia pileus* and *Beroë cucumis* in common, the accordance being thus as regards the Ctenophores "eine recht geringe, eine viel geringere, wie sie nach der Pfefferschen Reliktentheorie sein müsste, um so mehr da diese beide keine eigentlich bipolaren Formen... sind". With this I quite agree. There is really no case of bipolarity among the Ctenophores, the two forms named being, in fact, continuously distributed from the arctic to the antarctic region; nor do they only occur in deeper water in the intervening tropical regions, as is suggested by Moser (loc. cit.). This becomes evident from the facts recorded by the author herself. Thus the specimens of *Pl. pileus* recorded from the Seychelles are stated to have been taken at the surface; that the specimen from the North of Ascension was taken in a haul from 200<sup>m</sup>, can, of course, not prove the contrary. That these species may perhaps be less common in the tropical than in the more temperate seas, as Moser suggests (p. 171), is possible, though it can by no means be regarded as an established fact. But the main point in this matter is that the two species in question have been definitely shown to be continuously distributed from the arctic to the antarctic region.

<sup>1</sup>) The fact that *Beroë Forskålii* is recorded by O. Maas (Méduses. Expedition antarctique Française 1903—5 (Charcot). 1908. p. 16) from the Antarctic Sea does not alter the fact that the occurrence of this species in the North European Seas must be regarded as a proof of the existence of Gulf Stream water in the place, where it is found.

## Corrigenda.

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p. 60. line 14: for "*Lesueuria hyboptera* A. Ag." read "*Lesueuria vitrea* M. Edw."

p. 75. line 1 at top: for "(Moser)" read "Moser".

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Explanation of the Plates.

The following letters denote the same parts in all the Plates.

- |  |   |
|--|---|
| <i>b.</i> Basal surface.   | <i>inf.</i> Infundibulum.   |
| <i>br. c.</i> Branching peripheral canal system.                         | <i>i. t.</i> Interstitial tissue.   |
| <i>c.</i> Costæ.   | <i>l.</i> Lumen of the "chimney".   |
| <i>c. c.</i> Cavity of peripheral canals.                                | <i>m.</i> Egg-membrane.   |
| <i>c. g.</i> — - genital organ.  | <i>m. t.</i> Mesodermal tissue.   |
| <i>cmb.</i> Comb (swimming plate).                                       | <i>o.</i> Mouth-opening.  |
| <i>col.</i> Colloblasts.   | <i>ov.</i> Oesophagus.  |
| <i>c. tb.</i> Cavity of tentacle-basis.                                  | <i>o. f.</i> Opening from the "suboral" cavity into the lumen of the "chimney". |
| <i>cu.</i> Cupule.   | <i>ov.</i> Ovary.   |
| <i>c. z.</i> Zone of cells, forming the cupule.                          | <i>ot.</i> Otolith.   |
| <i>e.</i> Embryo.  | <i>p. f.</i> Polar field.   |
| <i>e. c.</i> Brood cavity for the embryo.                                | <i>s.</i> Apical sense organ.   |
| <i>ect.</i> Ectoderm.  | <i>sec. t.</i> Secondary tentacle.  |
| <i>end.</i> Endothelial lining of infundibulum.                          | <i>s. o.</i> Secondary mouth opening.   |
| <i>ent.</i> Entodermal lining of genital or tentacular cavity; Entoderm. | <i>spz.</i> Spermatozoa.  |
| <i>ep.</i> Epidermis.  | <i>st. f.</i> Stomodæal (pharyngeal) folds.                                     |
| <i>e. s.</i> Entodermal sac.   | <i>t.</i> Tentacle.   |
| <i>excr. c.</i> Excretory canal.   | <i>t. b.</i> Tentacle-base.   |
| <i>excr. o.</i> — opening.   | <i>t. o.</i> Opening of tentacle-sheath.  |
| <i>f.</i> Transverse furrow; "suboral" cavity.                           | <i>t. r.</i> Tentacle-root.   |
| <i>g.</i> Genital organ.   | <i>tr. c.</i> Transverse canal.   |
| <i>gl. c.</i> Gland cells.   | <i>t. sh.</i> Tentacle-sheath.  |
| <i>g. z.</i> Germinal zone.  | <i>ts.</i> Testis.  |
| <i>i.</i> Ectodermal invagination.                                       |   |

Plate I.

## Plate I.

The figures represent different specimens of *Tjalffella tristoma* Mrtsn.

- Fig. 1. Photograph of two specimens in their natural position on the stalk of *Umbellula Lindahli*; the upper one in side view, the lower one somewhat obliquely from above. The white corpuscles are the genital organs. The specimens were still in formaline when photographed. Natural size.
- 2. A young specimen, without embryos. Side view.  $\frac{8}{1}$ .
  - 3. A slightly older specimen, with one embryo. The specimen was cleared in xylol, the stomodæal folds thus becoming visible through the body wall. The two median genital organs are distinctly seen to consist each of two parts, viz. the median part being the ovary, the outer part the testis. The branching canal system is perhaps not correctly shown in all the outer branchings, these being not quite discernible in the cleared-up specimen. Side view.  $\frac{8}{1}$ .
  - 4. Specimen showing the right half in regeneration. No embryos. Side view.  $\frac{9}{1}$ .
  - 5. Young specimen, without embryos. The small size of the outer left genital organ perhaps indicates, that this part has been regenerated. (The lower corner to the left slightly restored). Side view.  $\frac{8.5}{1}$ .
  - 6. Fully developed specimen, seen from above.  $\frac{7}{1}$ . (Same specimen as Fig. 9).
  - 7. Specimen having lost the right "chimney" with the tentacle and the outer pair of genital organs; the regeneration has scarcely begun, but the edges of the rupture have closed. Side view.  $\frac{8.5}{1}$ .
  - 8. Specimen in regeneration. Side view.  $\frac{8}{1}$ .
  - 9. Fully developed specimen, with numerous embryos. Same specimen as Fig. 6. Side view.  $\frac{7}{1}$ . Some pigment is seen within the embryos, having become distinct through the clearing up of the specimen in xylol. The branching canal system, on the other hand, became indistinct through that process and is therefore represented in a somewhat diagrammatic way.



1. Photograph, 2-9. Th. Mortensen del.

Lith. Anst. v. E. A. Funke

*Tjalfiella tristoma* Mrlsn.



Plate II.

## Plate II.

All the figures represent embryos of *Tjalfiella tristoma*. All  $\frac{40}{1}$ .

- Figs. 1—3. Stage I. Fig. 1. from the oral side, showing the transverse furrow; 2. side view (from the tentacular plane), showing the costæ and tentacle rudiments; 3. from the aboral side showing the aboral organ, the costæ and tentacle rudiments. The small, irregularly placed spots are probably only artefacts, products of the preservation.
- 4—6. Stage II. 4. from the oral side, 5. side view (from tentacular plane), 6. from the aboral side. The combs have begun to appear.
- 7. Embryo slightly younger than Figs. 1—3, from the oral side. The transverse furrow is quite short, the oral opening being distinct. The aboral side of the specimen figured was as in Fig. 3.
- 8—11. Stage III. The fully developed young Cydippid, ready to leave the egg-membrane (but found lying within the membrane). 8. seen from the sagittal plane, 9. from above, 10. from the tentacular plane, 11. from the oral side. In fig. 9 are seen the ciliated ridges passing from the sense organ to the costæ. The tentacle is rolled up within the tentacle sheath.

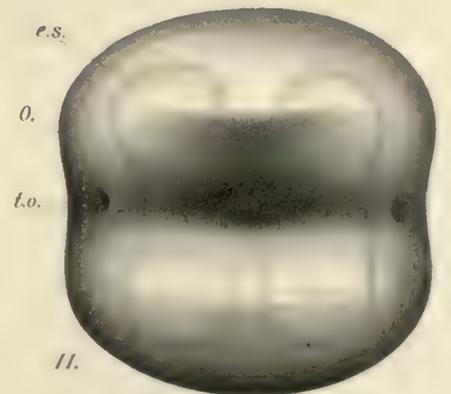
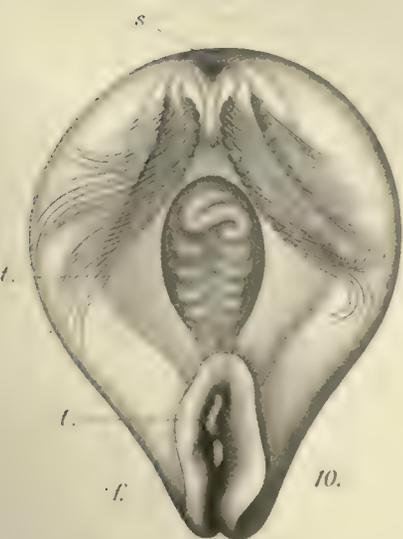
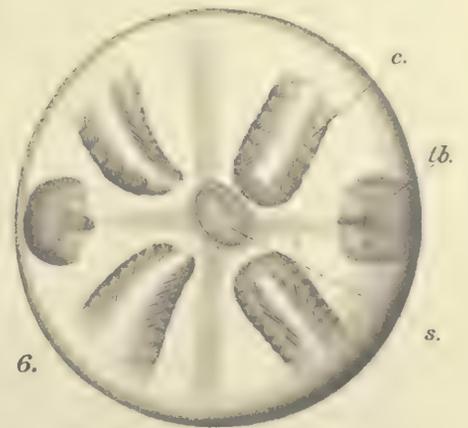
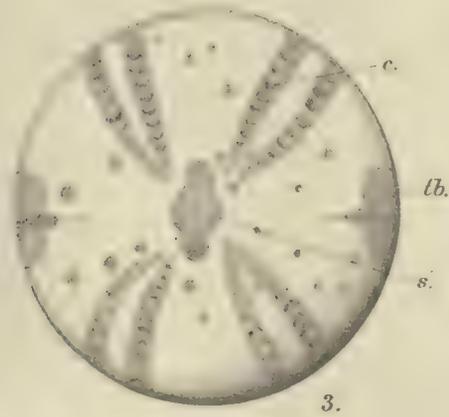
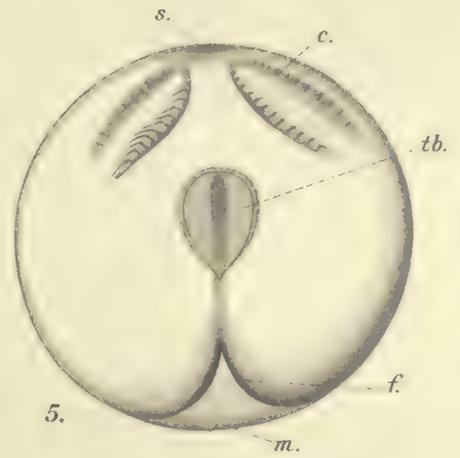
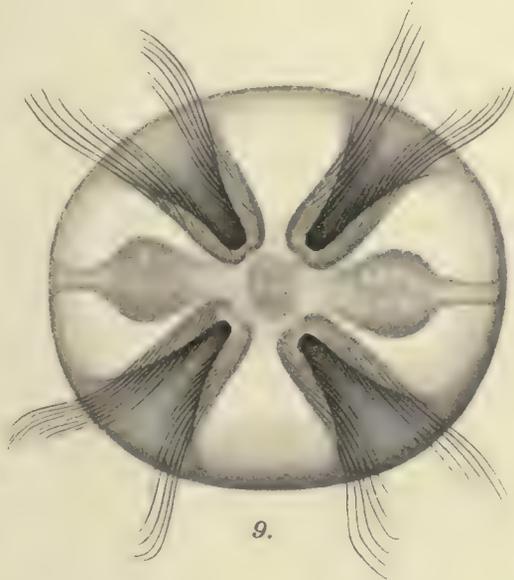
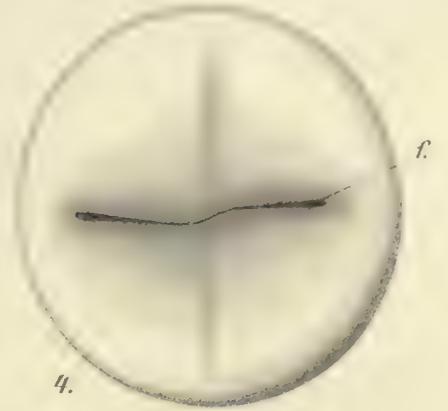
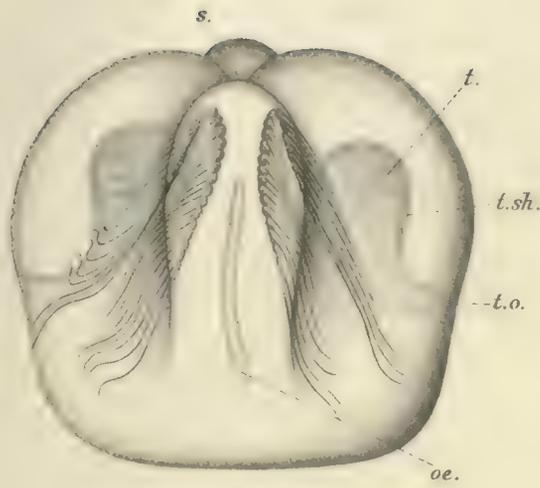
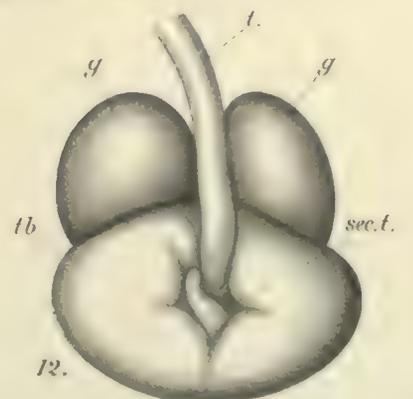
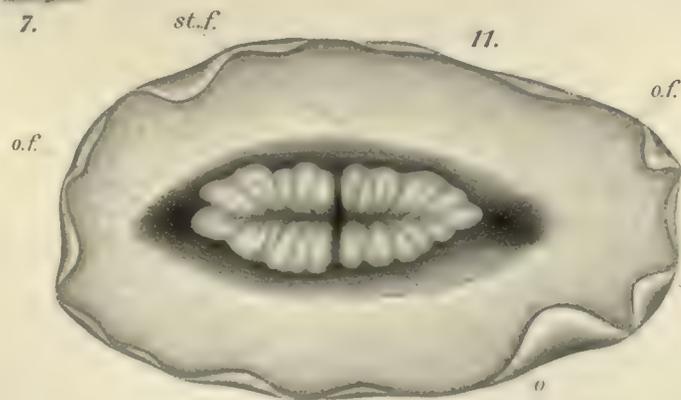
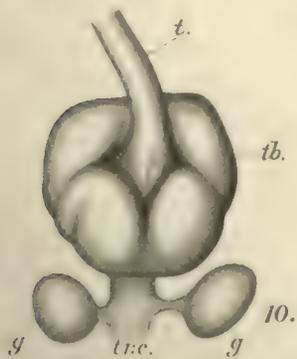
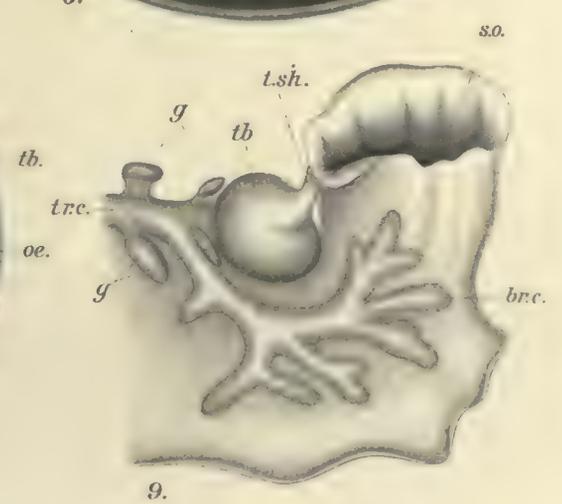
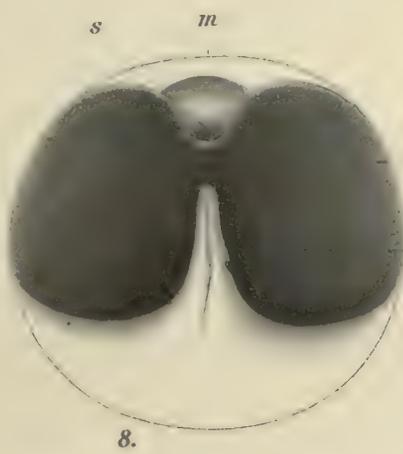
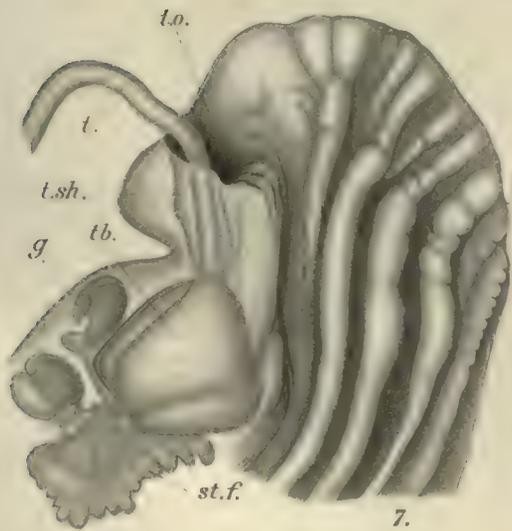
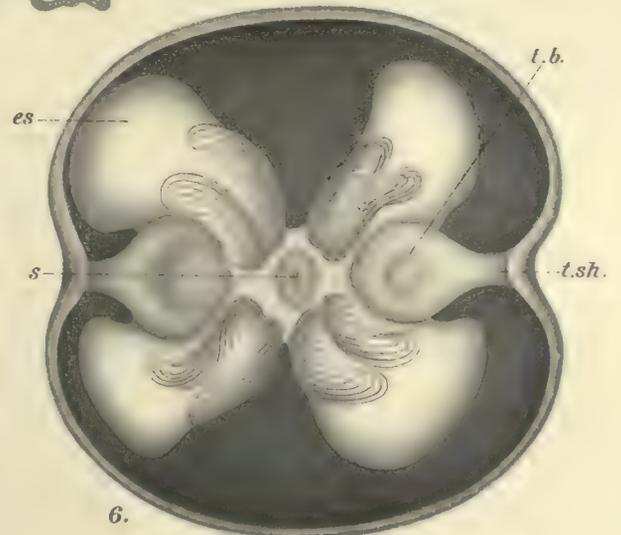
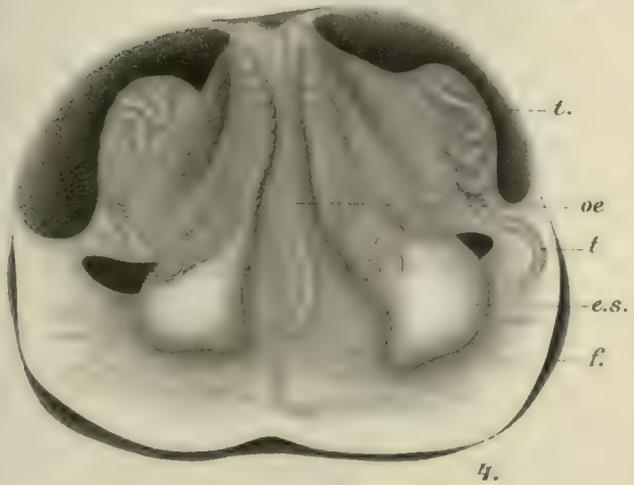
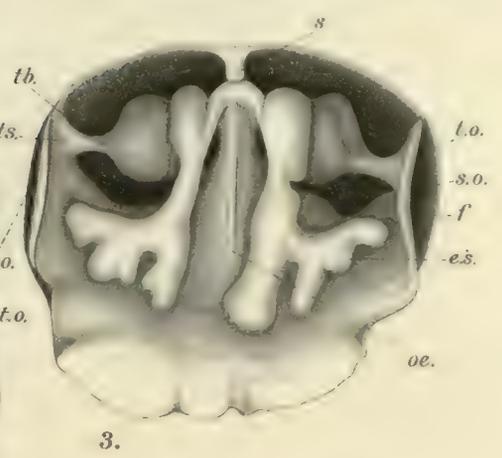
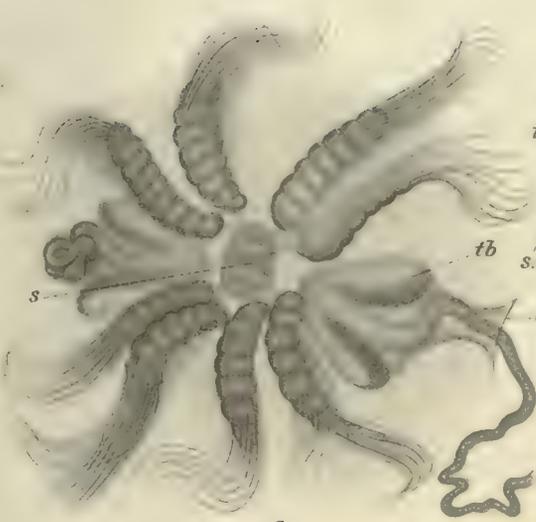
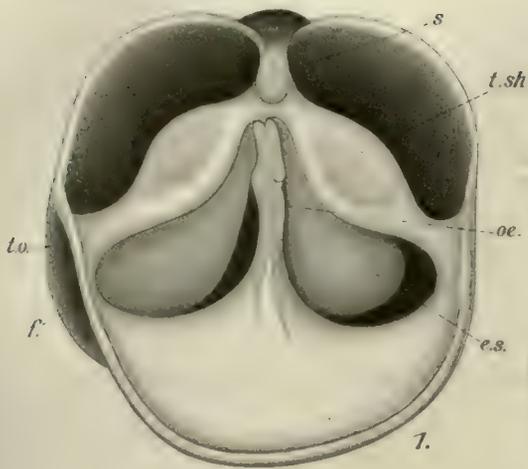




Plate III.

## Plate III.

- Fig. 1. Embryo in the stage III. The skin of the one side removed so as to show the tentacular sheaths; below these are seen the two entodermal sacs of the under side, those of the upper side having been removed.  $40/1$ .
- 2. The aboral region, with the costæ and tentacles, of an embryo in the Stage III. The skin folds over the costæ have been omitted, being indistinct in the flattened preparation. The left tentacle sheath was torn away and is therefore not represented in the figure. From the aboral organ are seen the ciliated ridges going to the costæ.  $58/1$ .
  - 3. Young specimen, after leaving the egg-membrane. The costæ have disappeared. The edges of the transversal furrow have united at the right side, the secondary mouth-opening having thus been formed; the upward growth of the secondary mouth-opening has also begun, though there is as yet no distinct "chimney". The skin of the side turning towards the spectator has been prepared away so as to show the branching of the entodermal sacs — the beginning of the branching peripheral canal system of the grown specimens.  $27/1$ .
  - 4. Embryo in Stage III, corresponding to that figured in fig. 1. — The skin partially removed so as to show the pharynx and the entodermal sacs, but the costæ have been left in place. The tentacles are seen rolled up within the tentacle sheath; the right tentacle is seen to protrude a little into the transverse furrow.  $45/1$ .
  - 5. Part of the basal surface of a grown specimen; the furrow closed. (Comp. Fig. 11).  $8/1$ .
  - 6. Embryo in Stage III, with the lobes spread out horizontally; seen from above. The skin has been removed so as to expose the entodermal sacs and the tentacle bases and sheaths. In the middle the skin remains, the aboral organ and the costæ lying in place.  $45/1$ . (The oesophagus was indistinct in the preparation and has therefore not been indicated in the figure).
  - 7. Part of the side wall of a "chimney" seen from the inside, showing the folding of the skin. The opening of the tentacle-sheath is seen; above the tentacle-base are seen the genital organs of the side looking towards the spectator, turned upwards, and below these part of the stomodæal folds are seen.  $17/1$ .
  - 8. Embryo in Stage II; the skin partly removed so as to show the configuration of the oesophagus and the invaginated portion of the transverse furrow. The interior was filled by a mass of large entoderm cells, but the exact relations of these and the existence of entodermal cavities could not be made out, owing to the — for this purpose — unsatisfactory preservation. Side view from the sagittal plane.  $38/1$ .
  - 9. Regenerating half of a grown specimen, showing the relations of the genital organs and the branching peripheral canal system to the main transverse canal (the perradial vessel). The epidermis has been removed. Side view, a little obliquely. The genital organs of the side away from the spectator pushed a little upwards so as to become visible.  $25/1$ .
  - 10. Tentacle and tentacle basis, seen from the apical side, of a young (regenerated) specimen. The small genital organs (only the subtentacular pair drawn) are seen to develop at the end of small branches from the transverse canal.  $25/1$ . (Comp. Fig. 12).
  - 11. The basal surface of a grown specimen. The furrow ("suboral" cavity) is opened so as to show the large stomodæal folds, in the middle of which is seen the narrow opening of the oesophagus (in the figure designated o). The hole (o. f.) at each end of the furrow represents the opening from the furrow into the lumen of the "chimneys".  $8/1$ . (Comp. Fig. 5).
  - 12. Tentacle and tentacle basis of a grown specimen, seen from the outer side. The small finger-shaped body at the base of the tentacle probably represents a secondary (abnormal) tentacle. (Comp. Fig. 10). The two large bodies lying over the tentacle basis are the two subtentacular genital organs.  $25/1$ .



Th. Mortensen del.



Plate IV.

## Plate IV.

- Fig. 1. Vertical section, along the transversal plane, through a grown specimen. <sup>22</sup>/<sub>1</sub>. The section is not median. The figure shows the four genital organs of the same side, the two median ones showing the arrangement of the ovary and testis, the ovary medially, the testis laterally placed. Below the outer genital organ is seen the tentacle-basis. The strongly folded lower side of the section represents the stomodæal folds. On the left side is seen the connection between the "chimney" cavity and the "suboral" cavity. The clear spaces below the genital organs and especially in the outer part to the right are sections through the branching peripheral canals.
- 2—4. Successive horizontal sections through the upper (apical) part of a grown specimen. <sup>17</sup>/<sub>1</sub>. In fig. 2 the section goes through the apical organ, in fig. 3 through the transverse main (perradial) canal, in fig. 4 through the upper part of the oesophagus. The designations excr. c. and s. in figs. 2—3 are not correctly placed. The small pearshaped body seen in the middle of the upper side in fig. 2 is the apical organ, which has become oblique through the contraction of the animal; the small ring below the apical organ is the excretory canal. The space in the middle of the figure is part of the gastrovascular system, as is also the space designated excr. c. in fig. 3. The two darker bodies in the middle of this figure, designated s (apical organ), likewise belong to the gastrovascular system (probably from the inner end of the oesophagus). — Otherwise the figures show the arrangement of the 4 pairs of genital organs, the ovaries being placed subsagittally and subtransversally, the testes interradially, after the usual ctenophoran type. The left subsagittal organ on the lower side apparently affords an exception, the ovary being interradian, the testis subsagittal. This is, however, an abnormality, due to a revolution, perhaps the result of the egg-formation. As seen from fig. 2, part of the ovary is in the normal place. In fig. 3 is seen the connection between the transverse canal and the cavity of the right subsagittal genital organ of the lower side; in fig. 4 is seen the connection between the transverse canal and the cavity of the tentacle basis. The sections do not cut the genital organs at the same level, owing to the contraction of the animal which has made it impossible to get perfectly horizontal sections through the whole of the organs. Also the tentacle basis to the left is seen (Fig. 4) to have been cut obliquely.

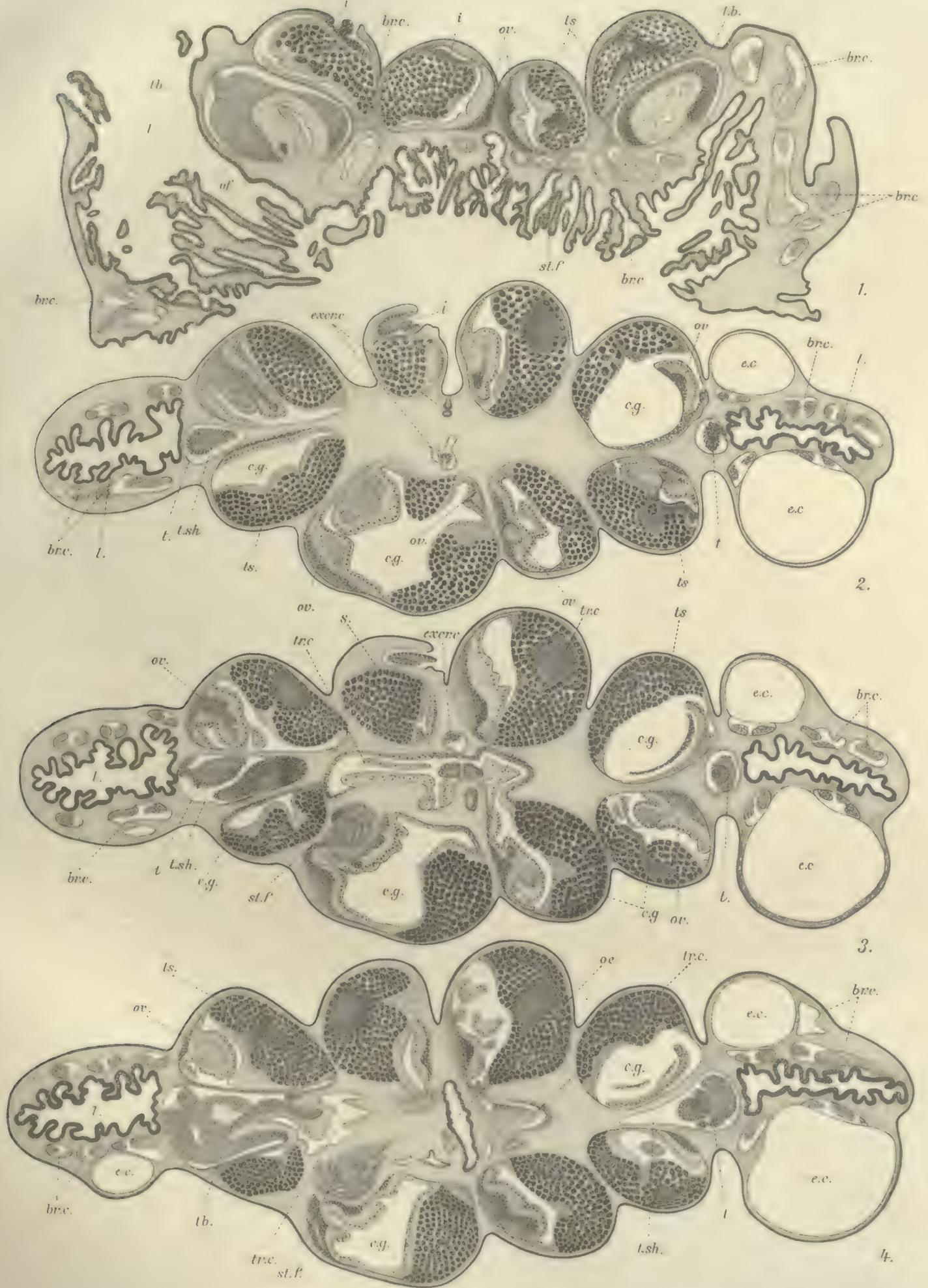




Plate V.

## Plate V.

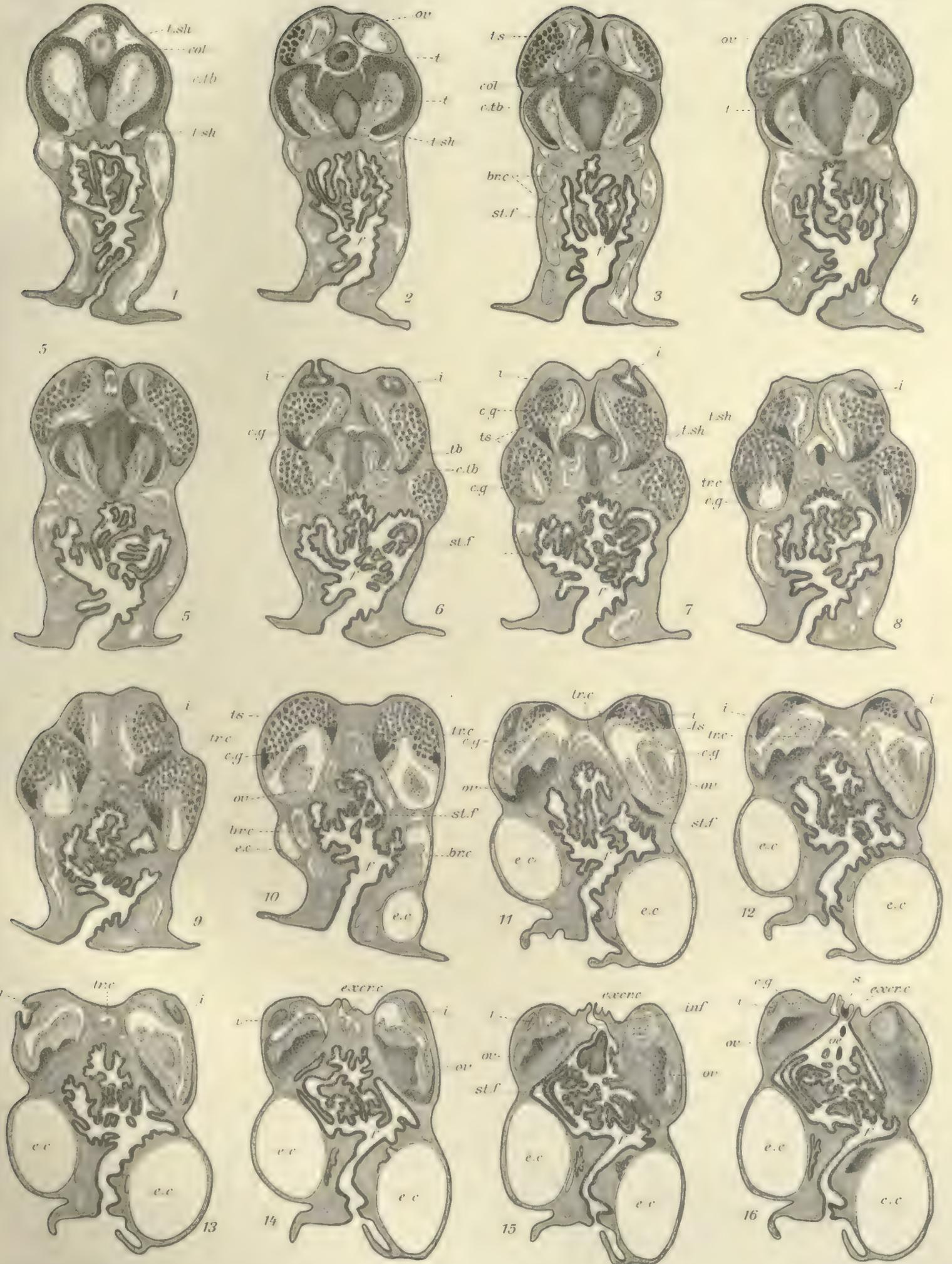
All the figures represent sections along the sagittal plane of a grown specimen of *Tjalfiella tristoma*, in consecutive order from the tentacle to the apical organ; all equally enlarged:  $\frac{22}{1}$ .

- Fig. 1. Section through the tentacle-base, outside the genital organs.
- 2—5. Sections through the outer (subtentacular) genital organs and the tentacle basis.
  - 6—8. The subsagittal (inner) genital organs appear below the outer ones (this position being partly due to the contraction of the specimen). The tentacle basis gradually disappears in these sections. Contemporaneously the invagination over the genital organs appears. In Fig. 6 the cavity of the two sides of the tentacle basis is seen to be in connection with the gastrovascular canals. In fig. 7 the same is seen to be the case with the cavities of the two outer genital organs.
  - 9. Inside the tentacle basis. The two canals are seen to lie separately.
  - 10. The two canals unite into one (the transverse canal). The outer genital organs have disappeared.
  - 11—12. Showing the connection of the cavity of the two inner (subsagittal) genital organs with the transverse canal. Further the ectodermal invagination over these genital organs is seen here (as also in fig. 13).
  - 13. The testicular portion of the subsagittal genital organs has disappeared, only the ovarial portion remaining.
  - 14—16. The excretory canals are shown. — Fig. 16 especially shows them, being almost exactly a median section. (Comp. Pl. VII. Fig. 1).

In figs. 10—16 is seen a brood cavity on each side near the basis. The content has not been drawn, being not sufficiently well preserved and the sections not having such a direction as to show anything of the embryonal structure clearly.

A detailed explanation of the figures otherwise seems unnecessary. An inspection of the figures in their consecutive order will show the interrelations of the different organs clearly enough.

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Th. Mortensen del.

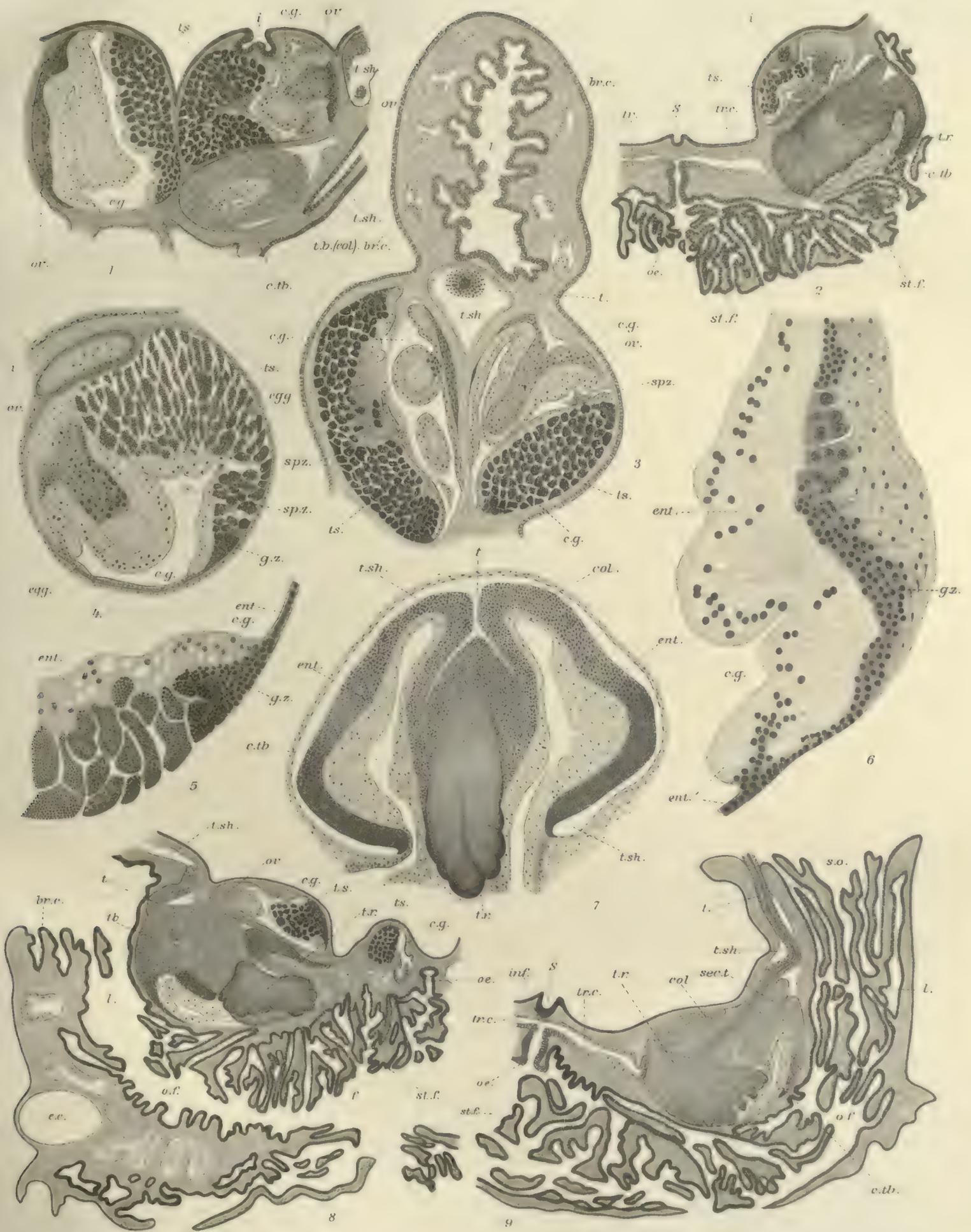
*Tjalstella tristoma* Mrlsn.



Plate VI.

## Plate VI.

- Fig. 1. Part of vertical lateral section (in the transversal plane), showing the relative position of the testes and ovaries. On the outer subtentacular genital organ is seen the ectodermic invagination; below the same is seen part of the tentacle-basis. The thick, dark lining to the right of the figure is the epithelium of the "chimney"-cavity.  $30/\text{I}$ .
- 2. Part of vertical, median section (in the transversal plane), showing the oesophagus, the apical organ, the transverse canal and the root of the tentacle, above which lies the inner part of the outer genital organ. Below are seen the stomodæal folds. The infundibulum can scarcely be said to exist here. (Comp. Fig. 9). The left transverse canal wrongly designated tr. instead of tr. c.  $22/\text{I}$ .
- 3. Part of horizontal section, showing the two outer, subtentacular genital organs and the "chimney". In the ovary of the left genital organ is seen an egg in formation, enclosed by its follicle. In the cavity of the organs are lying spermatozoa, especially in that to the left. In the right genital organ the cavity within the ovary is an abnormal formation, probably produced by the preservation.  $30/\text{I}$ .
- 4. Section through a genital organ (right subsagittal); from a vertical section in the transversal plane. At its upper side is seen part of the ectodermal invagination. In the lumen of the genital organ lies a small cluster of spermatozoa; in the ovary one egg is seen in formation.  $80/\text{I}$ .
- 5. Part of the testis from a vertical section along the transversal plane. To the right are seen the young sexual cells, passing without limit into the (entodermal) epithelial lining of the genital cavity. Towards the left of the figure the cells are seen to form the characteristic packets of spermatogonia. The outermost packets to the left consist of nearly ripe spermatozoa. The epithelial lining of the testis towards the genital cavity is more or less vacuolated. The position of this figure is not correct; the point ought to have been looking downwards.  $200/\text{I}$ .
- 6. Part of the ovary, from the same section, and same genital organ, from which fig. 5 is drawn. At the lower end the germinal zone is seen to pass without limit into the entodermal epithelium lining the genital cavity. The large nuclei in the upper part of the figure indicate that these cells are about to develop into eggs.  $200/\text{I}$ .
- 7. Horizontal section through the tentacle basis, showing the root of the tentacle and the colloblast-layer covering both tentacle and the tentacular vessels; further the entodermal lining of the tentacular vessels, having the same character as that of the genital organs.  $40/\text{I}$ .
- 8. Part of vertical, nearly median section, parallel to the transversal plane, showing the direct continuation of the "suboral" cavity (f.) into the lumen of the "chimney". In the right (subsagittal) genital organ the cavity is seen to be in connection with a branch from the transverse canal.  $22/\text{I}$ .
- 9. Part of vertical median section, parallel to the transversal plane. The tentacle is seen in longitudinal section (combined from 2—3 successive sections). The main transverse canals are seen in connection with the oesophagus; infundibulum rudimentary. A secondary tentacle is seen below the large, normal tentacle.  $30/\text{I}$ .
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Th. Mortensen del.

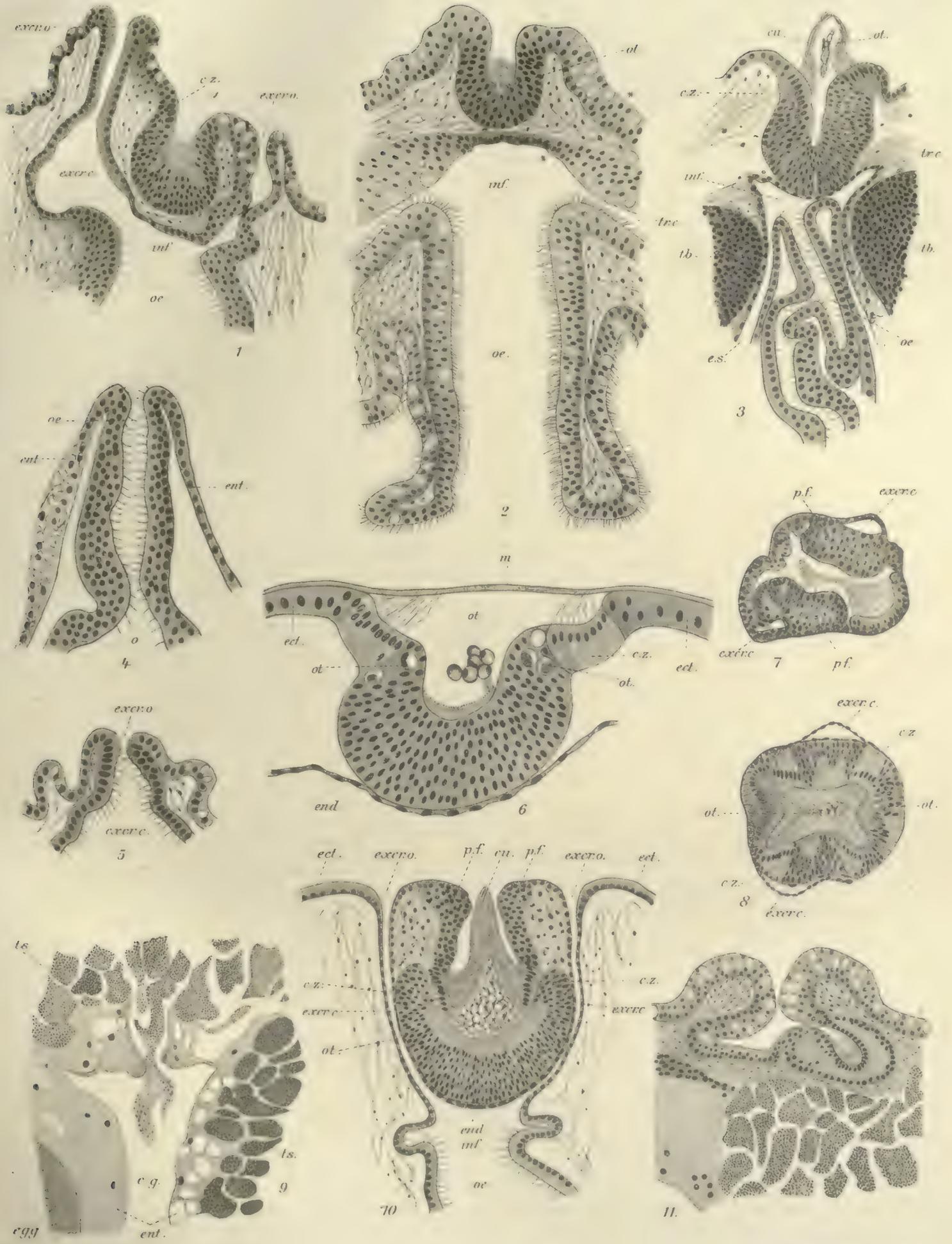
Tjalfiella tristoma Mrtsn.



Plate VII.

## Plate VII.

- Fig. 1. Vertical section, parallel to the sagittal plane, through the apical organ of a grown specimen (Comp. Pl. V. Fig. 16); showing the two excretory canals. The right one was not found open in its whole length, undoubtedly on account of a slight curve in its course (due to the preservation?). The apical organ is seen to be quite rudimentary; no distinct otolith is seen (Comp. Fig. 2), but a pair of otolith cells are seen within the cell mass. — The three larger nuclei seen at the upper side of the organ to the left side probably represent the zone of cells forming the cupule, which has disappeared. Cilia were not to be seen here in the excretory canals. (Not quite reliable in all the histological details, the preservation being insufficient for that purpose).  $175/1$ .
- 2. Vertical section, in the transversal plane, through the apical organ and the oesophagus of a grown specimen. The right side of the upper part of the figure from the \* and the right half of the oesophagus restored. In the middle of the apical organ is seen a small group of otolith cells lying partly imbedded in the epithelium.  $175/1$ .
- 3. Vertical section, in the transversal plane, through the apical organ and oesophagus of an embryo in the III. stage. (Comp. Fig. 10). The canal marked e. s. is the upper part of the entodermal sac.  $175/1$ .
- 4. Vertical section through the oesophagus (in the transversal plane) of an embryo in stage II (corresponding to Pl. III. Fig. 8). ent. — the median wall of the entodermal sac.  $240/1$ .
- 5. Vertical section through the excretory opening of a grown specimen.  $180/1$ .
- 6. Vertical section (in the transverse plane) of the apical organ of an embryo in stage II. The otolith mass is seen to be attached to a tuft of cilia, probably a rudimentary balancer. The zone of cells at the upper edge of the organ bears long cilia, which are to form the cupule. The mesodermal tissue is not yet developed. The endothelial membrane below the organ is the dorsal wall of the infundibulum. Otoliths are seen developing within some of the cells of the apical organ.  $280/1$ .
- 7—8. Horizontal sections (slightly oblique) through the apical organ of an embryo in Stage III. Fig. 7 at the level of the polar fields, fig. 8 below the polar fields. Outside the polar fields are seen the excretory canals.  $175/1$ .
- 9. Part of section through a genital organ, showing the discharging of the spermatozoa into the cavity of the genital organ.  $200/1$ .
- 10. Vertical section (in the sagittal plane) through the apical organ of an embryo in Stage III; showing the excretory canals. (Comp. Fig. 3).  $175/1$ .
- 11. Vertical section, parallel to the sagittal plane, through the ectodermal invagination over the genital organ. The entodermal lining of the genital organ was highly vacuolated; the vacuoles have been omitted in the figure. Some of the packets in the testis are seen to contain ripe spermatozoa.  $180/1$ .



*Tjalfiella tristoma* Mrlsn.

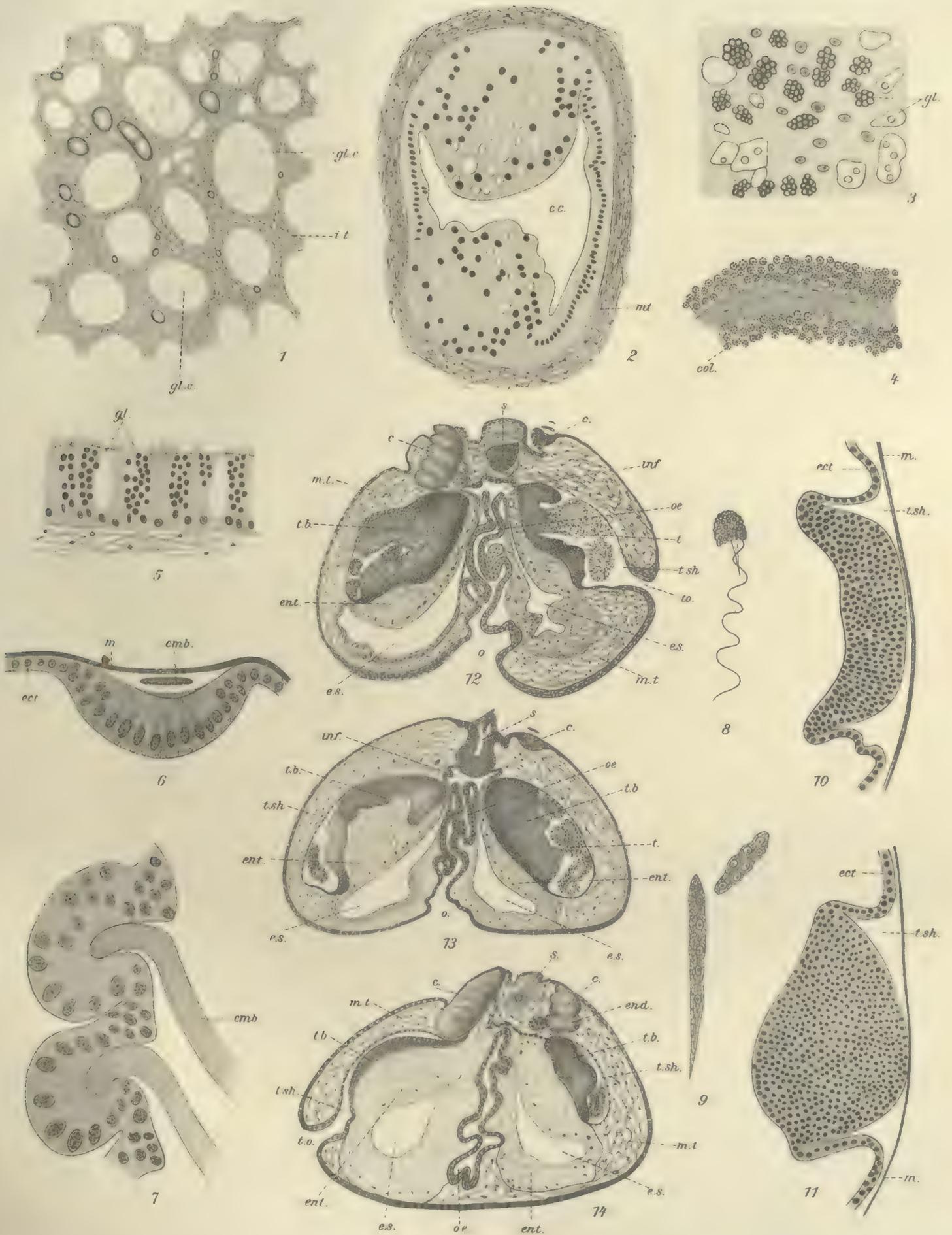
Edinb. A. Funke, Scania



Plate VIII.

## Plate VIII.

- Fig. 6. Epithelium from the "chimney", showing the numerous gland cells lying in the interstitial tissue.  $385/1$ .
- 2. Transverse section of one of the branching peripheral canals, showing the two lobes of high epithelium separated by a band of low epithelium. Cilia could not be observed. The cells of the lobes are somewhat vacuolated. c. c. cavity of the canal. m. t. mesodermal (muscular) tissue.  $200/1$ .
- 3. Epithelium from the stomodæal folds; showing different stages of the gland cells.  $415/1$ .
- 4. Longitudinal section of the tentacle, showing the muscular core and the colloblast layer.  $200/1$ .
- 5. Section of the skin of the chimney cavity; showing the cilia and gland cells (eosinophilous grains).  $385/1$ .
- 6. Transverse section of a costa, from an embryo in Stage II.  $415/1$ .
- 7. Longitudinal section of a costa, showing the base of two swimming plates. From an embryo in Stage III.  $530/1$ .
- 8. A colloblast.  $530/1$ .
- 9. Young muscle cells from the mesodermal tissue (of a grown specimen). Cell-limits are somewhat distinctly indicated. (After an unstained preparation directly from a formaline-specimen; the nuclei therefore appear as clear bodies within the granular mass of the cells).  $415/1$ .
- 10—11. Vertical sections through the tentacle-rudiment of an embryo in the II. Stage. 10 is lateral, 11 median. Shows the beginning formation of the tentacle-sheath. The nuclei are in places (fig. 10 in the lower part) serially arranged.  $175/1$ .
- 12—14. Three consecutive vertical sections, parallel to the transversal plane, through an embryo in the III. stage. Fig. 12 shows the opening of the right tentacle sheath, fig. 14 of the left. Fig. 13. — comp. Pl. VII. Fig. 3. For the rest the figures are easily understood from the accompanying letters.  $75/1$ . The limit between the large entodermal cells and the mesodermal tissue indistinct.
-



*Tjalstella tristoma* Mrtsn.



**Plate IX.**

## Plate IX.

Figs. 1—5. Successive horizontal sections through an embryo in stage II. The entoderm too badly preserved to be figured (the large vacuolated cells apparently fill the whole space between the ectoderm and oesophagus, but an entodermal cavity is doubtless present. Figs. 1—3 show the costæ, 2—3 the tentacle-rudiment. In fig. 2 the oesophagus is cut at the level, where it passes into the transversal furrow; the latter is cut at different levels in figs. 3—5. <sup>80</sup>/<sub>1</sub>.

— 6—14. Successive horizontal (slightly oblique) sections through an embryo in stage III, prepared out of the egg-membrane. <sup>80</sup>/<sub>1</sub>.

Fig. 6 goes through the upper edge of or above the apical organ, showing only the excretory canals. The epithelial lining around them is the epidermis, the apical organ having been rather sunken in the specimen sectioned. The substance lying between the two excretory canals is the cupule. (Comp. Pl. VII. Fig. 3).

Fig. 7. The section goes through the apical organ. (Comp. Pl. VII. Fig. 8).

Fig. 8. The section just touches the lower side of the apical organ (to the left side, the direction being slightly oblique), otherwise it goes through the infundibulum. To the right the tentacle apparatus begins to appear.

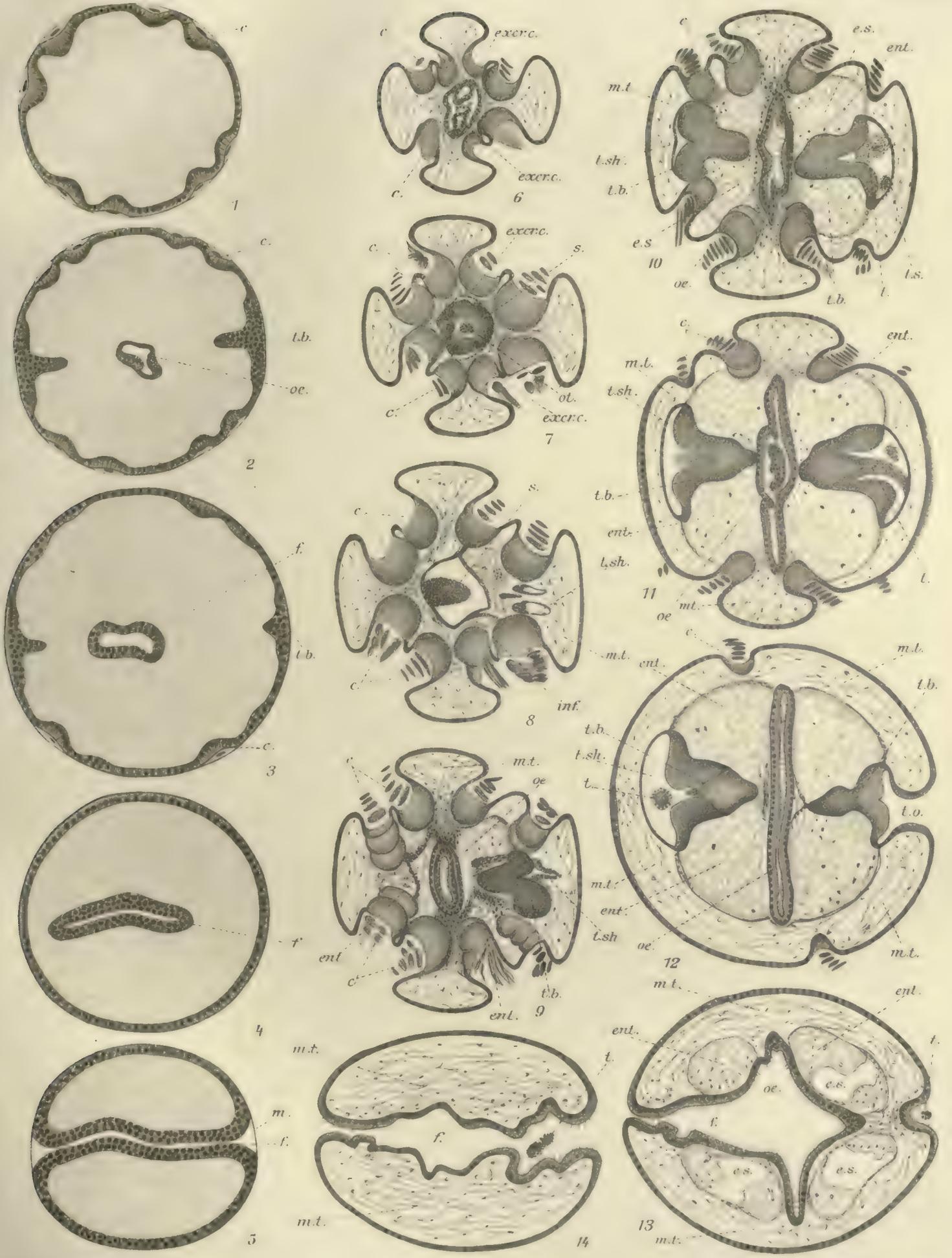
Fig. 9. The section goes through the upper end of the oesophagus. The right tentacle apparatus is seen.

Figs. 10—12 show the oesophagus, the four entodermal sacs and the tentacles.

Fig. 13 is at the level, where the oesophagus passes into the transverse furrow, fig. 14 passes through the furrow, below the oesophagus. The right tentacle is seen lying within the furrow. In figs. 6—12 are seen the costæ, lying in their furrows, the intercostal parts arching somewhat over them.

(The fig. 12 has perhaps become a little too large, belonging to the same section as the other figures; the reason is that the epidermis of the specimen has wrinkled to some extent; but these wrinkles, doubtless exclusively due to the preservation, have been eliminated and the natural shape reconstructed. The same has been the case with all the sections, of embryos as well as grown specimens, the artificial wrinkles having everywhere been left unreproduced, the natural course of the ectodermal line having been reconstructed).

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Th. Mortensen del.

Lith. Anst v. E. A. Fiske, Leipzig.

*Tjalsiella tristoma* Mrlsn.



Plate X.

## Plate X.

Figs. 1—9. Successive vertical sections, parallel to the sagittal plane, through an embryo in the stage III, prepared out of the egg-membrane.  $80/1$ .

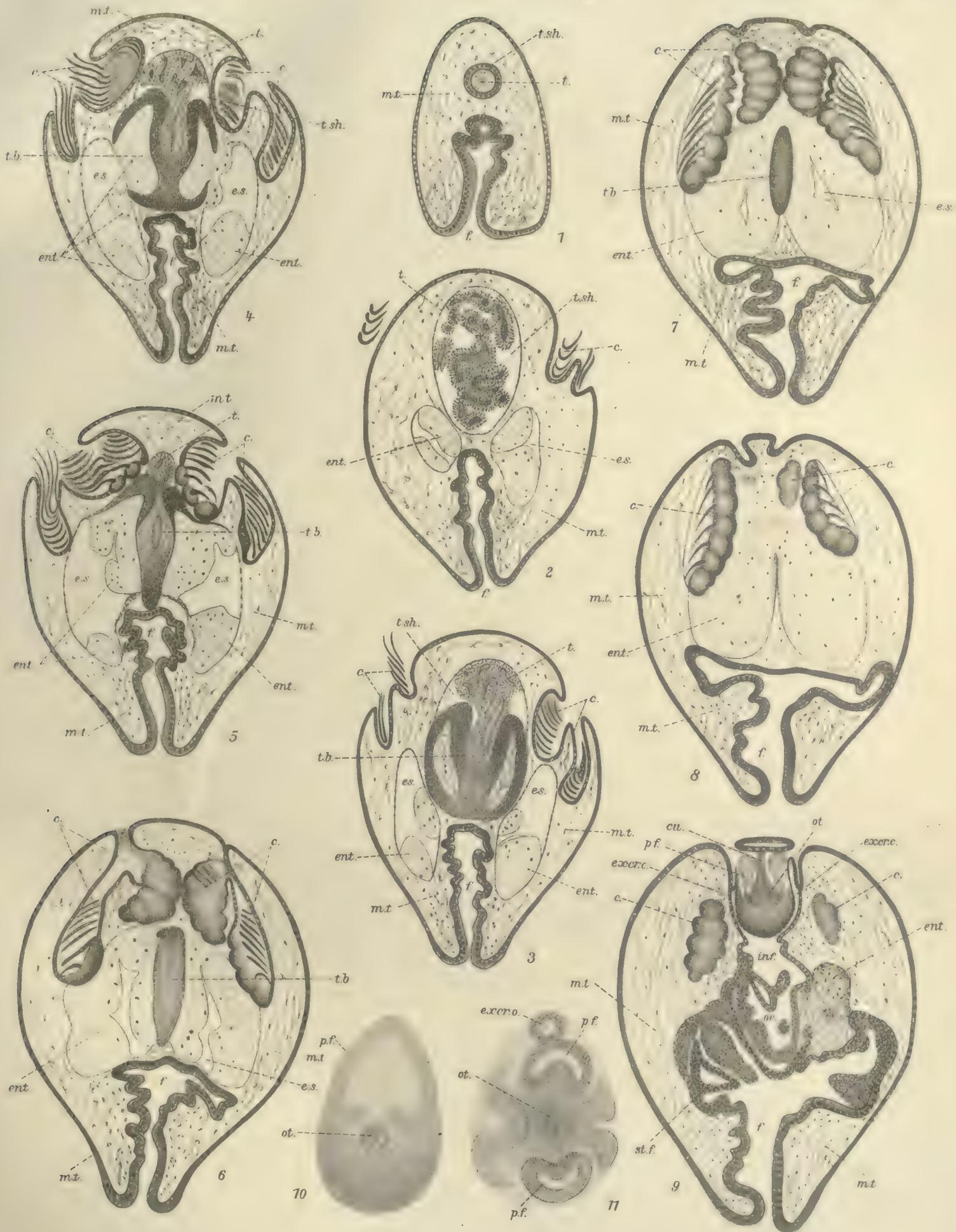
Fig. 1. The section goes through the outer part of the tentacle sheath.

Fig. 2. Further inwards, the section going through the coiled-up tentacle which lies within the tentacle sheath. (Comp. Pl. II. Fig. 8, Pl. VIII. Fig. 12). The outer end of the entodermal sacs is seen in the section; here the large entodermal cells are lying in two strands, as in the branching peripheral canal system.

Figs. 3—7 give successive sections through the tentacle apparatus and the entodermal sacs. Fig. 8 is inside the tentacle basis. In fig. 6 is seen the direct connection between the lumen of the entoderm sacs and the diverticula in the tentacle basis. Figs. 7—8 show the continuation of the costal sacs as low furrows running towards the apical organ.

Fig. 9. Median section, through the apical organ, the excretory canals, infundibulum and oesophagus. (Comp. Pl. VII. Fig. 10). The flat epithelial ring above the apical organ is the epidermis arching over the apical organ — not quite normally, due to the contraction on preservation. The situation of the costæ within the body in figs. 7—9 is only apparent; a comparison with the horizontal sections in Pl. IX easily explains how this arrangement has arisen through the intercostal parts arching over the deep lying costæ.

- 10. The apical organ of an embryo in stage III; seen in side view, from the sagittal side. Above the otolith is seen the polar field.  $220/1$ .
  - 11. The same as fig. 10 seen from above; showing one excretory pore, the other being indistinct in the preparation.  $220/1$ .
-



Th. Mortensen del.

Lith. Anst. v. A. Funke, Leipzig.

*Tjalfiella tristoma* Mrtln.



# INGOLF-EXPEDITIONEN

1895—1896.

## STATIONERNES PLADS, DYBDE OG BUNDTEMPERATUR.

Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur	Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur	Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur
1	62° 30'	8° 21'	132	7°2	24	63° 06'	56° 00'	1199	2°4	45	61° 32'	9° 43'	643	4°17
2	63° 04'	9° 22'	262	5°3	25	63° 30'	54° 25'	582	3°3	46	61° 32'	11° 36'	720	2°40
3	63° 35'	10° 24'	272	0°5		63° 51'	53° 03'	136		47	61° 32'	13° 40'	950	3°23
4	64° 07'	11° 12'	237	2°5	26	63° 57'	52° 41'	34	0°6	48	61° 32'	15° 11'	1150	3°17
5	64° 40'	12° 09'	155			64° 37'	54° 24'	109		49	62° 07'	15° 07'	1120	2°91
6	63° 43'	14° 34'	90	7°0	27	64° 54'	55° 10'	393	3°8	50	62° 43'	15° 07'	1020	3°13
7	63° 13'	15° 41'	600	4°5	28	65° 14'	55° 42'	420	3°5	51	64° 15'	14° 22'	68	7°32
8	63° 56'	24° 40'	136	6°0	29	65° 34'	54° 31'	68	0°2	52	63° 57'	13° 32'	420	7°87
9	64° 18'	27° 00'	295	5°8	30	66° 50'	54° 28'	22	1°05	53	63° 15'	15° 07'	795	3°08
10	64° 24'	28° 50'	788	3°5	31	66° 35'	55° 54'	88	1°6	54	63° 08'	15° 40'	691	3°9
11	64° 34'	31° 12'	1300	1°6	32	66° 35'	56° 38'	318	3°9	55	63° 33'	15° 02'	316	5°9
12	64° 38'	32° 37'	1040	0°3	33	67° 57'	55° 30'	35	0°8	56	64° 00'	15° 09'	68	7°57
13	64° 47'	34° 33'	622	3°0	34	65° 17'	54° 17'	55		57	63° 37'	13° 02'	350	3°4
14	64° 45'	35° 05'	176	4°4	35	65° 16'	55° 05'	362	3°6	58	64° 25'	12° 09'	211	0°8
15	66° 18'	25° 59'	330	—0°75	36	61° 50'	56° 21'	1435	1°5	59	65° 00'	11° 16'	310	—0°1
16	65° 43'	26° 58'	250	6°1	37	60° 17'	54° 05'	1715	1°4	60	65° 09'	12° 27'	124	0°9
17	62° 49'	26° 55'	745	3°4	38	59° 12'	51° 05'	1870	1°3	61	65° 03'	13° 06'	55	0°4
18	61° 44'	30° 29'	1135	3°0	39	62° 00'	22° 38'	865	2°9	62	63° 18'	19° 12'	72	7°92
19	60° 29'	34° 14'	1566	2°4	40	62° 00'	21° 36'	845	3°3	63	62° 40'	19° 05'	800	4°0
20	58° 20'	40° 48'	1695	1°5	41	61° 39'	17° 10'	1245	2°0	64	62° 06'	19° 00'	1041	3°1
21	58° 01'	44° 45'	1330	2°4	42	61° 41'	10° 17'	625	0°4	65	61° 33'	19° 00'	1089	3°0
22	58° 10'	48° 25'	1845	1°4	43	61° 42'	10° 11'	645	0°05	66	61° 33'	20° 43'	1128	3°3
23	60° 43'	56° 00'	Kun Planktonundersøgelser		44	61° 42'	9° 36'	545	4°8	67	61° 30'	22° 30'	975	3°0

Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur	Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur	Station Nr.	N. Brd.	V. Lgd.	Dybde i danske Fvn.	Bundtemperatur
68	62° 06'	22° 30'	843	3° 4	92	64° 44'	32° 52'	976	1° 4	118	68° 27'	8° 20'	1060	-1° 0
69	62° 40'	22° 17'	589	3° 9	93	64° 24'	35° 14'	767	1° 46	119	67° 53'	10° 19'	1010	-1° 0
70	63° 09'	22° 05'	134	7° 0	94	64° 56'	36° 19'	204	4° 1	120	67° 29'	11° 32'	885	-1° 0
71	63° 46'	22° 03'	46			65° 31'	30° 45'	213		121	66° 59'	13° 11'	529	-0° 7
72	63° 12'	23° 04'	197	6° 7	95	65° 14'	30° 39'	752	2° 1	122	66° 42'	14° 44'	115	1° 8
73	62° 58'	23° 28'	486	5° 5	96	65° 24'	29° 00'	735	1° 2	123	66° 52'	15° 40'	145	2° 0
74	62° 17'	24° 36'	695	4° 2	97	65° 28'	27° 39'	450	5° 5	124	67° 40'	15° 40'	495	-0° 6
	61° 57'	25° 35'	761		98	65° 38'	26° 27'	138	5° 9	125	68° 08'	16° 02'	729	-0° 8
	61° 28'	25° 06'	829		99	66° 13'	25° 53'	187	6° 1	126	67° 19'	15° 52'	293	0° 5
75	61° 28'	26° 25'	780	4° 3	100	66° 23'	14° 02'	59	0° 4	127	66° 33'	20° 05'	44	5° 6
76	60° 50'	26° 50'	806	4° 1	101	66° 23'	12° 05'	537	-0° 7	128	66° 50'	20° 02'	194	0° 6
77	60° 10'	26° 59'	951	3° 6	102	66° 23'	10° 26'	750	-0° 9	129	66° 35'	23° 47'	117	6° 5
78	60° 37'	27° 52'	799	4° 5	103	66° 23'	8° 52'	579	-0° 6	130	63° 00'	20° 40'	338	6° 55
79	60° 52'	28° 58'	653	4° 4	104	66° 23'	7° 25'	957	-1° 1	131	63° 00'	19° 09'	698	4° 7
80	61° 02'	29° 32'	935	4° 0	105	65° 34'	7° 31'	762	-0° 8	132	63° 00'	17° 04'	747	4° 6
81	61° 44'	27° 00'	485	6° 1	106	65° 34'	8° 54'	447	-0° 6	133	63° 14'	11° 24'	230	2° 2
82	61° 55'	27° 28'	824	4° 1		65° 29'	8° 40'	466		134	62° 34'	10° 26'	299	4° 1
83	62° 25'	28° 30'	912	3° 5	107	65° 33'	10° 28'	492	-0° 3	135	62° 48'	9° 48'	270	0° 4
	62° 36'	26° 01'	472		108	65° 30'	12° 00'	97	1° 1	136	63° 01'	9° 11'	256	4° 8
	62° 36'	25° 30'	401		109	65° 29'	13° 25'	38	1° 5	137	63° 14'	8° 31'	297	-0° 6
84	62° 58'	25° 24'	633	4° 8	110	66° 44'	11° 33'	781	-0° 8	138	63° 26'	7° 56'	471	-0° 6
85	63° 21'	25° 21'	170		111	67° 14'	8° 48'	860	-0° 9	139	63° 36'	7° 30'	702	-0° 6
86	65° 03' 6	23° 47' 6	76		112	67° 57'	6° 44'	1267	-1° 1	140	63° 29'	6° 57'	780	-0° 9
87	65° 02' 3	23° 56' 2	110		113	69° 31'	7° 06'	1309	-1° 0	141	63° 22'	6° 58'	679	-0° 6
88	64° 58'	24° 25'	76	6° 9	114	70° 36'	7° 29'	773	-1° 0	142	63° 07'	7° 05'	587	-0° 6
89	64° 45'	27° 20'	310	8° 4	115	70° 50'	8° 29'	86	0° 1	143	62° 58'	7° 09'	388	-0° 4
90	64° 45'	29° 06'	568	4° 4	116	70° 05'	8° 26'	371	-0° 4	144	62° 49'	7° 12'	276	1° 6
91	64° 44'	31° 00'	1236	3° 1	117	69° 13'	8° 23'	1003	-1° 0					





# THE DANISH INGOLF-EXPEDITION.

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# THE DANISH INGOLF-EXPEDITION.

VOL. V, PART 3

CONTENTS:

*OSKAR CARLGREN: CERIANTHARIA.*

PUBLISHED AT THE COST OF THE GOVERNMENT

BY

THE DIRECTION OF THE ZOOLOGICAL MUSEUM OF THE UNIVERSITY



COPENHAGEN.

H. HAGERUP.

PRINTED BY BIANCO LUNO.

1912.



# THE DANISH INGOLF-EXPEDITION.

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VOLUME V.

3.

## CERIANTHARIA.

BY

OSKAR CARLGREN.

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WITH 5 PLATES AND 16 FIGURES IN THE TEXT.



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PRINTED BY BIANCO LUNO.

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Ready from the Press October 5<sup>th</sup> 1912.

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The investigations of which I now publish an account, deal not merely with the scanty stock of Ceriantharia collected on the Ingolf Expedition, but with all northern species that I have received for investigation, chiefly from the museum of Copenhagen, the museum of Trondhjem and the natural history museum (Riksmuseum) at Stockholm. As the number of known Ceriantharia from the northern seas, even including the species I have described, is comparatively small, I have preferred not to scatter my account of these few species over two or possibly more publications, because a view as connected as possible of the morphology of the Ceriantharia, in the way set forth below, seems to be not without value, especially as this account is based on close study of a comparatively large number of species (see below) and in many points deviates considerably from the accounts previously published, such as v. Beneden's and Mc Murrich's. Through the kind courtesy of the editors of the scientific results of the Ingolf Expedition, I have been put in a position to publish my investigations in the reports of the Ingolf Expedition. For this I must express my gratitude, and at the same time I have to thank the heads of the respective departments of the museums whose collections I have used, above all Dr. Levinsen of Copenhagen, Professor Th  el of Stockholm, Professor Appel  of of Upsala formerly of Bergen, Dr. Svenander formerly of Trondhjem, and Dr. Broch of Trondhjem. On morphological grounds chiefly I have also taken account in the present work of *C. americanus*, though this species is found more in the south. The specimens of this species described are partly from the museum of Copenhagen, partly from Beaufort-station in North Carolina, the director of which, Dr. Aller, has sent me some specimens preserved in formalin, a kindness for which I tender my warmest thanks.

Simultaneously with this work I am publishing in *Mittheilungen a. der zoologischen Station zu Neapel* a paper describing the morphology of a larval form and a few adult forms of Ceriantharia already known. As account is taken of these forms also in the synopsis of the morphology (4th section), I would request any reader who takes a special interest in the structure of the Ceriantharia, to pay special attention to that work also.

I subdivide this paper into the following four parts.

- (1) A brief introduction comprising the literature of the subject, the geographical distribution, and a survey of the Ceriantharia of the north.
- (2) An account of the different species.
- (3) The classification of the Ceriantharia.
- (4) Concerning the morphology of the Ceriantharia.



## Section I.

### Literature and survey of the northern Ceriantharia.

The first species of Ceriantharia from northern waters was described by Gosse (1856) as *Edwardsia vestita*. Two years later (1858) he identified this form with *Cerianthus membranaceus*, a mistake which he rectified in 1859 when the species received the name it has since retained, *Cerianthus lloydii*. A summary of the exterior and life-conditions of the species was given by Gosse (1860). After being observed on the coasts of Great Britain, it was met with in 1861 by M. Sars on the Norwegian coast. Danielssen however in *Fauna littoralis Norvegiae* 1871 expresses the opinion that the form met with by Sars and afterwards by himself is a new species, which he calls *Cerianthus borealis*, a name which Verrill however had used (1873) for a species described by himself from North America. Carlgren (1893) shews that it had already been observed by S. Lovén (1839) on the west coast of Sweden. Hartlaub (1894) found it at Heligoland.

More or less detailed accounts of this species have been given by Carlgren (1893), v. Beneden (1898) and by Danielssen as early as 1888, though the last-named has referred it to *C. borealis*. Danielssen's account moreover is written in so peculiar a style and varies so much from all other accounts of the Cerianthidae, that one would be inclined to deny the identification of his *C. borealis* with *C. lloydii*, were not Danielssen's accounts of the Actiniae, as Mc Murrich (1893 p. 133) says, "beautiful examples of how not to do it". According to my investigations however the two forms are one and the same species, as Andres (1883) had already conjectured.

A small Cerianthid *Cerianthus vermicularis* Forbes from the Sound is described by Lütken (1860). Andres (1883) has given this species the name of *Cerianthus lütkeni*. Without doubt this is a young Cerianthid and probably nothing but a young *Cerianthus lloydii*. It is uncertain however whether *Cerianthus vermicularis* (Forbes in Johnston) is so also (Compare Andres 1883 p. 561).

New Cerianthidae are described by Danielssen (1890) from the Norwegian North-Atlantic Expedition under the names of *Cerianthus vogti* and *abyssorum*. But the descriptions are so incomplete that the classification of the species cannot be made out. As I understand them the two species are identical and fall under the genus *Cerianthus*. The systematic position also of the species described by Roule (1905), *Cerianthus lloydii* and *danielsseni*, the former of which to judge from the coloured drawing is not *Cerianthus lloydii* but probably a new species, cannot be determined. Although the description of the former is so incomplete, it might still be convenient to give it a special name *Cerianthus roulei*.

In 1889 Lütken claimed to have made the discovery that *C. membranaceus* was to be found in the Kattegat. In reality this was a mistake, as the specimens of Lütken are identical with a species I have described below, *P. multiplicatus*.

In addition to the above mentioned Ceriantharia, Levinsen (1893) has described a species which he called *Cerianthus danielsseni* — a name which Kingsley (1904 p. 347) had suggested for Danielssen's *C. borealis*. But in the first place it is identical with *C. lloydii*, and secondly it seems to embrace the species *P. multiplicatus* I describe below. The large specimens which Levinsen speaks of from the Kattegat are probably identical with the forms designated as "borealis" and "membranaceus" (see *P. multiplicatus*).

The name *Cerianthus borealis* was given by Verrill (1873) to a form from the Arctic regions of the Atlantic coast of North America. The anatomical structure of this species was dealt with, though very imperfectly, by Kingsley (1904). Another, more southern form was first observed by Agazziz (1859) and described later by Verrill (1862) under the name of *Cerianthus americanus*. It was investigated anatomically by Mc Murrich (1890) and (1910), though not so fully as might be desired.

Before the first adult, northern Cerianthidae had been described, a larval Cerianthid from the Norwegian coast *Arachnactis albida*, described by M. Sars (1846), was already known. In 1862 Agazziz found on the North American coast another form, *Arachnactis brachiolata*, and in 1890 Bourne mentioned a larval *Arachnactis*, which Fowler (1897) described as *Ar. bournei*. As I do not treat the larval forms in detail here, I refer the reader to my paper on "Actinienlarven" (Nordisches Plankton 1906).

To these species I have in the present treatise to add three which have not been described before: *Pachycerianthus multiplicatus*, *Arachnanthus sarsi* and *Botrucnidifer norvegicus*: three new genera *Arachnanthus*, *Botrucnidifer* and *Ceriantheopsis* are here described for the first time.

If we include the North American form *C. borealis* in our list of the northern and arctic Cerianthidae at present known, we get the following number of adult forms.

- (1) *Cerianthus lloydii* Gosse = *borealis* Danielssen = *danielsseni* p. p. Levinsen, Kingsley = *vermicularis* Lütken = *lütkeni* Andres.
- (2)     >     *vogti* Danielssen = *Cerianthus abyssorum* Danielssen.
- (3)     >     *borealis* Verrill (not of Danielssen).
- (4) *Pachycerianthus multiplicatus* Carlgren = *Cerianthus danielsseni* Levinsen p. p. = *membranaceus* Lütken.
- (5) *Arachnanthus sarsi* Carlgren.
- (6) *Botrucnidifer norvegicus* Carlgren.

Here belong the following forms whose place in the system it has not been possible to determine<sup>1)</sup>. Possibly one of them may be identical with one of the six already mentioned.

<sup>1)</sup> Still another Ceriantharia which was obtained by the "Michael Sars" Expedition 1910 (60° 57' N. 4° 38' W 1098 m. clay St. 102 — 9. 10. 1910), has brown labial tentacles and stomatodaeum, very deep furrows in the distal portion of the column, marginal tentacles twice as large as the labial tentacles, a directive labial tentacle, and the typical arrangement of the mesenteries. As only the most distal part of the specimens was secured — they were cut in two by the dredge at the lower border of the stomatodaeum — it is impossible to give a precise description of it. It appears however not to be identical with any of the Ceriantharia which I have described.

(7) *Cerianthus danielsseni* Roule.

(8) *Cerianthus? lloydii* Roule = *C. roulei* n. n.

Of these *Cerianthus lloydii* shews the widest geographical distribution known, Greenland, Spitsbergen, Nova Zembla, the Norwegian coast, the west coast of Sweden to The Sound, North Sea, the coasts of Great Britain. The range of distribution of *C. borealis* according to Parker (1900) is from the Arctic Ocean to Cape Hatteras. *Pachycerianthus multiplicatus* is known only from the Kattegat and the fjord of Trondhjem. *Arachnanthus sarsi* and *Botrucnidifer norvegicus* only from the fjord of Trondhjem in Norway. *C. vogti* only from a district lying west of the fjord of Trondhjem and westward of Lofoten (*C. abyssorum*), Roule's *Cerianthus danielsseni* is taken to the westward of Iceland and near Lofoten in Norway, and *C. roulei* is only known from Spitsbergen. After this general survey of the forms, I pass on to describe the species which I have investigated.

## Section II.

### Description of species.

Family **Cerianthidae**. Diagnosis see Section III.

Genus **Pachycerianthus** Roule. Diagnosis see Section III.

Species **P. multiplicatus** nov sp. Pl. 1, 2.

Syn.: *Cerianthus membranaceus* Lütken 1889 p. 362.

*danielsseni* p. p., Levinsen 1893 p. 397.

*Diagnosis*: A large species with 160—170 long marginal tentacles. The directive chamber and the contiguous chamber on either side of this probably without labial tentacles. Stomatodaeum of medium length. Siphonoglyph not wide, with insertions for 6 mesenteries. Hyposulcus short, with quite long, very narrow, but distinct hemisulci. The directive mesenteries very short. The protomesenteries 2 and 3 short, the former somewhat longer than the latter. Protomesenteries 2 sterile with region of the ciliated tract and cnido-glandular tract. The metamesenteries arranged distinctly in quartettes. The metamesenteries of the first cycles (*M*) very long extending to the aboral pole of the body with prolonged ciliated tract region and numerous craspedonemes reaching as far as the most aboral portion of the mesenteries, with very slight cnido-glandular region, fertile. The craspedonemes are most numerous and longest in the lowest part and here form not very distinct bunches. The metamesenteries of the 2nd cycle (*m*) short, of much the same length as the protomesenteries 2 and 3, with craspedonemes as with *M* and somewhat stronger cnido-glandular region, fertile. The metamesenteries of the 3rd (*B*) and 4th (*b*) cycles very short, corresponding in structure with protomesenteries 3, with insignificant craspedonemes and well developed cnido-glandular region, sterile, those of the 4th cycle somewhat shorter than those of the 3rd.

*Occurrence:* Norway Trondhjem fjord Rissen 130 m. slime, 21. 7. 1892 G. Svenander. 1 sp. (A). T. M.  
 » 1 sp. T. M.  
 Kattegat (No. 432) Joh. Petersen 1 sp. (B) labelled *C. borealis* Dan. Cop. M.  
 » (No. 432) » » 1 sp. (C) » *C. membranaceus* Cop. M.  
 » (No. 424) » » 1 sp. (D) » *C. borealis* Dan. Cop. M.  
 » (No. 318) » » 1 sp. (E) » » » Cop. M.

*Dimensions.* Sp. A. Length of body 15.5 cm., greatest breadth 3 cm. Length of marginal tentacles: the innermost 6.5 cm., the outermost 3.5 cm. Length of labial tentacles 1.4—1.7 cm. Length of stomatodaeum about 3 cm. — all measurements taken from preserved specimens.

*Colour:* According to the statement of Dr. Svenander, who dredged a specimen in Trondhjem fjord, the whole animal was of a faint flesh colour.

*Exterior aspect* (Pl. I, fig. 1). The body has the usual aspect of the Cerianthidae. The column shews longitudinal furrows as a result of contraction. Such may possibly be observed in the fully extended animal, as in the well extended upper portion feeble longitudinal furrows appear, which are specially well marked below the tentacles and there correspond to the insertions of the mesenteries. Aboral pore? The tentacles are long, the marginal and labial tentacles each 160—170. The marginal tentacles seem to be arranged in the same way as with *C. membranaceus*. As regards the grouping of the labial tentacles however, I cannot express myself with any certainty, as I did not like even in the slightest degree to mutilate the only well preserved specimen (A). As this specimen happened to be dissected along the line of the siphonoglyph some tentacle insertions were also damaged, which was a great difficulty in the investigation of the arrangement of the labial tentacles. In another specimen, which was fairly well preserved but strongly contracted, it seemed to me that some tentacles in the region of the directive mesenteries were wanting. Though it is possible that the directive chamber and the two contiguous chambers lack labial tentacles, I prefer to leave the arrangement of the labial tentacles in this species an open question.

The stomatodaeum is of medium length with feeble longitudinal furrows in the oral portion, in the aboral with deep furrows and between them high ridges running lengthwise. The aboral end of the stomatodaeum is bent towards the column in the sort of way often noticed in contracted Cerianthidae. The siphonoglyph is comparatively narrow, so that only 6 mesenteries are attached to it. The hyposulcus is very short, though the hemisulci are comparatively long, but so narrow that they look like filaments for the greater part of their course.

*Anatomical structure.*

Column: The ectoderm is thick with numerous nematocysts, with marked spiral thread. The length and breadth of the nematocysts vary considerably. The largest size had a length of 96  $\mu$  and a breadth of 27  $\mu$ , the smallest size was 58  $\mu$  long. The ectodermal musculature is very fully developed, in the highest part of the body the folds are twice as high as the rest of the ectoderm, but, as usual with the Cerianthidae, taper off considerably in the distal and proximal part of the animal. The mesogloea-lamellae supporting the muscles are very fine and are set extremely close together. The chief lamella of the mesogloea is thin. The endoderm is rather thinner than the epithelial portions of the ectoderm and in the region of the stomatodaeum furnished in sections with tongue-like pro-

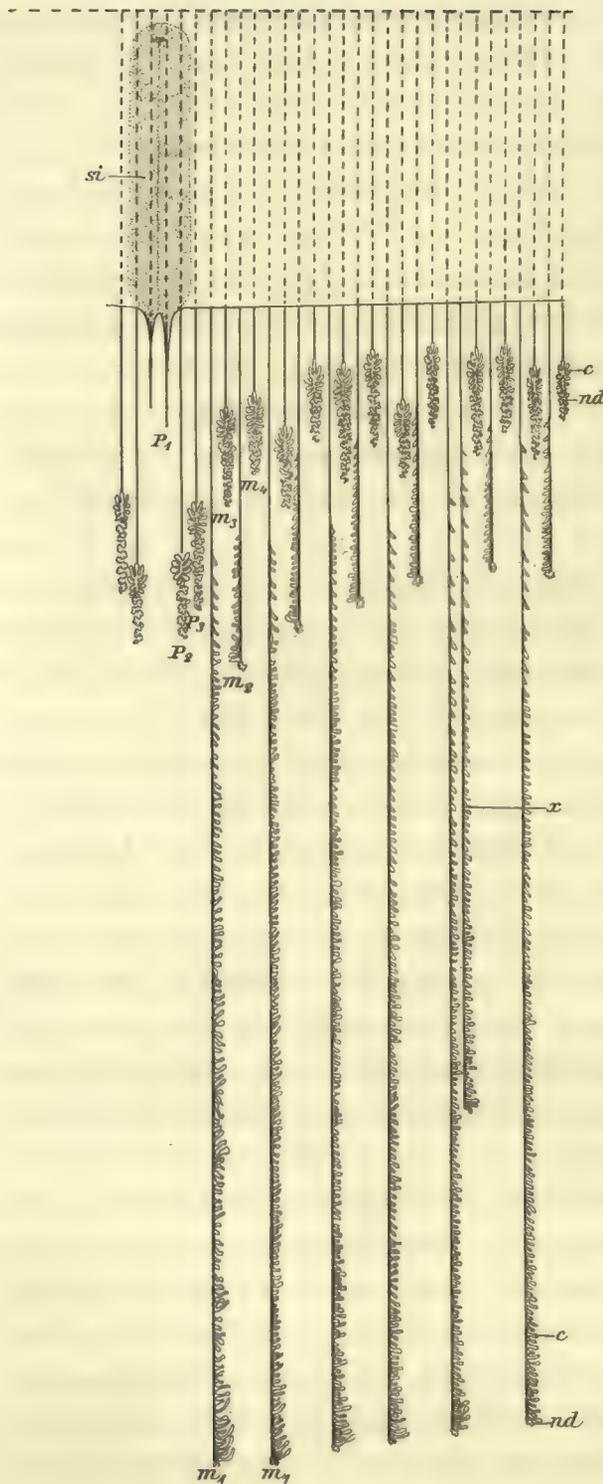
jections between the mesenteries. As they are not always clearly shewn, it is possible that they are produced by contraction. The endoderm is provided with numerous mucus cells and granular gland cells.

The ectoderm of the tentacles and oral disc contains numerous thin-walled nematocysts, spirocysts, and numerous nematocysts with much-coiled spiral thread, also a kind of thick-walled granulated capsules with long basal part of spiral thread (length  $53-65\mu$ ) and lastly thick-walled nematocysts but considerably smaller than the foregoing. The ectoderm of the tentacles is half the thickness of that of the column but considerably thicker than the mesogloea. The mesogloea is comparatively thick with higher folds on the inner side of the tentacles than on the outer, for which reason the longitudinal musculature is more developed on the inner side of the tentacles. Those of the radial musculature are strongly marked in the oral disc and the folds somewhat lower than the ectoderm. The endoderm of the oral disc on the other hand is thinner than the height of the muscle folds. (Pl. I, Fig. 3).

Stomatodaeum: The ectoderm is very high and folded and supported even in the upper portion by a mesogloea process of triangular cross section. The ectoderm is everywhere of the same structure with the exception of the very lowest part. The nematocysts with much-coiled spiral thread are numerous and about  $46-53\mu$  long and  $5\mu$  broad. In the aboral part are found also spirocysts and thick-walled nematocysts of about the length of  $36\mu$ . As usual the ectoderm contains numerous mucus and albumen gland cells which in the upper portion of the stomatodaeum are scattered about, but in the lowest portion like the nematocysts are clustered at the crest of the fold, whilst the furrows between the folds and the sides of these chiefly consist of supporting cells, an arrangement which is spoken of more fully under *C. lloydi*. The mesogloea folds are in the lowest part narrow in transverse section and long as usual with this species. The ectodermal musculature is very feeble, especially in the lowest portion of all where only scattered muscle cells appear; on the crests of the mesogloea folds in the most central part of the stomatodaeum the muscle lamella shews a tendency to be enclosed in the mesogloea, as here and there the muscle fibres are found enclosed in the mesogloea. The mesogloea contains only a few scattered cells.

The ectoderm of the siphonoglyph is high, not folded, with numerous homogeneous gland cells but with sparsely scattered nematocysts. The longitudinal musculature is very feeble. The mesogloea is thin in the middle but much thickened near the stomatodaeum. I have not observed any ciliated tracts on the hyposulcus, at least none are found in the aboral portion of the hyposulcus. A transverse section of a hemisulcus (Pl. I, Fig. 4) is very much like a transverse section of a median streak of the filament. The high ectoderm contains very numerous gland cells and more sparsely scattered nematocysts. These chiefly consist of thin-walled nematocysts but nematocysts with much-coiled threads too are found, as also thickwalled ones of the same dimensions as in the stomatodaeum. The longitudinal musculature in the hemisulci is feeble but plain.

Mesenteries: (Text-figure 1). I have counted the number of the mesenteries in 2 specimens. In ex. E were found 38 mesenteries of the 1st cycle, in ex. A I observed on the left side 17 large mesenteries of the 1st cycle which reached to the aboral portion of the animal, and 2 lesser ones, which reached to the middle of the space between the aboral border of the stomatodaeum and the aboral



Text-figure 1. Diagram of the arrangement of a part of the mesenteries with stomatodaeum and siphonoglyph in *Pachycerianthus multiplicatus*. Here as in the text-figures 4, 5, 7, the mesenteries are marked with lines in the region of the stomatodaeum; *nd* by *m*, *m*<sub>2</sub> etc. are rather too strongly marked. *x*: see text! The line below the mesenteries indicates here as in figures 4, 5, 7 the aboral end of the body. For the other signs of the figure see the explanation of the Plates.

extremity of the body. On the right side were found 19 large mesenteries of the 1st cycle besides 4 lesser ones, of which the 1st reached  $\frac{2}{3}$  the remainder  $\frac{1}{2}$  or  $\frac{1}{3}$  of the space just mentioned. The number of mesenteries in specimen E was therefore about 160, in A about 170.

The following description is chiefly based on specimen A, as the other specimens were not well preserved enough to be adapted for anatomical study. When I speak of the length of the mesenteries in relation to the length of the column, there is to be understood here, as in general with the Ceriantharia, only the portion of the mesenteries and column that lies below (aborally from) the aboral border of the stomatodaeum. Below, I have in most cases called the column below the end of the stomatodaeum the column in a strict sense.

Protomesenteries: The directive mesenteries are sterile and very short, the right mesentery rather longer than the left, the free edge is straight. The hemisulci run a long way down as a small filament of the directive mesenteries.

Protomesenteries 2 (Pl. 2, Fig. 1) are comparatively short and extend about a fourth part of the length between the lower border of the stomatodaeum and the aboral pole. The left mesentery is somewhat longer than the right. The region of the ciliated tracts is long, slightly folded with short craspedonemes. The cnido-glandular tract is little developed. The mesenteries are in the aboral part very small in comparison with other sterile mesenteries. On the mesentery reproduced appears an aboral small lobe, which at its extremity supports craspedonemes. They are sterile.

Protomesenteries 3 (Pl. 2, Fig. 2) are sterile, shorter than P. 2 and considerably broader in the craspedoneme- and cnido-glandular region. The right mesentery is rather longer than the left. The craspedoneme region is inconsiderable compared with the cnido-glandular tract. The latter is very

strongly developed here, more so than in any other mesentery. The end of the craspedoneme region forms here as with the metamesenteries of the 3rd and 4th cycles the most prominent portion, a long lobe with numerous craspedonemes on the oral side and with wavy coils of the cnido-glandular tract on the aboral side.

Protomesenteries 2 and 3 take with respect to their appearance a middle position between the metamesenteries of the 2nd and 3rd cycle.

The metamesenteries are arranged in the usual manner: 4 mesenteries in each quartette (1, 3, 2, 4—1, 3, 2, 4 etc.). Broadly viewed the length of the mesenteries diminishes in every group in proportion to its nearness to the multiplication chamber, which is shewn in the diagram of the arrangement of a part of the right side metamesenteries. One peculiarity is worth pointing out, namely, that between the 20th and 21st mesentery on the right side an extra mesentery has been developed (text-fig. I. x.) which has the same appearance as the metamesenteries of the 1st cycle, though it is rather shorter, but is distinguished from them by the fact that it is sterile like the metamesenteries of the 3rd and 4th cycles. This anomaly has nothing corresponding to it on the left side, as no such mesentery exists there. This however is not the only break in the regular diminution in the size of the mesenteries as they approach the multiplication chamber. Thus the mesentery of the 2nd cycle on the right side in the 6th group is longer than the corresponding mesentery in the 5th group. In the 16th group on the same side the mesentery of the 2nd cycle is considerably longer than the same mesentery of the preceding quartette and as long as the mesentery of the 2nd cycle in the 1st quartette — relations which remind us of those we meet with in *Cerianthus membranaceus* and *solitarius*.

The metamesenteries of the 1st cycle (Pl. 2, Fig. 6) are those which principally develop reproductive organs. They are very long and reach almost to the aboral portion of the body. With exception of the youngest of all they exhibit no difference in size and appearance. The reproductive organs are best developed in the middle portion, where they take up the greater part of the breadth of the mesenteries, rather feebler in the lowest part of the mesenteries and feeblest in the straight part of the ciliated tract region, where only scattered germ follicles are found. The ciliated tract region of the filament is straight for some distance under the stomatodaeum and then quickly passes over into a folded section, which soon sends out craspedonemes. These are in the oral part rather short (Pl. 2, Fig. 7), in the lower parts however considerably longer and more branched, especially towards the proximal end, where they terminate in a cluster of threads (*bm* Pl. 2, Fig. 8). At the bottom of the mesentery is found an extremely minute part, a cnido-glandular tract of precisely the same structure as the wavy part of the mesenteries of the 2nd and 4th cycle. In consequence of its slight extent it is not marked in Fig. 8. The more or less concave aboral border of the mesenteries has no filament, as usual with mesenteries of every kind.

The metamesenteries of the 2nd cycle (Pl. 2, Fig. 4) closely recall those of the 1st cycle though they are much shorter, to a certain extent they form a transition to the mesenteries of the 3rd cycle. The reproductive organs are only feebly developed on these mesenteries. As regards the length of the different mesenteries of this cycle they follow the general rule with the exceptions before mentioned. It is possible indeed that in other groups besides those mentioned, an irregularity in the ratio of the lengths of the mesenteries may occur, as in this, the only fully serviceable specimen, I have

not been able to study the mesenteries as closely as could be desired. The length of the mesenteries below the stomatodaeum is about  $\frac{2}{7}$ — $\frac{1}{5}$  of the distance between the aboral pole and the lower border of the stomatodaeum. The straight part of the ciliated tract portion of the filament is shorter than in the mesenteries of the 1st cycle, but rather longer than the craspedoneme region. The craspedonemes are but slightly branched, in the most aboral portion packed close together in a bunch as with the mesenteries of the 1st cycle. At the bottom is a small part, a cnido-glandular tract which in a number of mesenteries shews many coils, so that these mesenteries by their appearance suggest those of the 3rd and 4th cycle. The mesenteries are broadest in the aboral part.

The metamesenteries of the 3rd and 4th cycle (Pl. 2, Fig. 3, 5) agree in structure with the protomesenteries 3. They are distinguished, the one from the other, only by a slight difference of length and position. The difference in size between the mesenteries of the same cycle is inconsiderable in the various groups, but they follow roughly the usual rule, that they get smaller towards the multiplication chamber. The straight part of the ciliated tract region is quite short, then follows a slightly folded short region with craspedonemes which are continued on to a considerably projecting portion of the mesentery, where they correspond to the bunches of craspedonemes which are present on the mesenteries of the 1st and 2nd cycle. The bunch is less developed on the mesenteries of the 4th cycle than on those of the 3rd, and lies on the oral side of the projecting part of the mesentery, whilst the aboral side of it is taken up by the greatly coiled part of the cnido-glandular tract. At the extremity of the projection, the ciliated region and the cnido-glandular tract pass into one another. The mesenteries of the 3rd and 4th cycle are considerably broader than those of the 1st and 2nd cycle. The broadest part is where the ciliated region terminates in the cnido-glandular tract.

The mesenteries of the 1st cycle then are fertile and have a long craspedoneme region and a very short cnido-glandular region.

The mesenteries of the 2nd cycle are likewise fertile and have a shorter craspedoneme region and a short cnido-glandular region, sometimes with many coils. The mesenteries of the 3rd and 4th cycle are sterile and have a short craspedoneme region but on the other hand a strongly developed wavy cnido-glandular region.

The cnido-glandular tract is thus very feeble on the mesenteries of the 1st cycle, rather stronger on those of the 2nd, and well developed on the mesenteries of the 3rd and 4th cycle. whilst the reverse is the case with regard to the ciliated tract region and its craspedonemes.

The filaments in the region of the ciliated tracts recall, in point of structure, those in *Cerianthus lloydii* described below. The thin-walled nematocysts are very numerous in the lateral portions of the median streak, and very narrow but long nematocysts occur there also with very winding thread. There is not found here so pronounced a ciliated groove between the two lateral portions of the median streak as is found in *A. oligopodus*, but the middle parts consist principally of supporting cells combined with scattered gland cells and spirocysts. In the craspedoneme region the median streak shews no tendency to bipartition. Since the filament encases the free edge of the craspedonemes, it is of course cut through twice by a transverse section (Pl. 1, Fig. 5). The craspedonemes are thus constructed as in *C. membranaceus*. Nematocysts with coiled thread also occur here.

The cnido-glandular tract contains a multitude of small finely granular gland cells and very numerous mucus cells, and thus does not present the typical appearance found in other Ceriantharia which I have investigated (Fig. 6, Pl. I). The thick-walled nematocysts which are not marked in the figure are  $29-31\ \mu$  long and  $7\ \mu$  broad. Spirocysts occur very seldom, as also the long nematocysts above mentioned.

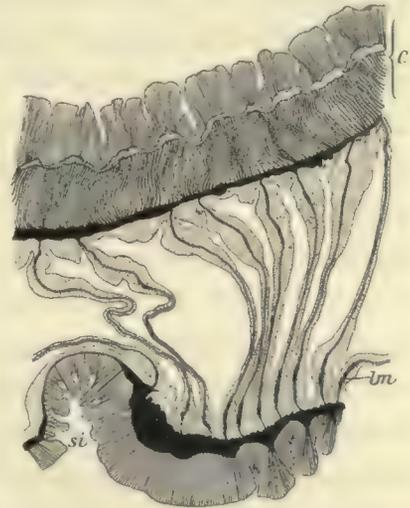
The musculature of the mesenteries is similar to that of *Cerianthus lloydii*; on the side of the mesenteries remote from the directives are found longitudinal muscles, on the near side, transverse ones. As for the directive mesenteries their musculature has not been investigated by me. (Textfig. 2, Pl. I, Fig. 2).

The mesogloea of the mesenteries is feeble as a rule and contains very thinly scattered though large cells, which often occupy a cyst-like space; in the craspedoneme region they are rather more numerous.

The endoderm is strong and provided with numerous remarkably homogeneous gland cells.

The specimen examined was hermaphrodite with well developed ova and spermatozoa.

*Systematic remarks.* In my paper in Nordisches Plankton (1906) I assumed that this form by reason of the large tentacles was the fully grown form of *Arachnactis albida*. This is not the case, however, as the anatomical investigation sufficiently shews. On the other hand it is not unlikely that *Arachnactis albida* is a larval form of *Arachnanthus sarsi* described below (compare this form).



Textfig. 2. *Pachycerianthus multiplicatus*. Portion of column, stomatodaeum and mesenteries.

Genus *Cerianthus* delle Chiaje. Diagnosis see Section III.

Species *Cerianthus lloydii* Gosse. Pl. 3, Pl. 4, figs. 4-5 Pl. 5, fig. 11.

*Edwardsia vestita* (Forbes) Gosse, 1856, p. 73.

*Cerianthus membranaceus* (Gmel.) Gosse, 1858, p. 419.

*Cerianthus lloydii* n. sp. Gosse, 1859, p. 50.

» » Gosse, 1860, p. 268, Pl. 6, fig. 8.

» » Gosse. Andres, 1883, p. 346.

» » » Pennington, 1885, p. 179.

» » » Sars, 1861, p. 262.

» » » (Koren) Danielssen, 1877, p. 80, note Pl. 4, figs. 8, 9.

» » » Carlgren, 1893 a Fig. 1, 1893 b, p. 120, fig. 39, 40, Pl. 10 fig. 1.

» » » Hartlaub, 1894, p. 203.

» » » E. van Beneden, 1898, p. 24, 25, fig. A, Pl. 1, figs. 1-4.

*Cerianthus vermicularis* Forb. Lütken, 1860, p. 199.

- » *lütkeni* n. n. Andres, 1883, p. 561.
- » *danielsseni* n. n. pro parte Levinsen, 1893, p. 397.
- » *danielsseni* n. n. Kingsley, 1904, p. 347.
- » *borealis* n. sp. Danielssen, 1879, Pl. 4, figs 8—9.
- »     » Dan. Danielssen, 1888, p. 13, Pl. 1.

? *Cerianthus* sp.? Breitfuss, 1904, p. 6.

*Diagnosis:* A large to medium sized species with tentacles of average development. Tentacles arranged in the main as in *C. membranaceus*, though a directive tentacle is lacking in the region of the labial tentacles. Siphonoglyph comparatively small, hyposulcus feebly developed, hemisulci quite long, distinct, but narrow. Directive mesenteries short. Protomesenteries 2 very long, extending right to the aboral pole, fertile with a well developed ciliated tract region, not however reaching much further down than to the aboral end of protomesenteries 3, with very long craspedion region. Cnido-glandular tract region comparatively feeble, wavy. Protomesenteries 3 rather short, with a ciliated tract region, which reaches as far as the termination of the directive mesenteries, and a long, wavy cnido-glandular tract region. Metamesenteries not clearly arranged in quartettes. Little difference between the metamesenteries of the 1st and 2nd cycle, all of which go down to the aboral pole. The metamesenteries of the 1st and 2nd cycle fertile, with rather shorter ciliated tract region than protomesenteries 2, this region being shorter in proportion to the nearness of the mesenteries to the multiplication chamber. The region of the cnido-glandular tract developed as with protomesenteries 2, as also the craspedion region. The metamesenteries of the 3rd and 4th cycle sterile, short, diminishing in length towards the multiplication chamber with a comparatively long ciliated tract region and an equally long cnido-glandular tract region, without craspedion region.

*Occurrence:*

Greenland. Tessiursars Vak, Anlistoivik fjord 3—10 fath., fine grey clay  $\frac{7}{7}$ , 1883, Sophia Exp. No. 522, 2 Ex. R. M.

» Fjord in the vicinity of the Sophias anchorage 6. 7. 1883, Sophia Exp. No. 521, 1 Ex. R. M.

» Discofjord, Iuannersvit 18 fath. sand and clay 27. 6. 1871. Ingegaard and Gladan-Exp. Lindahl many ex. R. M.

» 505 fath. 22. 2. 1890 Wandel No. 5, 1 ex. Cop. M.

Spitzbergen. Ice Fjord, Ekman Bay 40—43 m. Very loose, red clay. Bottom temperature  $-0.3^{\circ}$ . Spitzbergen-Exp. 1908, St. 113, 1 ex. R. M.

» In the coast of Cape Platen 40 m. Heligoland-Exp. 1898, St. 14, 1 ex. Berlin M.

? Barents sea. Breitfuss.

Kara sea Lat.  $70^{\circ} 57' 67^{\circ} 37'$  N. Zembla Exp. 1875, 1 ex. R. M.

Matochkin Sharr 20 fath. sand and clay 13. 7. 1875 N. Zembla Exp. 1875, 2 ex. R. M.

Norway. Trondhjem fjord, Rødberg 50—100 m. Aug. 1898 Östergren and Arvidsson 1 small ex. R. M.

Molde 30—50 fath. (*Cerianthus borealis*) Bergen Mus., Cop. M., R. M.

Bergen, the great Lungegaardsea 20 fath. (*Cerianthus borealis* Dan.)

Hardanger Varaldsö 50—60 fath. (*Cerianthus borealis* Dan.)

Skagerak 380—400 fath. brown clay 10.6.1879. Gunhild Exp. 1879 St. 5, 1 ex. R. M.

Väderöarne Lovén 1875 1 ex. Goës 1 ex. North Coralreef July 1899, Sandberg 1 ex. R. M.

Kattegat. Gulmar fjord Strömmarne. Skatholmen Carlgren June 1894 many ex.

» Théal 1879, Zool. Stat. 1896, 1898. Bonden Carlgren 1891 R. M.

» Fittebojen, Gotenb. Mus.

Lilla Middelgrund. Gunhild 1879 1 ex. R. M.

Kullen, Mølle 1832 S. Lovén 1 very small ex.

Hellebæk Lütken 1 small ex. (*Cerianthus Danielsenii* Lev.) Cop. M.

» Jungersen 1 small ex. ( » » » ) Cop. M.

North Sea. Heligoland from Prof. Hartlaub 1 ex. R. M.

Further distribution. British Isles (Gosse).

*Dimensions.* In the largest specimen (Ice fjord 1908) the length of the body is about 15 cm. Breadth of same 1—1.2 cm. Length of marginal tentacles up to 3.5 cm. Length of labial tentacles up to 1.5 cm.

*Colour.* Column more or less white, commonly tending to yellow (pale buff to ochre), immediately below the ring of tentacles often inclining to chestnut, paler or deeper. The outer tentacles are transparent, the base surrounded by a white ring that runs down in a point to the oral disc. Inside this the oral disc has often a darker chocolate-coloured portion with more or less plain, often broken bands of chocolate to chestnut-brown. These bands often run together and form larger, brown portions that take up the sides of the tentacles. Between these darker bands are found elongated patches of opaque white.

The labial tentacles deep chestnut or chocolate-brown to bright almost opaque white; on the outer side is found a longitudinal white or dingy white portion so that, seen from this side, the tentacles give the appearance of being opaque white with chocolate-coloured edges.

The oral disc is transparent with the parts between the attachment of the mesenteries more or less opaque white, but this does not go as far up as the tentacles. The directive chamber has plain marks of opaque white. The stomatodaeum is of the same colour as the column, though it has a somewhat darker brownish-yellow. The siphonoglyph is lighter.

The above account of the colouring is based on the observation of 4 specimens from Bohuslän, Sweden.

Danielssen says (1888) that the column in *C. borealis* i. e. *C. lloydii* is whitish-yellow and the oral disc rather darker. The tentacles have a brownish tinge,

*Exterior aspect.* The column has the characteristic form of the Cerianthidae, without aboral pore. The tentacles are of medium length and very short for the size of the animal. In specimens whose tentacles are undergoing regeneration, it seems on cursory inspection as though the tentacles might be covered by the upper border of the column (compare Danielssens drawing Fig. 3, Tab. 1, 1889), which is not the case. The marginal and the labial tentacles in the larger specimens number each about 70, in smaller specimens a lesser number is found. The number of marginal and labial tentacles respectively is not likely to exceed 70, as the longest specimen (from the Spitzbergen Expe-

dition 1908) has no more, notwithstanding that this specimen was considerably larger than other specimens with an equally large number of tentacles. The labial tentacles are considerably shorter than the marginal. As to the arrangement of the marginal tentacles, that of younger specimens agrees with the arrangement indicated by v. Beneden; in older specimens 4 tentacle rings are plainly to be seen. Just as in *C. membranaceus* the 4th cycle is sometimes differently coloured from the other three, and in the present case the tentacles of the 4th cycle are also rather smaller than those of the 3rd, and lie when fully extended a little outside those of the third cycle. The arrangement of the marginal tentacles reckoning from and including the directive chamber, is as follows.

in younger individuals: 2 (dt) 3, 2, 1 | 3, 2, 3, 1 | 3, 2, 3, 1 | 3, 2, 3, 1 | etc.

in older individuals: 2 (dt) 4, 3, 1 | 4, 2, 3, 1 | 4, 2, 3, 1 | 4, 2, 3, 1 | etc.

The tentacles lying nearest the directive tentacle (dt) are in older specimens a little displaced outwards.

The labial tentacles are arranged in 4 cycles according to v. Beneden  $o | dt | 3, 2, 4 | 4, 1, 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 |$  etc. The 8 specimens examined by me shew a rather different arrangement, which has no significance however for the determination of the species, partly because it is very hard to decide to which cycle the tentacles nearest the directive chamber belong, and partly because the position is variable. I have found the arrangement to be:  $o | dt | 4(3), 2, 3 | 4, 1(2), 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 |$  etc. The arrangement of the labial tentacles then may probably be expressed by the following formula.

$$o (dt) 4, 2, 3 | 4, 1, 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 | \text{etc.}$$

$$(3) (4) (2)$$

In a few specimens examined some tentacles were torn away and regenerated, in others all the top of the column and stomatodaeum was torn away and undergoing regeneration with small, newly formed tentacles. The specimen which Danielssen (1889) has figured, is evidently in the like state.

The oral disc is of the usual appearance.

The stomatodaeum is of medium length, faintly furrowed longitudinally, in the most aboral part with very deep longitudinal furrows. The siphonoglyph is deep, but comparatively small, as, besides the directive mesenteries, only the 2 nearest protomesenteries are attached to the siphonoglyph and that only in the middle portion of it. Only the directive mesenteries are orally and aborally attached to the siphonoglyph. The hyosulcus is small, the hemisulci are distinct and in the lower part resemble filaments.

#### *Anatomical description.*

The anatomy of this species has been treated by me previously in 1903, but very imperfectly, as I had then only a single and that a badly preserved specimen for examination. I showed however, that the musculature of the mesenteries had an arrangement, which made it extremely likely that the siphonoglyph in the Cerianthidae was not ventral but dorsal, and that quite a number of mesenteries went right down to the aboral pole. Afterwards v. Beneden also gave a sketch of the anatomy, though only incidentally. Among other things he has given a sketch of the arrangement of the mesenteries and the grouping of the tentacles (1908, Text-fig. A, p. 25) which in various points however requires supplementing. For, among other things, v. Beneden has not noticed the cnido-

glandular tract in the mesenteries of the 1st and 2nd cycle, and in the protomesenteries 2. Lastly, Danielssen has treated the anatomy of *C. borealis*, a species that has turned out to be identical with *C. lloydii* (see below). If that description should be regarded as correct *C. borealis* would be a form extremely divergent from the other known Ceriantharia, to judge by everything. Danielssen's description must be considered for the most part wrong. In what follows I take hardly any account of that description and I do this all the more because, on reviewing the Actiniaria described by Danielssen, I have been brought to the conclusion that Danielssen's descriptions of the anatomical facts concerning these are in the highest degree untrustworthy.

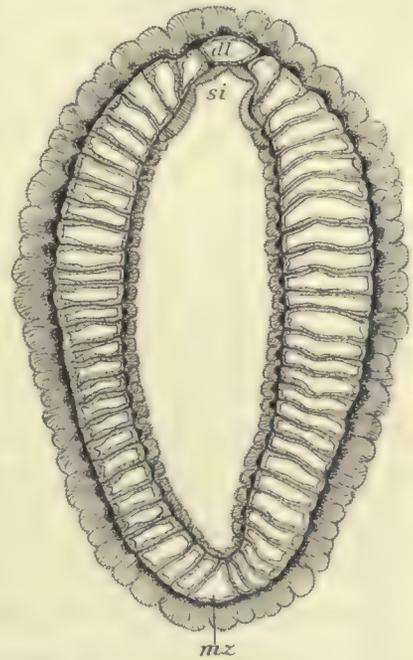
The column: Ectoderm thick with extremely numerous nematocysts principally of the kind with much coiled spiral thread — the longest I measured attained a length of  $72\mu$  and a breadth of  $14\mu$ ; but probably still longer nematocysts occur. In addition there is a sprinkling of thick-walled, very small nematocysts about  $41\mu$  long. The longitudinal musculature is very strongly developed except in the most distal portion.

The tentacles in an outstretched state with somewhat thin ectoderm. The ectoderm of the outer tentacles contains nematocysts which are principally spirocysts. The nematocysts of the inner tentacles agree with those of the stomatodaeum, though spirocysts are quite numerous. The largest thick-walled ones were about  $41-43\mu$  long.

The oral disc is like the tentacles in structure, though the radial musculature is stronger.

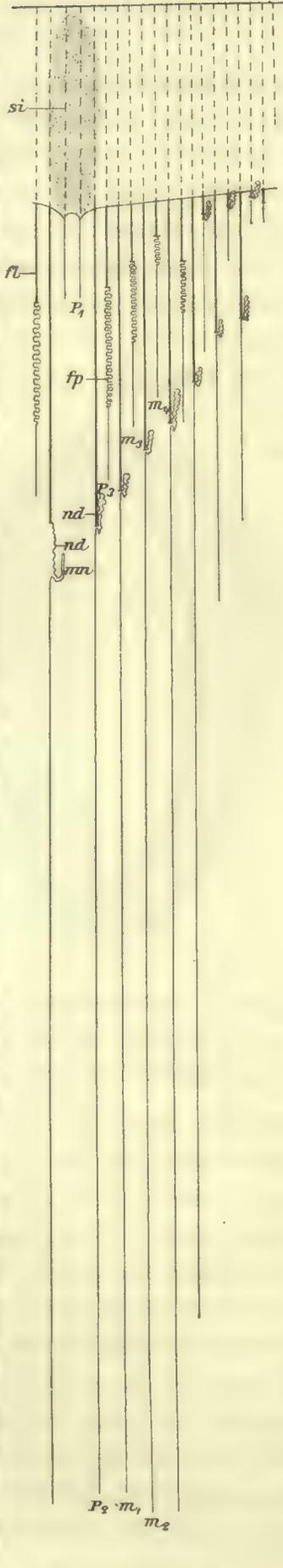
The stomatodaeum (Fig. 1-5, Pl. 3) also shews the structure characteristic of the Cerianthidae in general. The ridges are formed of thickenings of the ectoderm in the highest part of the stomatodaeum, in the aboral part where the ridges are considerably higher they are supported by mesogloaeal enlargements (Pl. 3, Fig. 2, 4). The ectoderm in the upper part of the stomatodaeum contains 3 kinds of thick-walled nematocysts, some being about  $46-48\mu$  long, and broad, some about  $34\mu$  long, and broad, and lastly some  $19-22\mu$  long, but narrow. Of these the last class is the rarest, the first the most numerous. In addition spirocysts are found but are not particularly numerous. The ectoderm supported by mesogloaeal processes is provided at the summit of the ridge with gland cells and a sprinkling of nematocysts, whilst the sides of the ridges and the furrows between the ridges chiefly contain supporting cells. At the bottom of the furrows and the transition to the filaments the ectoderm is more strongly ciliated than higher up (Fig. 3, Pl. 3). The nematocysts in the aboral part of the stomatodaeum agree with those in the oral, the large ones about  $41-43\mu$  long, the smaller more thinly scattered than in the oral part. The longitudinal musculature of the ectoderm is feebly developed.

The siphonoglyph (*si*) contains, besides supporting cells, only solitary nematocysts, but numerous mucus cells, particularly numerous on the border towards the stomatodaeum (Fig. 5, Pl. 3). An ectodermal longitudinal musculature is almost entirely absent. The hyposulcus contains very numerous



Textfig. 3. Transverse section of *Cerianthus lloydii* in the upper part of the stomatodaeum. For the signs see explanation of the figures.

Textfig. 4. Diagram of the arrangement of a part of the mesenteries and stomatodaeum of a young specimen of *Cerianthus lloydii*. The lines across the mesenteries indicate the extremities of the ciliated tracts. For the signs see explanation of the Plates.



mucus cells as well as very numerous granular gland cells and spirocysts; it is therefore not so differentiated as the siphonoglyph. The hemisulci are distinct, very long and narrow in the lower part, filament-like as in *P. multiplicatus*, and provided with numerous spirocysts and mucus-cells, but with thick-walled nematocysts also.

The mesenteries: The arrangement of the mesenteries and filaments is shewn in fig. 5, Pl. 4 and the schematic text-fig. 4, which is based on a series of sections of a young specimen. Van Beneden's diagram (1898, Fig. A p. 25) on the other hand is based on a rather older specimen. As van Beneden seems not to have taken notice of the cnido-glandular tract of the mesenteries of the 1st and 2nd cycle, these are not marked on his figure.

The directive mesenteries are short. The free part does not attain the length of the stomatodaeum, and is considerably shorter in younger specimens. The hemisulci possess no differentiated ciliated tract.

The protomesenteries 2 are fertile and reach to the aboral pole. The ciliated tract region extends further down than on other mesenteries, but is nevertheless comparatively short and attains at most a length of  $1\frac{1}{2}$  times the stomatodaeum. The cnido-glandular tract region is short, on a thread-like outgrowth of the mesentery more or less resembling an acontium. The craspedion region is very long.

The protomesenteries 3 are sterile, short, and scarcely reach to the beginning of the cnido-glandular tract region of protomesenteries 2. The ciliated tract region is short and smaller than in the mesenteries just mentioned. The region of the cnido-glandular tract is better developed in these than in any of the other mesenteries and has many coils.

The metamesenteries of the 1st and 2nd cycles are almost equally well developed, the older reach right down to the aboral pole, the younger go a longer or shorter distance down the column. The ciliated tract region is comparatively short, the region of the cnido-glandular tract slight as on protomesenteries 2, with which the mesenteries of the 1st and 2nd cycle agree generally in structure. The younger the mesenteries are, the shorter is the ciliated tract region and the more oral the situation of the cnido-glandular tracts; the cnido-glandular tract is found furthest towards the aboral side of the animal in protomesenteries 2. These metamesenteries are all fertile with the exception of the very youngest.

The metamesenteries of the 3rd and 4th cycles are sterile and agree in appearance and structure with protomesenteries 3. The

difference in length between the two cycles is slight. They are all short, shorter than protomesenteries 3 and diminish in length towards the multiplication chamber. In contrast with the metamesenteries of the 1st and 2nd cycle, they have no development of the craspedia.

The number of the metamesenteries comes to about 70 in the larger specimens.

The filaments: The ciliated tract is specially well marked in protomesenteries 2 and the metamesenteries of the 1st and 2nd cycles, rather more feebly in the others. The median streak contains numerous spirocysts and shews especially in the metamesenteries of the 1st and 2nd cycle in the distal part a distinct tendency to bipartition, though by no means so pronounced as in *Arachnactis lobiancoi*. The mesogloal processes, on which the chief part of the ciliated tracts rest, arise however, as in the majority of species for inst. as in *C. membranaceus*, from the middle lamella of the mesentery and not from the mesogloal fold of the median streak. In transverse section the median streak is broad with 2 strong mesogloal folds projecting towards the sides. The outline shews in the middle a very deep depression and the ectoderm is rather thinner than at the sides, and in the same way the gland cells and nematocysts are fewer in the middle than at the sides, and in this way also the median streak shews signs of dividing into 2 tracts, and perhaps more markedly than in *C. membranaceus*. In the metamesenteries of the 3rd and 4th cycles this differentiation is less advanced, so that the filaments sometimes have the same appearance as in Botrucnidifer (Fig. 5, Pl. 4). The longitudinal musculature in the median streak is well developed. The ciliated tract region of the filaments is straight without craspedonemes.

The cnido-glandular tract is of the usual structure with numerous gland cells, and thick-walled nematocysts broadening towards the base, of 31—34  $\mu$ 's length. Whilst it has very wavy coils in the mesenteries of the 3rd and 4th cycles and also in protomesenteries 3, it is straight or slightly coiled in the metamesenteries of the 1st and 2nd cycles and in protomesenteries 2 and in the case of the latter is strongly suggestive of v. Beneden's acontia. Like these and the craspedonemes the mesenterial process, on which the filament rests, shews an ascending and a descending limb of the filament separated by the endoderm of the mesentery. The latter is very slight at the extremity of the process, so that the two limbs of the filament almost press upon each other (giving the process a structure which agrees with that of the acontium as I have described it below — a description which differs not a little from v. Beneden's but agrees in the main with Cerfontaine's), higher up however towards the base of the process, this part gets distinctly larger. In fig. 4, Pl. 4, which represents a transverse section taken some way from the extremity of such an acontium-like process in protomesenteries 2, we see at the sides the two intersected filament-parts of the cnido-glandular tract with their thick-walled nematocysts and gland cells separated by a part of the endoderm. It is noticeable too that the part of the mesogloea that belongs to the filaments shews a tendency to part off from the mesogloea of the endoderm, a circumstance which is of interest for the study of the structure of the "acontium" in other species. Longitudinal musculature is absent in the cnido-glandular tract.

The craspedia, that is to say the parts of the median streak that lie below (aborally) from the cnido-glandular tract, are very well developed in the upper part (Fig. 6, Pl. 3), and taper away more and more towards the aboral pole. In their upper part are found, besides homogeneous and granular gland cells, numerous spirocysts, in the lower part appear also the large thick-walled nematocysts



*Diagnosis.* Medium-sized species with 30—40 marginal tentacles and about the same number of labial tentacles. Marginal tentacles very long, arranged in at least 2, probably more cycles, set very close together. Labial tentacles half the length of the marginal tentacles; their arrangement is: 4 (dt) | 0, 2, 3 | 4, 1, 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 | . . . . The distal portion of the column with well marked furrows corresponding to the mesenterial attachments. Siphonoglyph narrow, hyposulcus distinct but small, hemisulci very long but narrow. Protomesenteries 2 very long, reaching right to the aboral pole, fertile, with well developed ciliated tract region, which is rather longer than protomesenteries 3, short cnidoglandular tract region and long craspedion region. Protomesenteries 3 about  $\frac{1}{3}$  of the length of the body, reckoning from the aboral end of the stomatodaeum to the aboral pole. The metamesenteries developed as in *Cerianthus lloydii* with similar arrangement of the parts of the filaments. Ciliated tract region straight, without craspedonemes.

*Occurrence.* 64° 2' N. 5° 35' E. 911 m. Clay. Temperature at bottom — 1,1° NNAE., St. 87, 22. 8.

1876 (*C. vogti*).

68° 6' N. 9° 44' E. 1159 m. » » » » — 1,3° NNAE., St. 251, 9. 8.

1877 (*C. abyssorum*).

*Dimensions.* *C. vogti*: Length of body 80 mm., breadth in distal portion 20 mm., in proximal portion 6 mm., according to Danielssen: the corresponding dimensions for *C. abyssorum* are given by Danielssen as 65, 25 and 8 mm.

*Colour.* According to Danielssen "The body is pale yellow with a pale rose-red play of colour (*C. vogti*); pale brownish but its uppermost margin is for a few millimetres of its breadth, white (*C. abyssorum*). The marginal tentacles are upon their aboral side a beautiful rose-red, and on the adoral side light-brown; the oral tentacles are a beautiful chestnut brown colour, also the oral disc, but with lighter coloured radii (*C. vogti*); the oral disc is dark brown with a lighter coloured annulus round the oral aperture (*C. abyssorum*).

*The outward appearance* is rather well described by Danielssen. The species has the characteristic form of Ceriantharia, but is rather broader in the distal than in the proximal region. According to Danielssen, an aboral pore is found. The most distal portion of the body has very deep furrows corresponding with the mesenterial attachments. The marginal tentacles are very long in comparison with the size of the animal. They are arranged in at least two cycles, probably more, but as the tentacle cycles are very closely set and the specimen is not very well preserved it is almost impossible to determine the number of cycles. The labial tentacles are about half the length and breadth of the marginal tentacles. A directive labial tentacle is certainly found, situated very high up and ought to belong to the 4th cycle or perhaps to the 3rd. On the other hand, the two chambers contiguous to the directive chamber on either side appear, as far as I can see, to be without labial tentacles. That this is really so, finds support in the fact that on such an hypothesis the remaining labial tentacles fall into a typical arrangement, which would not be the case, if we suppose, beside the existing tentacles, others proceeding from these two chambers as well. According to my observations, the labial tentacles would be arranged in the following manner

4, (dt) 0, 2, 3 | 4, 1, 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 | etc.

In *C. abyssorum* I have not been able to observe the grouping of the tentacles in the vicinity

of the directive chamber. In the latter Danielssen has not noticed that all the marginal tentacles were torn off at the base, as is obvious from Danielssen's figure 7, Pl. 5, which is in accordance with the preserved specimen, on which only labial tentacles were found intact. The tentacles marked in Danielssen's figure are labial and not marginal tentacles as Danielssen states. Between the marginal and labial tentacles a very large part of the oral disc is devoid of tentacles and shews radial furrows corresponding to the attachments. The stomatodaeum is long and furrowed longitudinally, in the lower part with mesogloal ridges. The siphonoglyph is narrow with only 2 couples of mesenteries attached. The hyposulcus is small but well marked. The hemisulci are very long, but narrow and look like filaments.

*Anatomical structure.* Though the specimen of *C. vogti* at my disposal was not internally as well preserved as might be wished, I have been able, I hope, to fix the most important of the larger anatomical details. The lowest part of the animal however was very much macerated, so that I am unable to state whether differentiation of craspedonemes occurs there, though in my opinion it may be taken not to be the case. Consequently I cannot give any diagram, nor is it necessary, as it looks as if the mesenterial arrangement corresponds with that of *C. lloyii*, although *C. vogti* has nothing like as many mesenteries as that species. As I did not want to spoil the specimen, the finer anatomical details given below are incomplete, and all the more so, that even as regards the tissue the object examined was very much macerated.

The column is of the usual structure. The ectoderm contains numerous larger and smaller nematocysts with very irregularly coiled thread. Some of the largest capsules reached a length of as much as  $72\mu$  and a breadth of  $17\mu$ . The ectodermal musculature is not particularly well developed for a Cerianthid.

The ectoderm of the marginal tentacles contained extremely numerous spirocysts (maximum length  $60\mu$ ) and in addition thick-walled nematocysts (length  $24\mu$ ). The ectoderm of the labial tentacles agrees, as to the occurrence of nematocysts, with that of the stomatodaeum, though the spirocysts are much more numerous and the other nematocysts more sparse. The spirocysts are smaller than in the outer tentacles.

The ectoderm of the stomatodaeum is of the usual structure. The nematocysts consist of very numerous capsules with irregular, strongly coiled thread (length  $31-41\mu$  breadth  $7\mu$ ), and in addition are found very numerous spirocysts, small thick-walled nematocysts (length about  $24\mu$ ) and thick-walled capsules with quite well marked base of the spiral threads. The last are common and attain a length of  $43\mu$  and a breadth of  $7\mu$ .

The mesenteries. The directive mesenteries are short with a well marked hemisulcus (see above).

Protomesenteries 2 go down to the aboral pole, and are fertile, with a long ciliated tract region, which reaches a little further down than protomesenteries 3. Then succeeds a short, poorly developed cnido-glandular tract region and finally a long craspedion region. Protomesenteries 3 are sterile, and attain a length of about  $\frac{1}{3}$  of the length of the body between the aboral end of the stomatodaeum and the aboral end of the animal. They are formed like the metamesenteries of the 3rd and 4th cycles.

The grouping of the metamesenteries seems to resemble most closely that of *C. lloydi*. The fertile metamesenteries of the 1st and 2nd cycles go down to the aboral pole and shew about the

same proportions among the various divisions of the filaments as in that species. The ciliated tract region is long, the cnido-glandular tract inconsiderable and the craspedion region long.

The metamesenteries of the 3rd and 4th cycles are sterile and developed as in *C. lloydii*. The metamesenteries decrease considerably in length towards the multiplication chamber, but whether any break occurs in the uniformity of decrease I cannot say with certainty, at least there is no very marked break of the kind.

The region of the median streak looks very much like that of *C. lloydii* and is of about the same extent. Certainly the ectoderm is much macerated, yet from the appearance of the mesogloea in the filament it may be concluded that the filament was constituted very much as in *C. lloydii*, the mesogloea lamellae issuing from the main lamella of the mesentery. An initial partition of the median streak takes place here also, though perhaps the ciliated groove between the two portions of the median streak is less well marked. The spirocysts are very numerous, and there occur besides a sprinkling of thick-walled nematocysts with plainly marked bases of the spiral threads (length about 29  $\mu$ ).

The cnido-glandular tract on the metamesenteries of the 1st and 2nd cycles is feebly developed, to about the same degree as in *C. lloydii*. Besides very thinly scattered spirocysts are found numerous thick-walled nematocysts of the same size and appearance as in the median streak.

The region of the craspedion was badly preserved, so that it was impossible to get an adequate idea of its structure.

The particular specimen examined was hermaphrodite. Danielssen declares the species to be bi-sexual, but this is not so. The same author makes several other strange statements, amongst the rest about the mesenterial musculature. As far as I have been able to make out, *C. vogti* does not deviate in general structure from the other Ceriantharia.

*Systematic Remarks.* It admits of no doubt that *C. vogti* and *C. abyssorum* are the same species. Danielssen says, "that *C. abyssorum* differs from *C. vogti* is probable from the number and nature of the tentacles, from the colour of the long tube in which the animal dwells, and finally, from the extremely different locality in which it was found". These characters however are not such as to serve as a valid ground of division for the erection of two distinct species. To take the number of the tentacles in the first place, the coincidence here in the two species is almost exact. It must be borne in mind however, that Danielssen omitted to observe that all the marginal tentacles in *C. abyssorum* had been torn away and only the labial tentacles left (see above). The colour is approximately the same. The other two characters have no significance as distinguishing marks.

*C. vogti* seems in its internal structure to recall *C. lloydii* very closely, though it has a narrower siphonoglyph. But externally the two species are very different. *C. vogti* has deep furrows in the distal portion of the column, which do not appear in *C. lloydii*; in proportion to the size of the animal the tentacles are considerably longer in the former than in the latter. In *C. vogti* is found a directive labial tentacle which is absent in *C. lloydii*: on the other hand there are no labial tentacles in *C. vogti* issuing from the chambers contiguous to the directive chamber, whilst *C. lloydii* is in this respect of the normal structure.

Genus *Ceriantheopsis* nov. gen. Diagnosis see Section III.

The only known species is  
***C. americanus*** (Verr.) Pl. 5, fig. 1—6.

..... Agassiz, 1859, p. 24.

*Cerianthus americanus* Verrill, 1862, p. 32.

» » Verrill, 1863, p. 56.

» » Verr. Andres, 1883, p. 560.

» » » Mc. Murrich, 1890, p. 134.

» » » Parker, 1910, p. 756, fig. 21.

» » » Mc. Murrich, 1910, p. 16, fig. IV, Pl. 1, fig. 14.

» » » Pax, 1910, p. 167.

*Diagnosis:* Large size with about 100—125 marginal tentacles and about as many labial tentacles. The marginal tentacles very long. Arrangement of tentacles: marginal tentacles in 4 or possibly only 3 cycles  $\begin{matrix} 2 \text{ (dt) } 4, 3, 1 \\ 3 \end{matrix} \left| \begin{matrix} 4, 2, 3, 1 \\ 3 \end{matrix} \right| \begin{matrix} 4, 2, 3, 1 \\ 3 \end{matrix} \left| \text{etc.} \right.$  and labial tentacles in 4 cycles  $2 \text{ (dt) } 4, 1, 3 \left| 4, 2, 3, 2 \left| 4, 3, 1, 2 \left| 4, 3, 1, 2 \left| \text{etc.} \right.$  Stomatodaeum small with attachments for only 4 mesenteries. Hyposulcus absent, hemisulci rather long. The directive mesenteries rather short with no development of ciliated tract. Protomesenteries 2 fertile, reaching to the aboral part of the animal with well developed craspedonemes, and narrow prolonged cnido-glandular tract resting upon a process. Protomesenteries 3 short with well developed craspedonemes and cnido-glandular tract region. Arrangement of metamesenteries *mBm* in clearly marked quartettes. *M* agree in structure with protomesenteries 2, are fertile, long, the longest reach to the aboral pole, increasing in length towards the multiplication chamber, though with breaks in one or two places (at the 3rd, 5th and possibly the 7th quartette); *m* fertile, short, the free border twice as long as the free part of *B* and *b*, with rather larger cnido-glandular tract than *M*s, in other respects like *M*. *B* and *b* sterile, very short, with longer cnido-glandular tract region and shorter craspedoneme region. This is especially the case with *b*. The region of the ciliated tracts is constructed on type 2 in the oral part. The region of the craspedia is long in *M* and protomesenteries 2, shorter in *m*. In protomesenteries 2 and the longest metamesenteries *M* the craspedia in the most aboral part form a small craspedoneme, which contains very numerous thick-walled nematocysts.

*Occurrence:* Beaufort N. Carolina. Copenhagen Museum 1 ex.; several examples from Director Aller. Distribution according to Parker (1900): from Cape Cod to Florida.

*Dimensions.* Length 60—70 cm., disc of nearly 4 cm. Verrill. — Length in the largest specimens 20 cm., diameter through the middle 1.5—2 cm., the disc 1.8—2.5 cm. Length of outer tentacles 3.4 cm. of the labial tentacles 1.8—2.5 (Mc. Murrich). The specimens I examined had a length of 7—8 cm. in their preserved state.

*Colour.* "The color of the column is some shade of brown varying from pale chocolate-brown to deep purplish brown. The upper part is always darker than the lower and in some cases the column is marked with longitudinal lines of a lighter shade than the ground colour. The marginal tentacles are of a paler brown than the column except the outermost, which are purplish blue. The oral tentacles in all specimens I observed were pure white; Verrill on the other hand, describes

them as being darker than the marginal ones, and marked with white longitudinal lines. In the Beaufort specimens, however, the tentacles of both series are unmarked by lines, spots or annulations. The disc is yellow with white lines crossing it radially." Mc. Murrich (1890, p. 135).

*Exterior aspect.* The body shews the typical Cerianthid structure and is provided with an aboral pore. When contracted the column has plain longitudinal furrows.

The tentacles are large and very long. The arrangement is the typical one. In a specimen with 98 marginal tentacles and the same number of labial ones, the arrangement was as follows.

49 MT . . . . 1, 3, 2, 4 | 1, 3, 2, 4 | 1, 3, 2, 4 | 1, 3, 2, 4 | 1, 3, 2, 4 | 1, 3, 4, 2, 4, 3, 1 | 4, 2, 3, 1 | 4, 2, 3, 1 | 4, 2, 3, 1 | 4, 2, 3, 1 | . . . . 48 MT  
 49 LT . . . . 2, 1, 3, 4 | 2, 1, 3, 4 | 2, 1, 3, 4 | 2, 1, 3, 4 | 2, 3, 2, 4 | 3, 1, 4, 2, 4, 1, 3 | 4, 2, 3, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 | 4, 3, 1, 2 | . . . . 48 LT

Whilst the arrangement of the labial tentacles in 4 cycles was very clear, the distinction between the marginal tentacles of the 3rd and 4th cycles was very hard to see. Possibly it might be more correct to distinguish only 3 cycles of marginal tentacles, a question that cannot be answered however with full confidence save by examination of fully extended specimens. Another specimen shewed the following arrangement.

Marginal tentacles 91	45 M. T. Dt.	45 M. T.
Labial tentacles 89	44 L. T. Dt.	44 L. T.

The stomatodaeum is very long. But its relative length to the column is hard to determine in consequence of the great contraction not only of the column but of the stomatodaeum in particular. The stomatodaeum is furrowed longitudinally. In the most aboral portion, these furrows as in the Cerianthidae in general get distinctly deeper. The siphonoglyph which begins immediately beneath the labial tentacles is small in comparison with the size of the animal, as only 4 mesenteries are attached to it. The hyposulcus is not developed, whereas filament-like hemisulci are found well developed.

*Anatomical description.*

The anatomy of this species has been already described by Mc. Murrich both in an earlier work of the year 1890, and also recently (1910). In various points however Mc. Murrich's investigations require supplementing. This is specially the case with the mesenterial filaments and their structure. As appears from the description given below my observations do not always accord with this investigator's. As the structure of column, tentacles and oral disc agree with those of other Cerianthidae, I do not treat these organs in much detail.

The ectoderm of the column contains very numerous nematocysts with coiled spiral thread (length up to  $70\mu$ ). In the ectoderm of the marginal tentacles are found numerous thick-walled nematocysts (length  $26-31\mu$ ) whilst spirocysts are more rarely met with. The converse is the case in the ectoderm of the labial tentacles. Here the spirocysts are very numerous, whilst the thick-walled nematocysts are fewer and smaller than in the marginal tentacles (length  $19\mu$ ).

The stomatodaeum is constructed as in other Ceriantharia. The ectodermal ridges in the upper part are very prominent and contain, besides gland cells, thick-walled nematocysts, that attain a length of  $31-36\mu$ . If spirocysts occur here, they are very rare. The furrows between the ectodermal ridges are lined with a not very thick ectoderm, which contains, besides supporting cells, no small number of gland cells. The longitudinal musculature of the stomatodaeum is well developed. The

longitudinal ridges in the aboral part are, as in *C. lloydii*, supported by mesogloea processes, which is not the case in the oral part. The structure of the ridges agrees that of *C. lloydii*. Here very numerous spirocysts occur. Thick-walled nematocysts of a length of 24—31  $\mu$  are not infrequent. The ectoderm of the siphonoglyph is prominent and contains specially numerous, closely packed homogeneous gland cells (mucus cells).

The ectoderm of the hemisulci consists in the oral part chiefly of strongly ciliated supporting cells; outwards from the pair of directive mesenteries the homogeneous gland cells become more numerous, and a number of thin-walled nematocysts also occur; aborally the gland part gets predominant till at last it gradually disappears. The extension of the hemisulci upon the mesentery is indicated here also by the strong ciliation (Fig. 4, pl. 5). The hemisulci do not form a filament-like part, as in *P. multiplicatus*, but usually line only one side of the mesentery. A ciliated tract on the outside is not developed, contrasting on this point with the genus *Arachnanthus*. The longitudinal musculature of the hemisulci is faint, with the exception of the part which lies below the cnidoglandular cell portion, where it is strong.

The arrangement of the mesenteries is given in detail by Mc. Murrich (1910). In the main my observations agree with this investigator's, though to some degree the details vary. Not only the regions of the ciliated tracts but also those of the cnidoglandular tracts lie in all mesenteries comparatively close to the lower border of the stomatodaeum, so that the craspedion region on the longer mesenteries, is specially long.

Protomesenteries 1: The directive mesenteries are comparatively short, without ciliated tracts. For the extension of the hemisulci on these mesenteries, see above.

Protomesenteries 2 are long and reach nearly to the aboral pole of the animal. The ciliated tract region is straight at the beginning, but lower down forms first short then longer, closely set craspedonemes. The region of the cnidoglandular tract is prolonged and forms a winding band (fig. 5 pl. 5). The region of the craspedia is very long and takes up the greatest part of the free border of the mesentery. In the most aboral part it forms a threadlike process (fig. 6, pl. 5). They are fertile.

Protomesenteries 3 are short though distinctly longer than the metamesenteries of the 3rd and 4th cycles. The ciliated tract region with its craspedonemes ends higher up than on protomesenteries 2. The region of the cnidoglandular tract is more strongly developed than in those mesenteries. As usual with the Cerianthidae they are sterile.

The metamesenteries are arranged on the formula *mBMb*, that is, in every quartette there is first a mesentery of the 2nd cycle, then one of the 3rd, next one of the 1st and lastly one of the 4th. As Mc. Murrich considers that the metamesenteries begin with the 5th pair of mesenteries, counting from the directive chamber, the mesenterial arrangement is according to his formula *BMbm*. A deviation from this rule would occur, if we may judge from Mc. Murrich's figure (IV 1910) of the arrangement of the mesenteries, in the 1st quartette where *B* takes *b*'s place, and conversely. As far as I can tell, however, from specimens examined, this is not the case, for this group also shews the typical arrangement. It is characteristic of this species, and of the whole genus perhaps, that the metamesenteries of the 1st cycle increase in length towards the multiplication chamber, as Mc. Murrich has shewn and I can confirm. Still in several places there occurs with a certain regularity a

break in this increase of the length in the mesenteries. In Mc. Murrich's figure this break occurs at the 3rd and 5th quartette. In one of the specimens examined by me however, this was not so clear, as the 4th metamesentery of the 1st cycle was a little shorter than the 3rd. My specimen also suggests the inference, that possibly a further break occurs at the 7th group in larger specimens.

As regards the metamesenteries of the 2nd cycle, there is no sign of such an increase of length in the mesenteries towards the multiplication chamber, nor yet is this the case with the metamesenteries of the 3rd and 4th cycles. The mesenteries of the 2nd cycle decrease towards the multiplication chamber according to my observations; in the 6th quartette according to my terminology a break first occurs, so that we there find a mesentery as long as or longer than that in the 5th group. The mesenteries of the 3rd and 4th cycles stand in much the same relation. Here too breaks occur, but because these mesenteries do not extend far below the stomatodaeum and because of their contraction, I cannot definitely state whether this break takes place at definite quartettes. However it appears as though the mesenteries of the 3rd and 4th cycles were distinctly feebler in the 1st than in the 2nd quartette. Very probably variations in proportionate length between the different quartettes occur in the mesenteries of the 2nd as well as of the 3rd or 4th cycle, but to investigate this closely access should be had to fully extended specimens in the very best preservation. Presumably also the cnido-glandular tracts of the mesenteries of the 3rd and 4th cycles in the quartettes lie at regular, though varying distances from the lower border of the stomatodaeum, but this cannot be clearly determined with contracted specimens.

The metamesenteries of the 2nd cycle compared with those of the 1st are short. Their free border is about twice as long as in those of the 3rd and 4th cycles. But an exception occurs in the first metamesentery of the 2nd cycle (Protomesentery 4, Mc. Murrich) which is the longest mesentery of this category and attains a length of about half the free border of the longest mesenteries. The metamesenteries of the 3rd and 4th cycles are short, and their free border below the stomatodaeum is not more than the length of the stomatodaeum.

As regards the subdivision of the filaments, there are found, as regularly among the Ceriantharia, both ciliated tracts and cnido-glandular tracts in all metamesenteries. In addition, on all metamesenteries are also found craspedonemes (called in Mc. Murrich's first work 1890 *acontia*) and in the metamesenteries of the 1st and 2nd cycles and in protomesenteries 2 *craspedia* as well.

The subdivision of the filaments in the metamesenteries of the 1st cycle (*M*) agrees with that found in protomesenteries 2. The same is the case with the metamesenteries of the 2nd cycle (*m*); the cnido-glandular tract however is more developed in these mesenteries. Those of the 3rd cycle (*B*) resemble, as to the filaments, those of the 2nd, but have a more developed cnido-glandular tract. The mesenteries of the 4th cycle (*b*) have a specially well developed cnido-glandular tract but feeble craspedonemes in the region of the ciliated tracts, which in this case is very short.

The structure of the filaments agrees in the main with that found in *C. membranaceus*. In the upper part of the region of the ciliated tracts, the median streak (spirocyst-glandular tract) is divided into 2 parts separated by a more undifferentiated part (median streak Mc. Murrich 1910). The lateral portions of the median streak shew the typical structure, i. e. they contain numerous thin-

walled nematocysts (spirocysts) and a sprinkling of thick-walled ones (length  $26\ \mu$ ) and gland cells which are principally large mucus cells. The "median streak" of Mc. Murrich, which is more strongly ciliated than the lateral portions, is not deeply sunk, as the ectoderm is rather high, but broad; between the supporting cells, mucus cells are interspersed now and then. The mesogloea and the musculature stand as in *Cerianthus lloydii*.

In the craspedoneme region the median streak is simple. In the coarser and shorter craspedonemes the endoderm between the ascending and the descending limbs of the filament is pretty well developed: in the long narrow craspedonemes the endoderm is very slight.

The cnido-glandular tract contains thick-walled nematocysts (length  $24\text{--}26\ \mu$ ) in great numbers. In addition nematocysts are found which are very small and without visible spiral-thread base. The like occur also in the threads, craspedonemes, of the craspedia. In protomesenteries 2 and the metamesenteries of the 1st and 2nd cycle the filament forms — as in *C. lloydii* — aborally from the cnido-glandular tract a more feebly developed part, which I have named craspedion region. In *M* this part is especially long. The craspedion (fig. 3, pl. 5), which is plainly distinct from the endoderm of the mesentery, shews much the same structure as the median streak. The nematocysts are principally spirocysts and the gland cells principally mucus cells. In the most aboral part there is found on the largest mesenteries of the 1st cycle a more or less threadlike appendage (fig. 6, pl. 5 *mf*), in other words the craspedion ends as a simple craspedoneme, which is formed by an ascending and a descending limb of the craspedion separated by an endoderm portion (fig. 1, 2, pl. 5). Just as the most aboral part of the craspedia in *C. lloydii* shews a mixed character, in as much as thick-walled nematocysts there present themselves in great numbers, so here the ectoderm of the craspedia contains thick-walled nematocysts (length  $(22\text{--}26\ \mu)$ ) in very large numbers, whilst the thin-walled ones are very rare in the greater part of the thread and become less so only at the base. The granular gland cells also are more numerous here than higher up on the craspedion, at the same time that the craspedion gets more sharply differentiated from the endoderm, in other words the craspedion thread acquires a structure approaching that of the cnido-glandular tract. Compare further the section IV.

As for the reproductive organs, they appear on protomesenteries 2 and on the metamesenteries of the 1st and 2nd cycles within the craspedia regions. Mc. Murrich states 1891 that the species would be found bi-sexual. This is certainly not the case. Both in Aller's specimens from Beaufort and in a specimen from the same locality belonging to the Museum of Copenhagen both male and female organs were found in the same individual. Certainly the ova in several specimens were comparatively small, but there is no possible doubt that the species is hermaphrodite. Mc. Murrich's statement is consequently based either on insufficient examination or else on the fact, that he chanced upon a specimen whose male organs had not been developed. For the Cerianthidae are probably proterandrous hermaphrodites. Still it seems to me that even in this case at least traces of the male organs ought to have been observed.

Family **Acontiferidae** Diagnosis see Section III.Genus **Arachnanthus** nov. gen. Diagnosis see Section III.**A. Sarsi** n. sp.

*Diagnosis:* (Marginal tentacles long, tapering very gradually towards the point? Labial tentacles well developed? Directive chamber and the contiguous chamber on either side of this without labial tentacles?) Stomatodaeum of medium length with very long hyposulcus that reaches past the middle of the animal and exceeds the stomatodaeum in length. The directive mesenteries comparatively long but do not extend farther than the middle of the hyposulcus. The protomesenteries of the 2nd cycle of the length of the hyposulcus, probably sterile, without cnido-glandular tract. Protomesenteries 3 about the length of the directive mesenteries with very short ciliated tract-region and very long cnido-glandular tract region. The metamesenteries of the 2nd cycle almost as well developed as those of the 1st (*M*). The oldest mesenteries of the 1st and 2nd cycle long, reaching not quite down to the aboral end of the animal, fertile, with long ciliated tract region. The 1st metamesentery on each side with an "acontium". The metamesenteries of the 3rd (*B*) and 4th (*b*) cycle short, about the length of protomesenteries 3, sterile, with very short ciliated tract region and very prolonged cnido-glandular tract, *b* slightly shorter than *B*. The musculature of the mesenteries comparatively well developed.

*Occurrence.* Trondhjem fjord. Röberg Indalbay 140 m. Silted sand with shells and small stones 18.6.1901. I. Arvidsson, R. M., 1 ex.

*Dimensions* in extended state: Length 4.7 cm., greatest breadth 0.8 cm.; in preserved state: length 3.2 cm., breadth 0.7 cm. N.B. the uppermost part of all was torn away.

*Colour* according to Arvidsson. "Mouth (stomatodaeum or oral disc?) dark brownish-black. Column yellowish-white with yellowish-brown longitudinal stripes, which are absent in the front. The most distal portion is fairly transparent, so that the stomatodaeum and the white mesenteries gleam through".

*Exterior aspect.* Body of the form characteristic of Ceriantharia. Of tentacles no trace is found, but this does not signify that we have here a species devoid of tentacles; in all probability the tentacles have been torn off together with the topmost part of the body, whereupon the stomatodaeum has coalesced with the column. For the stomatodaeum quite distinctly passes straight into the column and no oral disc is discoverable. Thus the animal is plainly in a state of regeneration as far as the front part is concerned. The stomatodaeum is well developed and of the structure characteristic of the Acontiferidae. The siphonoglyph is very broad. The hyposulcus is very long, exceeding the length of the stomatodaeum, and also very broad. The upper half is attached to the directive mesenteries in the form of a broad groove, whilst the aboral half is free. The lower free border is rounded, so that no differentiated hemisulci are found (See the diagram. Textfig. 5).

*Anatomical structure.* As I have only had one specimen for study, I did not like to dissect it fully, especially as the mesenteries are not very well preserved. The description of the anatomical structure therefore remains incomplete.

The column is like the other Ceriantharia in structure. The ectoderm is very thick and

contains, besides supporting cells, principally nematocysts with coiled spiral thread (the length of the nematocysts varies greatly and may reach to  $103\ \mu$ ) and mucus cells. The nematocysts are more numerous in the upper part and the mucus cells in the lower part of the column where they are closely packed together. The ectodermal musculature of the column is extremely developed; for the

size of the animal it is the most strongly developed longitudinal musculature that I have observed in any of the Ceriantharia.

The stomatodaeum has the same structure as in *Arachnanthus oligopodus*. The ridges in the aboral part therefore are not supported by mesogloal processes. The ectoderm is very thick and contains nematocysts of various forms, now resembling those found in the column, now spirocysts, now thick-walled and granulated, larger ( $55\text{--}60\ \mu$ ) and smaller ( $31\text{--}41\ \mu$ ). The siphonoglyph is of the usual structure with specially numerous mucus cells on the boundary of the stomatodaeum. The ectodermal musculature of the stomatodaeum and siphonoglyph is feeble but distinct.

The mesenteries (Textfig. 5):

The directive mesenteries are comparatively long.

Protomesenteries 2 agree in appearance with the metamesenteries of the 1st and 2nd cycle (In consequence of the animal's contraction all these mesenteries are somewhat folded. See diagram). The ciliated region is long, but so far as I have been able to see from the anatomical examination, the region of the cnido-glandular tract is absent, as in *A. oligopodus*. On the other hand there is a craspedion region. They extend to about the same length as the hyposulcus and are sterile.

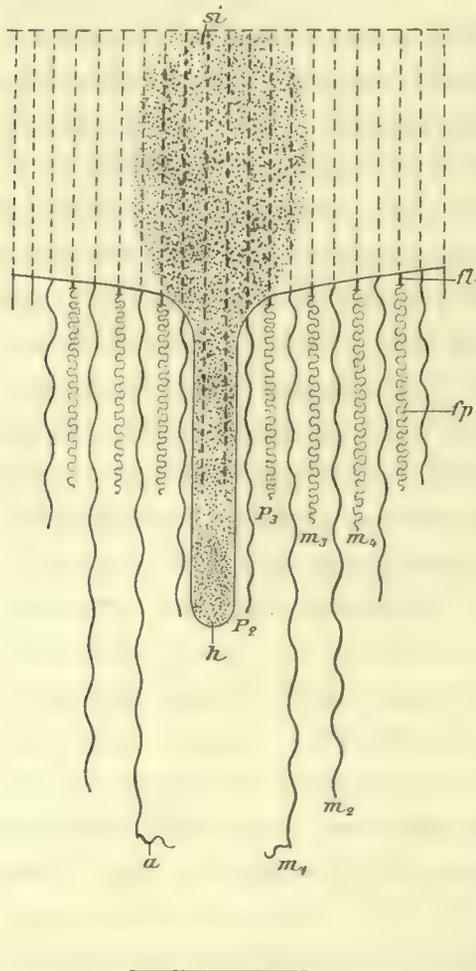
Protomesenteries 3 are sterile and rather longer than the directive mesenteries; the ciliated tract region is very short, the cnido-glandular tract region on the contrary very long and very wavy.

The metamesenteries of the 1st and 2nd cycles are little distinguished in length from each other, to judge from

Textfig. 5. Diagram of the arrangement of mesenteries and the stomatodaeum in *Arachnanthus sarsi*. For signs see explanation of the figures. The boundaries between the ciliated tracts and the craspedia regions at  $m_1$   $m_2$  etc. are not marked as it was impossible to observe them without microscopic examination.

the first two couples. The same is true of the metamesenteries of the 3rd and 4th cycles. The metamesenteries of the 1st and 2nd cycles are more than twice as long as those of the 3rd and 4th. The longest of the former reach almost down to the aboral part of the body, whilst the latter run to half or two-thirds of the length of the hyposulcus. I have not found any decided grouping of the metamesenteries in quartettes. The metamesenteries decrease in length towards the multiplication chamber, but this is not so clear with the mesenteries of the 3rd and 4th cycles.

The metamesenteries of the 1st and 2nd cycles are furnished with a long ciliated tract region.



Whether a cnido-glandular tract region is to be found I cannot determine with certainty. Probably there is none, but on the other hand the ciliated tract region is continued in to a craspedion region. Metamesenteries 1 bear "acontia". On the other mesenteries no such formations are found, though it is likely enough that in older specimens they are borne by a further couple of mesenteries.

The regions of the ciliated tracts in the metamesenteries of the 3rd and 4th cycles are particularly short, whilst the cnido-glandular tract is remarkably coiled, and very long. Almost the whole of the free border of the mesentery is taken up by the cnido-glandular tract.

As to the structure and arrangement of the mesenterial filaments and their differentiations there seems to be a correspondance with *Arachnanthus oligopodus*. Though I cannot indicate the boundary between the regions of the ciliated tracts and the craspedia regions on protomesenteries 2 and on the metamesenteries of the 1st and 2nd cycles, the craspedia regions seem to have about the same extent on these as in *Arachnanthus oligopodus*. The median streak is constructed as in that species, as also the craspedia and the "acontia". As the description of the structure of the region of the ciliated tracts, of the craspedia regions and the "acontia" finds its place in the morphological description of Ceriantharia (Section 4) I have not thought it needful to go into their structure in detail here. The thick-walled nematocysts in the cnido-glandular tract have a length of about 26—36  $\mu$ . In the endoderm of the mesenteries occur, especially in the lower part, large curved nematocysts of as much as 72  $\mu$  in length.

The mesenterial muscles shew the typical arrangement and are strongly developed, particularly if we take into consideration the small size of the animal. They are quite distinct along the whole length of the stomatodaeum, and are the best developed muscles I have observed in any Ceriantharia.

The metamesenteries of the 1st and 2nd cycles are fertile with feebly developed reproductive organs, the rest sterile. The species is hermaphrodite.

*Systematic remarks.* Though the tentacles are torn away on the only specimen discovered, so that it is impossible to attempt to study their arrangement, yet from the other morphological facts the inference might be drawn that this species is the adult animal of the larval Ceriantharium described by Sars, *Arachnactis albida*, or at least is very closely related to this larval form. The descriptions of this larval form given by Vanhöffen (1895) and v. Beneden (1898) as well as my own investigations of the same form, an account of which is given below, agree very largely with *A. sarsi*. In fig. 4 Plate 1 in Vanhöffen's work is represented an *Arachnactis albida* which is very like the specimen described above. In particular the appearance of the stomatodaeum is strongly suggestive of the stomatodaeum in the species I have here described, as also the appearance of the "acontia". The anatomical study which I have made of the "acontia" in *A. albida* also tends to shew that we have the same species before us. The colour markings too of the two forms agree very well together. It is noticeable moreover that the specimen of *A. sarsi* in respect to the number of the mesenteries ranks but little above the largest known specimens of *A. albida*. There is only a difference of a few couples of mesenteries.

However as it cannot be positively settled whether the species here described is the adult animal of *A. albida*, and as it does not seem advisable to identify them without convincing proof, I have preferred to give this species a new name *A. sarsi*. I do this the more readily as there seems

to be a rather great difference between *A. albida* and *A. sarsi*, in that the former's protomesenteries 2 are provided with extremely well developed cnido-glandular tracts, which I have not been able to discover in the latter. However, as the specimen of *A. sarsi* is not in every respect well preserved, and is so scanty, I must leave the connection of *Arachnanthus sarsi* and *Arachnactis albida* an open question. In the diagnosis above I have bracketed the arrangement and appearance of the tentacles, as these characters are only transferred from the free swimming larval stage of *A. albida*.

Lastly, I must mention that in a previous work (Nordisches Plankton 1906) I wrongly suggested that the adult species answering to *Arachnactis albida* was to be looked for in a gigantic Cerianthid (in fact the species here described *Pachycerianthus multiplicatus*). This hypothesis has not been confirmed by the anatomical investigations, although the appearance, great length and probably also the arrangement of the tentacles are much the same in *P. multiplicatus* and *A. albida*.

### Family **Botrucnidiferidae** Diagnosis see Section III.

#### Genus **Botrucnidifer** nov. gen. Diagnosis see Section III.

##### **B. norvegicus** n. sp. Pl. 4, fig. 6—8, Pl. 5, figs. 9—10.

*Diagnosis.* A small species with rather few tentacles. The marginal tentacles 34 at most, the labial tentacles 17 at most: the labial tentacles are consequently considerably fewer than the marginal ones. In relation to the size of the animal the tentacles are of moderate length. Arrangement of tentacles: Marginal tentacles 1 (dt) 4, 3, 1 | 3, 2, 3, 1 | 3, 2, 3, 1 | 3, 2, 3, 1 . . . . . Labial tentacles 0 (dt) 0, 1, 1 | 1, 1, 1, 1 | . . . . . The labial tentacles not developed above directive chamber and the contiguous chamber on either side of it. The stomatodaeum of medium length. The siphonoglyph narrow but deep, with only the directive mesenteries attached to it, with no hyposulcus, and very slight hemisulci. The directive mesenteries very short, with no differentiation of filament. Protomesenteries 2 fertile, reaching right down to the aboral end of the animal, with a region of the ciliated tracts, a region of the cnido-glandular tract, a long craspedion region, and a small botrucnid region. Protomesenteries 3 sterile, rather shorter than the former and resembling them, but with shorter craspedion region and larger botrucnid region. The metamesenteries of the 1st and 2nd cycles are like protomesenteries 2, but shorter, the difference in length between the mesenteries of cycles 1—4 in the same quartette is not so great as in other Ceriantharia. The regions of the ciliated tracts of medium length in all mesenteries and without craspedonemes. The cnido-glandular tracts in protomesenteries 2 and 3 and the metamesenteries are not very far from the stomatodaeum. In metamesenteries 2 they are about as far from the lower border of the stomatodaeum as the length of the stomatodaeum itself. Well developed craspedion region especially in protomesenteries 2 and the metamesenteries of the 1st and 2nd cycles. The botrucnids in the most aboral portion of the mesenteries, most developed in protomesenteries 3 and the metamesenteries of the 3rd and 4th cycles.

*Occurrence:* Norway, Trondhjem fjord among branches of Lophohelia and Paragorgia.

- » » » Röddberg 50—100 m., Aug. 1898, Arvidsson, R. M.
- » » » Skarnsund Indalbay, 100—200 m., Sept. 1898, Östergren.  
R. M., U. M.
- » » » Rissen, about 200 fathoms in Oculina colonies 31. 7. 1902.  
Svenander, R. M., T. M., U. M.
- » » » Galgenæsset. Rocky ground. On dead Oculina T. M.
- » » » without specified locality T. M.

*Dimensions.* A couple of the largest preserved specimens measured: specimen 1—3.2 cm. in length and 0.4 cm. in breadth. Specimen 2—3.6 cm. in length and 0.3 cm. in breadth. Marginal tentacles 0.35 cm. long, labial tentacles 0.2 cm.

*Colour.* According to Dr. Arvidsson's account. Body colourless, transparent, the oral part very faintly flesh-coloured. Tentacles faintly flesh-coloured.

*Exterior aspect.* The body has the appearance characteristic of the Ceriantharia. There is probably an aboral pore.

The tentacles are comparatively short, conical, the labial tentacles distinctly shorter than the marginal. The arrangement varies somewhat according to the age of the animal. In a small-sized specimen with 20 marginal and 10 labial tentacles the arrangement was as follows.

marginal tentacles	1, 2		1, 2, 1, 2		1, 2, 2, 1, 2, 2, 1		2, 1, 2, 1		2, 1, 2	
labial tentacles	,	1, 1, 1		1, 1, 0, 0, 0, 1, 1		1, 1, 1,				

3 older specimens shewed the following arrangement

Sp. 1.	26 marginal tentacles	3		1, 3, 2, 3		1, 3, 2, 3		1, 3, 4, 1, 4, 3, 1		3, 2, 3, 1		3, 2, 3, 1		3, 2, 3
	16 labial tentacles		1, 1		1, 1, 1, 1		1, 1, 0, 0, 0, 1, 1		1, 1, 1, 1		1, 1,			

The tentacle arrangement of specimen 2 (with 30 marginal and 16 labial tentacles) agrees with that of sp. 1. A third example shews some variation

32 marginal tentacles	2, 3, 1, 3		2, 3, 1, 3		2, 3, 1, 3		2, 3, 4, 1, 4, 3, 2		3, 1, 3, 2		3, 1, 3, 2		3, 1, 3, 2		3,
17 labial tentacles		1, 1		1, 1, 1, 1		1, 1, 0, 0, 0, 1, 1		1, 1, 1, 1		1, 1, 1,					

which comes to an interchange of the 1st and 2nd tentacle cycles. Which of the two is the typical grouping is hard to say and can hardly be determined with certainty except from living subjects, as the tentacles of the 1st and 2nd cycles are very close together. The number of the marginal tentacles will probably not exceed 34. Characteristic points are the great difference in the number of the marginal and labial tentacles, and the arrangement of the marginal tentacles in several cycles of the labial tentacles in one only.

The stomatodaeum is short, about  $\frac{1}{6}$  of the length of the body, longitudinally furrowed, and with special distinctness in the aboral part. Only the directive mesenteries are attached to this very narrow siphonoglyph. The hyposulcus is extremely slight, as also the hemisulci.

*Anatomical description.*

The column shews the usual structure. The numerous nematocysts with much coiled thread are comparatively short in relation to the breadth, and of 2 sizes  $36-43\mu \times 5-7\mu$ ;  $24-26\mu \times 7\mu$ .

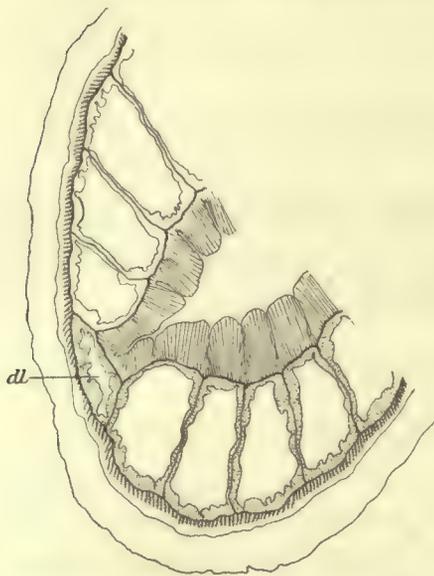
In addition, thick-walled nematocysts occur very rarely (length  $24-26\mu$ ). The ectodermal musculature is moderately developed (text-fig. 6), and is much feebler than in specimens of *Cerianthus lloydii* of the same size. The connective tissue processes too on which the muscles rest are thinly scattered.

The structure of the tentacles shews no deviation from the Cerianthid type. The bulk of the nematocysts consists of spirocysts. In addition, thick-walled granulated nematocysts are very frequently found. They are rather larger in the marginal than in the labial tentacles ( $34-36\mu$ ,  $24$  or  $26\mu$ ). The ectoderm attains a considerable thickness; the ectodermal muscles are slight.

The structure of the oral disc agrees with that of the tentacles; the radial musculature is rather more developed.

The structure of the stomatodaeum agrees with that of the stomatodaeum of *Cerianthus lloydii*,

save that the mucus cells are rarer. The nematocysts are thick-walled in the upper portion and agree with those of the labial tentacles: in the aboral portion they are thick-walled, transparent, and considerably larger ( $48 \times 12-14\mu$ ). The spirocysts are thinly scattered. The ridges developed in the midmost portion of the stomatodaeum are broader and only half as high as in *C. lloydii*. As a result of this, the mesogloal processes are broader and shorter than in that species.



Textfigure 6. *Botrucnidifer norvegicus*. Transverse section through a portion of the column and stomatodaeum with the mesenteries at the upper part of the stomatodaeum. dl directive chamber.

The structure of the siphonoglyph also agrees in the main with that of other Ceriantharia, though it is less differentiated from the rest of the stomatodaeum. The mucus cells are sparser than in *C. lloydii*. The structure of the hyposulcus and hemisulci does not differ from that of the siphonoglyph.

The mesenteries (text-fig. 7). The directive mesenteries are small and insignificant, with no distinct hemisulcus.

Protomesenteries 2 reach right down to the aboral pole, and are the longest of the mesenteries. The region of the ciliated tracts is about half as long again as the stomatodaeum. The region of the cnido-glandular tract shews no characteristic wavy coils but rests on a folded, very long process issuing from the mesentery just where the region of the ciliated tracts ends. The region of the ciliated tracts goes some way up the process. The region of the craspedion is long, going right down to the botrucnid in which the filament region ends. The botrucnids are smaller than on other mesenteries (invariably?). Fertile.

Protomesenteries 3 do not extend as far as the former, but still only terminate a little way from the aboral pole. The region of the ciliated tracts is rather shorter and the botrucnid region considerably longer than in protomesenteries 2. Sterile. Otherwise they resemble the mesenteries just mentioned.

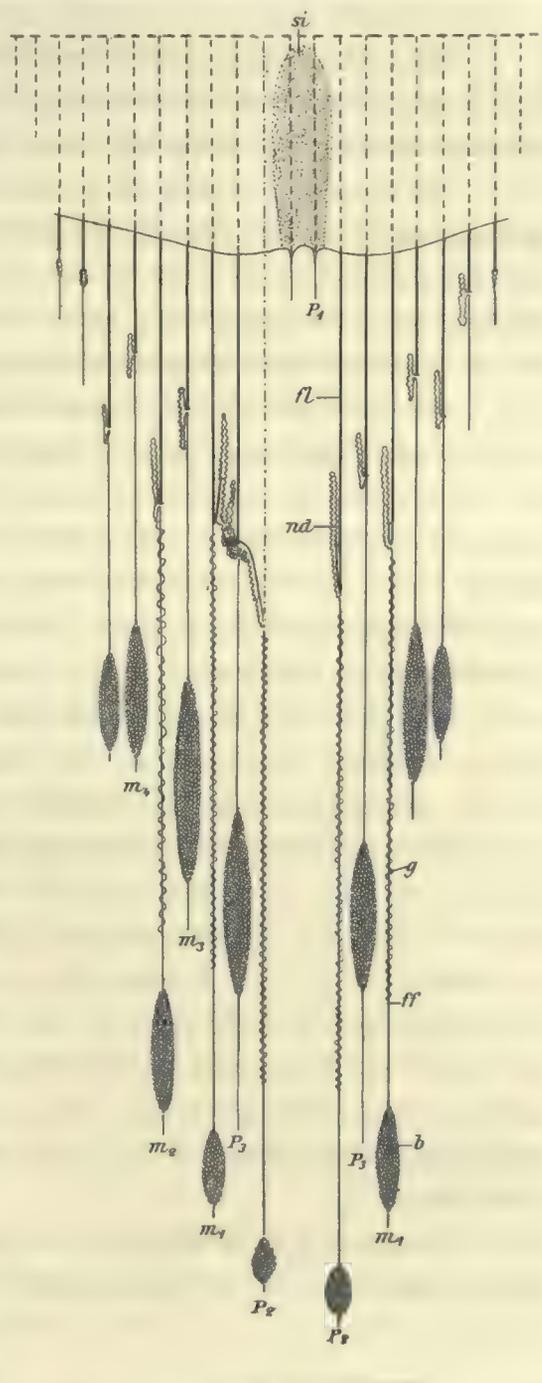
The metamesenteries of the 1st and 2nd cycles, which are fertile, are long, and the latter slightly shorter than the former in the same quartette. If those of the 2nd cycle are not fullgrown, the difference is naturally greater. The termination of the 1st metamesentery is intermediate between

the terminations of protomesenteries 2 and 3. In other points they agree in structure with protomesenteries 2. They diminish in length towards the multiplication chamber. The botrucnids are larger than in protomesenteries 2.

The metamesenteries of the 3rd and 4th cycles are sterile and shorter than the preceding, though when full-grown the oldest ought to reach a long way down. They decrease as usual towards the multiplication chamber. As too few metamesenteries of the 3rd and 4th cycles are developed, it is hard to say whether the difference in length between them is considerable or not. As far as can be judged from the development of the mesenteries, it seems not to be so. The metamesenteries of the 3rd and 4th cycles otherwise agree in structure with protomesenteries 3.

From the specimen represented (Textfig. 7) we see that the mesenteries of the left side are more developed than on the right, which is most unusual with the Ceriantharia. A further peculiarity is to be found in the fact that the highest part of protomesentery 2 on the left side is not found and its cnido-glandular tract has cohered with protomesentery 3 on the same side. (The upper part, which is missing, is marked throughout by lines and dots). Presumably the animal has been damaged in an embryonic state, before the mesenteries took shape, and regeneration has brought about the irregularity as regards protomesenteries 2, as well as the better growth of the mesenteries on this side. Other specimens examined are normal.

**The filaments:** The region of the ciliated tracts is well marked off and distinct. The mesogloal processes that support the ciliated tracts issue from the chief lamella of the mesentery as in *C. lloydii* and several others. The median streak is more semicircular in shape, in a few cases slightly flattened towards the sides. No trace of bipartition of the median streak can be detected. The ectodermal cells in the middle of the median streak are not lower than in other parts of the streak. The gland cells and nematocysts are evenly distributed. The spirocysts are very numerous and in addition thick-walled nematocysts ( $46\mu$ ) occur though rarely. The mesogloea in transverse section is something like a rounded spade or tongue with a narrower



Textfigure 7. *Botrucnidifer norvegicus*. Diagram of mesenteries and stomatodaeum. The line of dashes and dots on the left side indicates that this part of the mesentery (protomesentery 2) is lacking. For signs see explanation of the Plates.

base, and here and there the mesogloea forms a little process towards either side. The musculature is not developed.

The cnido-glandular tract shews but little tendency to wavy coils, but encloses as a folded tract a long process of the mesentery. The thick-walled nematocysts, which are not particularly numerous have a length of 43—48  $\mu$  and a breadth of 12  $\mu$ . Smaller nematocysts (24—26  $\mu$ ) occur as well.

The craspedion regions (Pl. 5, fig. 10) are well developed, long on protomesenteries 2 and the metamesenteries of the 1st and 2nd cycles. On protomesenteries 3 and the other metamesenteries they are less developed, which is connected with the fact that these mesenteries below the cnido-glandular tract are considerably smaller and shorter than the first-named mesenteries. The homogeneous gland cells are numerous, the nematocysts sparse.

The botrucnids (Pl. 4, fig. 6) are well developed. Each botrucnid grain, cnidorage, (fig. 7, 8, Pl. 4) is ball or egg shaped and jointed to the mesentery by a shorter stem. The mesogloea of the mesentery ramifies like the branches of a tree, of which one branch goes to each botrucnid grain. The mesogloea enters the stem of the grain like a thread and broadens out at the base of the grain in cup-like form. For the mesogloea seems to expand a little way at least up the periphery of the grain, thus forming a shallow, more rarely a deep cup. Here and there it looks as though there were a prolongation of the mesogloea edge in threads entering more deeply into the grain. The epithelium on the sides of the cup as also on the stem is very thin; in the cup however, besides supporting cells and an occasional mucus cell, are very large thick-walled nematocysts (length 43—48  $\mu$  breadth 12  $\mu$ ) and also spirocysts (4  $\mu$ ) in large numbers in the periphery.

The botrucnidae are consequently not, as v. Beneden says (1908 p. 32), simply epithelial in character; on the contrary they have like the filament a ground work of mesogloea, that even forms a more or less clear cup-like structure. They are presumably ectodermal formations, and looked at as a differentiation of the filament, they are probably homologous with the "acontia" — views which I have developed in detail below in the 4th section, and which are in conflict with v. Beneden's, who regards the botrucnidae as endodermal formations. On the other hand it is possible that a part of the loosened cnidorages consists only of epithelium, as v. Beneden states. In such a case a loosening, probably disruption of the grain would have taken place just outside the mesogloea. See further section 4.

The mesenterial muscles are feebly developed, but shew no variation in arrangement from the other Ceriantharia which I have described. The species is hermaphrodite.

## Larval forms.

*Arachnactis albida* M. Sars

Pl. 4, Fig. 1—3, Pl. 5, fig. 7—8.

For diagnosis and literature concerning this form and other northern Cerianthid larval forms see Carlgren: Actinien larven, Nordisches Plankton 1906.

Locality: 61° 41' N., 10° 17' W., 625 fathoms, 14. 8. 1895, St. 42, Ingolf-Exp., 3 ex. (A).  
 61° 42' N., 9° 36' W., 545 " " 14. 8. 1895, St. 44, " " " " 1 ex. (B).

The specimens found were in the following stages of development.

A<sub>1</sub>. Stage with 11 marginal tentacles, of which the 5th from the directive chamber on the right side is larger than the one on the left, which is very small. The 4th couple of marginal tentacles in course of formation.

A<sub>2</sub>. A little later stage than in fig. 1 (Nordisches Plankton (XI, p. 71), on the right side however is a small 5th tentacle in a rudimentary stage.

A<sub>3</sub>. The directive tentacle of the marginal tentacles not yet in formation. 4 marginal tentacles on the right side, of which the one nearest the multiplication chamber is small: on the left side 3 large ones and signs of a 4th by the multiplication chamber, 4 labial tentacles arranged in couples. (The earliest known stage of *A. albida*, reproduced in Nordisches Plankton XI, p. 7, fig. 1 a).

B = A<sub>1</sub>.

With respect to the animal's exterior, such exhaustive descriptions have already been given by a number of writers, that there is no need for me to go into the subject in detail. I have investigated however in a large number of instances (169), principally from the Valdivia Expedition, the arrangement of the tentacles. Though I intend later to give a full account of the results in tabular form, I will nevertheless mention here the following ascertained facts, which corroborate van Beneden's observations.

(1) From the 4th to the 6th couple inclusive of the marginal tentacles the right tentacle in each couple begins to form before the left (the animal being viewed with the oral side upwards and the directive chamber turned away from the observer).

(2) From the third to the fifth couple inclusive of the labial tentacles the same facts are observable as with the marginal tentacles (see 1).

(3) The directive tentacle of the marginal tentacles appears only after the 4th couple of marginal tentacles has appeared, commonly before the 5th tentacle on the right side: sometimes it appears simultaneously with it.

(4) In no instance are labial tentacles developed above the directive chamber and the contiguous chamber on either side.

*Anatomy.* The anatomy has been closely studied by Vogt (1888), Vanhöffen (1895) and later more thoroughly by van Beneden (1908). But even the last account needs no little supplementing, and specially so in the case of the stomatodaeum and its differentiation, and also of the mesenterial filaments and mesenterial musculature.

The stomatodaeum is very long with a sharply differentiated siphonoglyph, to which at least 2 and more commonly (in larger specimens) 3 couples of mesenteries are attached. The hyposulcus is very long and increases in length as the animal grows larger. Vanhöffen has given a good figure in his work (fig. 4, pl. 1, 1895) of the hyposulcus. The hemisulci are small in younger examples, in older ones they seem to disappear entirely in proportion as the hyposulcus increases. In one large specimen with 20 mesenteries the directive mesenteries went as far down as to the lower border of the hyposulcus.

The stomatodaeum shews a similar structure to *Arachnanthus oligopodus* and *sarsi*. The longitudinal furrows of the stomatodaeum are here also unsupported by mesogloal processes. They are gradually transformed into the filaments as shewn in fig. 1—3, Pl. 4. The siphonoglyph contains extremely numerous mucus cells, especially in the upper part. The structure of the hyposulcus resembles the siphonoglyph's, save that the mucus cells are less numerous. On the free border of the hyposulcus a filamentous differentiation runs almost to the aboral end of it. The ectoderm of the border contains numerous spirocysts and shews the same histological structure as the median streak. A mesogloal process supports a ciliated tract exactly as in *Arachnactis lobiancoi* and *Arachnanthus oligopodus*.

The mesenteries. Van Beneden (1898) has given one or two good figures of their arrangement. The oldest example represented by him was provided with 17 mesenteries. As to the subdivision of the filaments my observations agree with van Beneden's. The "pelotons" of the filaments are my cnido-glandular tracts, the upper straight-lined part is the region of the ciliated tracts, the lower part also straight-lined below the cross stroke is the region of the craspedia (not marked on metamesenteries 3 — mesenteries 5 — in van Beneden's fig. II), which van Beneden does not distinctly mark, but merely as a single filament tract.

The region of the ciliated tracts in transverse section resembles that of *Arachnanthus oligopodus* and *Arachnactis sarsi*. The median streak has the same structure as *Arachnanthus*. A little way below the stomatodaeum it is divided into 2 distinct portions separated from each other by a well marked groove containing supporting cells. The groove is deep especially in large specimens or else much flattened out like a broad plate—presumably the difference in appearance depends on a difference of contraction in the filament. Besides, the ectoderm of the median streak is formed of the characteristic cells. The mesogloal processes, which support the portion of the ciliated tracts that lies towards the column, issue from the mesogloal portion of the median streak, not from the main lamella of the mesentery.

The cnido-glandular tract ("peloton") has the enlargement pointed out by van Beneden and has the usual structure of thick-walled nematocysts and granular elongated gland cells, lying close together.

The craspedion portion shews the same division as the median streak in the region of the ciliated tracts. It is either deep (fig. 7, pl. 5) or else flattened out rather. In the most aboral part it is comparatively slight and shews no division. A well developed craspedion region is found on all the more developed mesenteries of the 1st and 2nd cycles.

The so-called "acontia" have a structure exactly corresponding to that in *Arachnanthus oligopodus* and *sarsi* (see further 4th section). Here too they are formed of a part of the ectodermal filament, which contains mucus cells closely packed together. I have not observed any increased agglomeration of nematocysts in the endodermal part of the "acontia". On the other hand large curved nematocysts are found in the endoderm of the mesenteries (*n* fig. 7. Pl. 5) especially in the aboral part of the mesenteries. The appearance of the acontia to the naked eye is shewn by Vanhöffen (fig. 3, Pl. 1, 1893).

As regards the arrangement of the musculature, I have been able, by means of two examples

which were remarkably well preserved and in the same stage of development (with 17 mesenteries), to establish the fact that the arrangement which occurs in the adult Ceriantharia, is found also in *A. albida*. The muscle arrangement on the mesenteries was specially clear in one specimen, which was strongly but uniformly<sup>1)</sup> contracted throughout. All the mesenteries including the directive had the transverse muscles extended upon the side towards the directive chamber, whilst the longitudinal muscles were developed on the side remote from them (fig. 8, Pl. 5). My diagram (1893 a) of the muscle arrangement on the mesenteries will thus be of value even in the matter of the directive mesenteries.

*Systematic Remarks.* As I have already pointed out, this larval form is possibly that of *Arachnanthus sarsi*. The dissimilarity of structure in protomesenteries 2 is sufficiently great however, to compel us to leave the question undecided. In any case *A. albida* is a larval form falling under the same genus as *Arachnanthus*, which cannot be said of *Arachnactis bournei* and *brachiolata* (compare p. 41). For further treatment of this larval form I refer to "Nordisches Plankton".

### Section III.

## Classification of the Ceriantharia.

As the earlier descriptions of Ceriantharia are very imperfect, and indeed some of the more recent also, it is particularly difficult to obtain a fair conception of a good many Cerianthid species. It is extremely probable of course that many of these are genuine species, for the Ceriantharia do not seem to be so deficient in species as was formerly believed, and as Pax (1910) — though without close study of the facts — still thinks probable. That there must be several species shewing considerable divergencies in the adult state, may be concluded moreover from van Beneden's, in many respects, meritorious work on Cerianthid larval forms in the Plankton Expedition (1898). Van Beneden shewed that two distinct types of larval forms might be distinguished:

(1) *Acontifères* having acontia.

(2) *Botrucnidifères*, provided with special stinging organs called Botrucnidae.

As genera of Acontifères van Beneden accounted:

*Arachnactis, Ovactis, Dactylactis, Solasteractis, Apiactis, Peponactis,*

As genera of Botrucnifères:

*Cerianthula, Hensenanthula, Calpanthula.*

In *Solasteractis, Apiactis* and *Peponactis* van Beneden found no acontia. Still he did not make a distinct group of them, doubtless for the reason that he believed, that these larval forms would also develop acontia at a later stage. For in his diagnosis of these three genera we find the attribution "Aconties absentes ou tardives".

<sup>1)</sup> The mesenteries were also strongly contracted similarly to the column. Such specimens are plainly the best for the study of the mesenterial musculature, whilst the specimens which shew strong contraction of the column without contraction of the mesenteries are the worst for purposes of research. For in the latter the mesenteries become so folded through the contraction of the column that it is particularly difficult to get an idea of the arrangement of the musculature.

The first division of adult Ceriantharia on an anatomical basis has been recently (1910) made by Mc. Murrich in his work on the Ceriantharia of the Siboga Expedition, in which he takes account of larval as well as of full grown forms.

Mc. Murrich's classification of Ceriantharia (1910) is of the following nature.

1 Suborder Acontiferae van Beneden.

Ceriantharia in which the second or fourth protocnemes, or in some cases both these mesenteries, are provided with acontia at least during the early stages of development. The deuteroconemic marginal tentacles appear in the same order as the mesenteries to which they correspond.

1. Family *Cerianthidae*.

Acontiferae in which the second couple of protocnemes are the telocnemes. The succeeding protocnemes are represented by a brachycnemic couple, usually sterile, and by a macrocnemic couple. Acontia are borne in larval stages upon the telocnemes and in some cases also upon the macrocnemic protocnemes.

Genera: *Cerianthus*, *Apiactis*<sup>1)</sup>, *Solasteractis*, *Peponactis*.

Genus *Cerianthus* Delle Chiaje.

Acontiferae living imbedded in mud or sand and provided with a sheath consisting of felted nematocysts and mucus: mesenteries and tentacles usually numerous, so that the quartette arrangement of the deuteroconemes is distinct.

Type: *Cerianthus membranaceus*.

2. Family *Arachnactidae*.

Acontiferae in which the fourth couple of protocnemes, counting from the mid-ventral line, form the telocnemes. The second and third couples of protocnemes are sterile. Acontia are borne in larval stages by the fourth protocnemes, but never by the second.

Genera: *Pachycerianthus*, *Arachnactis*, *Dactylactis*, *Ovactis*.

Genus *Pachycerianthus* Roule.

Arachnactidae living imbedded in mud or sand and provided with a sheath composed of felted nematocysts and foreign substances. Mesenteries and tentacles usually numerous and the quartette arrangement of the deuteroconemes distinct.

Type: *Pachycerianthus benedeni* Roule.

Suborder 2. Botrucnidiferae (van Beneden).

Genera: *Botruanthus* nov. gen. (Type *Botruanthus benedeni* (Torrey and Kleeberger), *Cerianthula*, *Hensenanthula*, *Calpanthula*).

Though like Mc. Murrich I am fully conscious that we cannot at present make a satisfactory division of the Ceriantharia, I am still of opinion that by the help of the accounts here given of the morphology of the Ceriantharia, Mc. Murrich's scheme may be considerably improved upon in various points. But before I pass on to my own suggestion for the grouping of the Ceriantharia, it might be well to look carefully into Mc. Murrich's division. This shews that Mc. Murrich retains van Beneden's division of the Cerianthidae into 2 groups Acontiferae and Botrucnidiferae.

<sup>1)</sup> As the scope of my work includes principally adult forms, I do not insert here the diagnosis of larval genera.

In the first sub-order he includes not only the forms that possess "acontia" but also those which in the adult state are known not to possess any, e.g. *Cerianthus membranaceus* and several species of *Pachycerianthus*. As far as I can see, Mc. Murrich has here fallen into error, for there is nothing in the development of the Ceriantharia to point to the "acontia" being larval organs, that afterwards disappear in the full-grown individuals. On the contrary it is possible that the "acontia" in some cases shew themselves quite late in the course of development, and most probably their number increases with the growth of the animal. In reality Mc. Murrich's diagnosis of Acontiferae conflicts seriously with van Beneden's.

Whilst Mc. Murrich says of Acontiferae that "they are provided with acontia at least during the early stages of development", we find in van Beneden's diagnosis of the three genera *Solasteractis*, *Apiactis* and *Peponactis*, that the acontia are "absentes ou tardives", a view quite contrary to Mc. Murrich's. As we know besides that the majority of Ceriantharia, so far anatomically described, lack acontia and botrucnidae alike, we have at once a strong reason for removing these Ceriantharia from the group Acontiferae. It seems to me necessary therefore to expel the whole of Mc. Murrich's Cerianthidae family, and a great part of the Arachnactidae family as well, from Acontiferae, thus reducing it so considerably, that it would only be found to include some adult forms. In my opinion then Cerianthidae should be divided into three groups.

- (1) those that possess neither botrucnidae nor "acontia".
- (2) those that possess "acontia" but not botrucnidae.
- (3) those that possess botrucnidae but not "acontia".

To the first group belong Mc. Murrich's Cerianthidae and a part of his Arachnactidae.

Mc. Murrich divided Acontiferae into 2 families Cerianthidae and Arachnactidae. In the former the second couple, reckoning from the directive chamber, would be the longest mesentery couple (the telocnemes) of the protomesenteries, in the latter family on the other hand the fourth couple would be "the telocnemes". This characterisation does not seem to me quite satisfactory even if we apply it only to the two adult genera included by Mc. Murrich, *Cerianthus* and *Pachycerianthus*, and this among other reasons because the fourth couple in my opinion belongs not to the protocnemes but to the metacnemes (deuteroconemes, metamesenteries). Between *Cerianthus* and *Pachycerianthus*, which are doubtless real genera, there is a distinct difference however, as Mc. Murrich has clearly recognized, namely, that whilst in the genus *Cerianthus* the second couple of protocnemes is long, fertile and similar to the metacnemes of the 1st cycle (*M*), in the genus *Pachycerianthus* on the other hand, the same couple is short, sterile, and provided with a well developed cnido-glandular tract like the metacnemes of the 3rd and 4th cycles (*B, b*).

Mc. Murrich's diagnoses, too, of the genera *Cerianthus* and *Pachycerianthus* are not so distinct as might be wished. As to the genus formulated by Roule and accepted by Mc. Murrich, *Pachycerianthus*, it is extremely difficult to form from Roule's description an adequate idea of the mesenterial appendages (the filaments and the "acontia"), with which it is far more important to be acquainted than with some of the generic characters mentioned by Roule. Roule (1904) characterises the genus in this way "cloisons courtes, deux seules d'entre elles ( $S_3 =$  fourth couple) parviennent dans l'extrémité aborale. Cloisons directrices épaisses donnent à la lage directrice la forme d'un canal

cylindrique. Disposition biseptale font alterner des cloisons fertiles acontifères avec des cloisons stériles privées d'aconties et portant des fils mésenteriques sur leur craspèdes. Musculature endodermique à peine représentée. Paroi de la colonne épaisse et consistante, à cause du développement pris par la musculature longitudinale et par la mésoglée." In his description of the type *P. benedeni* Roule adds the following concerning the filaments and acontia, after mentioning that filaments (craspèdes) are found on all mesenteries, except the feeblest. "Seulement et en alternance les unes ont des fils mésenteriques sur leur craspèdes et les autres n'en portent point. Les cloisons ainsi privées sont fertiles, dénuées de fils mésenteriques, elles possèdent par contre des aconties sur une assez grande part de leur extrémité inférieure; leur série débute par  $S_3$  et continue par les numéros d'ordre impaire  $S_5, S_7, S_9$ ".

According to this the fertile mesenteries would bear "acontia" whilst the sterile mesenteries would be provided with craspedonemes. If Roule's view were correct, *Pachycerianthus* would thus be a genus coming under Acontiferae. But this, I think, can hardly be the case, as I suspect that Roule had not clearly grasped the true nature of an "acontium". My supposition is supported too by the expression of Roule's just quoted, that the acontia are found "sur une assez grande part de leur (des cloisons) extrémité inférieure". As far as at present known, the acontia are never distributed over the mesenteries in such a way; it seems likely therefore that Roule has confounded them with the craspedonemes of the region of the ciliated tracts. *Pachycerianthus benedeni* might thus stand as the type of a genus included in the first Ceriantharia family, that which does not possess acontia nor botrucnidae. To this genus would belong *P. fimbriatus* Mc. Murrich, *C. lloydi* Gosse and others (see tables below p. 44—47) but not *C. oligopodus*, for which a new genus must be set up, unless a larval genus is taken for this form, which is not likely to be so good, as the development of the species and consequently the connection between the larval and the full-grown form is not quite certainly known. I call this genus *Arachnanthus* and take as its type *A. oligopodus* (Cerf.), as this species is the best known.

I now suggest therefore a different division of Ceriantharia, based on a thorough anatomical study of different species. Besides the genus *Arachnanthus* just mentioned, we now institute two more new genera *Botrucnidifer* and *Ceriantheopsis* (Types *B. norvegicus* n. sp. and *C. americanus* Verr.). Very likely this division may also have to be modified later when a larger number of species of Ceriantharia have passed under close anatomical investigation. But by starting from those features which I have indicated in the diagnosis of families and genera below, it may be possible gradually to secure a satisfactory classification of Ceriantharia. My suggestion for the division of Ceriantharia is of the following nature.

#### Fam. I *Cerianthidae*.

Ceriantharia without "acontia" and without cnidorages and botrucnidae.

##### Genus I. *Pachycerianthus* Roule.

Cerianthidae whose 2nd couple of protocnemes are short, sterile and provided with an extremely well developed region of the cnido-glandular tract. Arrangement of metacnemes (= deuteroconemes Mc. Murrich) in each quartette *M, B, m, b*, (1, 3, 2, 4) more or less distinct.

Type: *Pachycerianthus benedeni* Roule.

Genus 2. *Cerianthus* delle Chiaje s. str.

Cerianthidae whose 2nd couple of protocnemes are long, fertile and provided with a small region of the cnido-glandular tract. Arrangement of the metacnemes in each quartette *M, B, m, b* more or less distinct. *M* diminishing in length towards the multiplication chamber, occasionally with some breaks in this diminution.

Type: *Cerianthus membranaceus* Spall.

Genus 3. *Ceriantheopsis* nov. gen.

Cerianthidae, whose 2nd couple of protocnemes are long, fertile and provided with a very small region of the cnido-glandular tract. Arrangement of metacnemes in each quartette *m, B, M, b* more or less distinct. *M* increasing in length towards the multiplication chamber, with (or without?) some breaks in this increase.

Type: *Ceriantheopsis americanus* (Verrill).

Larval genera: *Solasteractis* E. van Beneden.

?*Apiactis* E. van Beneden.

?*Peponactis* E. van Beneden.

Family 2 *Acontiferidae*<sup>1)</sup>.

Ceriantharia with acontium-like threads from the craspedion region, whose ectoderm chiefly consists of mucus cells, on two or more mesenteries.

Genus 4. *Arachnanthus* nov. gen.

Acontiferidae whose 2nd couple of protocnemes are comparatively short and sterile. Metacnemes of the 1st and 2nd cycles (*M, m*) without region of the cnido-glandular tract but with "acontia" on the best developed. Arrangement of metacnemes in each quartette *M, B, m, b* more or less distinct.

Type: *Arachnanthus oligopodus* (Cerfontaine).

Larval genera: *Arachnactis*<sup>2)</sup> M. Sars.

*Ovactis* E. van Beneden.

*Dactylactis* E. van Beneden.

?*Apiactis* E. van Beneden.

?*Peponactis* E. van Beneden.

Family 3. *Botrucnidiferidae*.

Ceriantharia with cnidorages mostly aggregated in botrucnidae; without "acontia".

<sup>1)</sup> This name ought properly to be replaced by another, since, as I have shewn below, the "acontia" of the Ceriantharia do not answer to the "acontia" of the Actiniaria.

<sup>2)</sup> Mc. Murrich is probably right in his view that *Arachnactis bourni* and *A. brachiolata* must be removed from the genus *Arachnactis*. If the first is the larval form of *Cerianthus lloydii*, which is extremely likely, it naturally cannot retain its place under the family Acontiferidae. Unfortunately the known larval stages of this species are all so early that "acontia", even if they do appear eventually, have not had time to form. For the oldest larval stage observed by me had only 5 couples of mesenteries only 3 of which possessed filaments. The couple on which "acontia" ought to appear, if such really do form, had only feebly developed filaments. The classification of *A. bourni* remains therefore for the present uncertain. The same holds true also of *A. brachiolata*.

Genus 5. *Botrucnidifer* nov. gen.

Botrucnidiferidae with botrucnidae in the most aboral part both of protocnemes 2, protocnemes 3 and of macro- and microcnemes (brachycnemes). Metacnemes and protocnemes 2 with region of the cnido-glandular tract. Protocnemes 2 long, fertile. Arrangement of metacnemes in each quartette *M, B, m, b* more or less distinct.

Type: *Botrucnidifer norvegicus* n. sp.

Genus 6. *Botruanthus* Mc. Murrich.

Botrucnidiferidae with cnidorages (botrucnidae?) dispersed over the craspedonemes and bunches irregularly. The region of the cnido-glandular tract on protocnemes 2 and metacnemes *M* and *m*? Protocnemes 2 (short?) — rather long, (sterile?). Arrangement of metacnemes in each quartette *M, b, m, B*, more or less distinct. (Diagnosis on the basis of Torrey and Kleeberger's description).

Type: *Botruanthus benedeni* (Torrey and Kleeberger).

Larval genera: *Cerianthula* E. van Beneden.

*Hensenanthula* E. van Beneden.

*Calpanthula* E. van Beneden.

As I have not treated the larval forms thoroughly in this work, I refer for further details to the works of E. van Beneden (1898) and Mc. Murrich (1910). As to the place assigned to the larval forms, it does not differ much from Mc. Murrich's. Still it seems to me rather doubtful where to insert the larval genera *Apiactis* and *Peponactis*. For whilst van Beneden has described these larval forms as not possessing "acontia", Mc. Murrich has found these in some new species which he ascribes to these genera. Should Mc. Murrich's larval forms really possess "acontia", and at the same time have to be referred to van Beneden's genera *Apiactis* and *Peponactis*, these genera must then be classed under the family Acontiferidae and not under Cerianthidae. But it is not beyond the range of possibility that Mc. Murrich's "acontia" are nothing more than thread-like cnido-glandular tracts or slightly differentiated craspedonemes of the craspedion region, which, as I shew in this work, may have, as far as exterior goes, in certain Ceriantharia (for example in *Pachycerianthus solitarius* and *Ceriantheopsis americanus*) an appearance strongly suggestive of the "acontia". To settle this point however close study of the type specimens would be required. It is possible besides that van Beneden also has not always clearly distinguished such a craspedoneme of the cnido-glandular tract or of the craspedion from "acontia" but has described as "acontia"<sup>1)</sup> all formations which resemble them. I give expression to this suspicion, because van Beneden, as I believe I have shewn (compare section 4), did not have a clear conception of the structure of the "acontia". In that case either the whole or a part of the larval genera of Ceriantharia must undergo revision.

<sup>1)</sup> If the term "acontia" is extended to embrace not only the typical formations in *Arachnactis albida*, *Arachnanthus oligopodus* and *sarsi*, but also the craspedonemes of *Ceriantheopsis americanus* issuing from certain craspedia, which in their outward conformation, though not in their inner structure suggest the "acontia", then of course it will be necessary that the whole genus *Ceriantheopsis* should be transferred to the family Acontiferidae. By "acontia" would then be understood every threadlike organ issuing from the craspedion that is more or less differentiated in structure from the craspedion. For the present however I believe it will be more advisable to distinguish the "acontia" from the less differentiated craspedonemes of the craspedion region. Compare also the acontium-like craspedonemes issuing from the region of the ciliated tracts in *Pachycerianthus maua*.

As is known (Busch 1851), the larval form of *Cerianthus membranaceus* appears not to have a long period of development, but to sink quickly to the bottom. It may also be possible, therefore, that the most larval forms of the Cerianthidae family are not planktonic for any long period, and that the larval forms, which are more adapted for the planktonic mode of life, belong principally to the families Acontiferidae and Botrucnidiferidae.

Besides the generic characters given above, there are undoubtedly a number of others that will prove to be of significance for the discrimination of genera. In the above however I have endeavoured to give the genera as extensive a range as possible in order not to run the risk of having to suppress certain characters afterwards. However as these more secondary characters may be of use for a future characterisation of the genera, they are stated here.

Genus *Pachycerianthus*: Species as a rule with rather numerous mesenteries. Breadth of siphonoglyph and length of hyposulci vary. The median streak with a tendency at least to break up into two streaks. The mesogloal processes of the ciliated tracts issue from the main lamella of the mesentery. Mesenterial threads (craspedonemes) and bunches of the ciliated tracts may or may not be found. The region of the craspedion may or may not be found. The cnido-glandular tract on mesenteries *M* and *m* sometimes threadlike, from its exterior suggestive of the "acontia" and of the craspedonemes of the ciliated tract.

Genus *Cerianthus*: Species as a rule with numerous mesenteries. Siphonoglyph narrow. Hyposulcus as a rule small. The median streak and mesogloal processes of the ciliated tracts as with *Pachycerianthus*. Mesenterial threads (craspedonemes) and bunches in the region of the ciliated tracts may or may not be found. The region of the craspedion may or may not be found.

Genus *Ceriantheopsis*: Species with numerous mesenteries. Siphonoglyph narrow. Hyposulcus small. Median streak with marked tendency to divide into two lateral portions. The mesogloal processes of the ciliated tracts issue from the main lamella of the mesentery. Craspedonemes and bunches in the region of the ciliated tracts occur. The region of the craspedion is present, long. Protocnemes 2 and the longest metacnemes with a craspedoneme from the most aboral part of the region of the craspedion.

Genus *Arachnanthus*: Species with a small number of mesenteries. The 2nd couple of protocnemes without cnido-glandular tract region. Number of metamesenteries not large. Very broad siphonoglyph and long hyposulcus. With distinct filament region on hyposulcus. Median streak divided up into 2 streaks sharply marked off. The mesogloal processes that support the ciliated tracts issue from the mesogloal folds of the median streak. The region of the craspedia on *M* and *m* well developed. Without mesenterial threads (craspedonemes) and bunches in the region of the ciliated tracts.

Genus *Botrucnidifer*: Species with a small number of mesenteries. Siphonoglyph narrow, feeble hyposulcus. Median streak simple, not subdivided. The mesogloal processes of the ciliated tracts issue from the main lamella of the mesentery. Long craspedion region. Mesenterial threads (craspedonemes) and bunches in the region of the ciliated tracts not developed.

Genus *Botruanthus*: Species with very numerous mesenteries. Siphonoglyph very broad. Hyposulcus of medium development. Conformation of the median streak? Mesenterial threads (craspedonemes) occur. Craspedion region?

	Arrangement of the marginal tentacles	Arrangement of the labial tentacles	Approximate number of marginal tentacles	Directive labial tentacle	The ridges of mesogloea at the aboral end of the stomatodaeum
Family 1. Cerianthidae.					
<i>Pachycerianthus solitarius</i> (Rapp.).....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	2 (dt) 3 I 3, 4 2 3 2, 4 3 I 2,....	70	present	present
» <i>aestuarii</i> (Torrey a. Kl.).....	1 (dt) I I I, I I I I, I I I I,....	?	35	?	?
» <i>johnsoni</i> » ».....	?	?	100	?	?
» <i>fimbriatus</i> Mc. Murr.....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	2 (dt) 3 I 2, 4 2 3 2, 4 3 I 2,....	numerous	present	present
» <i>multiplicatus</i> Carlgr.....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	0 (dt) 0...?	175	absent?	present
» <i>monostichus</i> Mc. Mur.....	2 alternating cycles	1 cycle	50	present	?
» <i>benedeni</i> Roule.....	»	?	125	?	?
» <i>maua</i> (Carlgr.).....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	0 (dt) .....? ..... 4 3 I 2,....	150	absent	present
<i>Cerianthus membranaceus</i> Spall.....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	2 (dt) 3 I 3, 4 2 3 2, 4 3 I 2,....	140	present	present
» <i>lloydii</i> Gosse.....	2 (dt) 3 2 I, 3 2 3 I, 3 2 3 I,.... 2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	0 (dt) 3 2 3, 4 I 3 2, 4 3 I 2,.... 4 2 4 2	70	absent	present
» <i>vogti</i> Dan.....	at least in 2 cycles	4 (dt) 0 2 3, 4 I 3 2, 4 3 I 2,....	36-40	present	?
» <i>valdiviae</i> Carlgr. (n. sp.).....	probably in 2 cycles	0 (dt) I 2 3, 2 3 2 3, 2 3 2 3....	35	absent	present
» <i>ambonensis</i> Kwietn.....	3 cycles	?	130	?	?
» <i>sulcatus</i> Kwietn.....	2 (dt) I 2 I, 4 2 3 I, 4 2 3 I,....	2 (dt) 4 I 3, 4 I 3 2, 4 3 I 2,....	180	present	?
» <i>taedus</i> Mc. Murr.....	1 (dt) 2 I 2, I 2 I 2, I 2 I 2,....	2 (dt) 4 3 I, 3 4 2 I, 3 4 2 I,....	55	present	?
» <i>borealis</i> Verr.....	?	?	150	?	?
<i>Ceriantheopsis americanus</i> (Verr.).....	2 (dt) 4 3 I, 4 2 3 I, 4 2 3 I,....	2 (dt) 4 I 3, 4 2 3 2, 4 3 I 2,....	100-125	present	present
Family 2. Acontiferidae.					
<i>Arachnanthus oligopodus</i> (Cerf.).....	1 (dt) I I I, I I I I.....	0 (dt) I I I, I I I I,....	20	absent	absent
» <i>sarsi</i> Carlgr.....	1 (dt) I I I, I I I I...?	0 (dt) 0 I I, I I I I?	21?	absent?	absent
( <i>Arachnactis albida</i> Sars).....	1 (dt) I I I, I I I I,....	0 (dt) 0 I I, I I I I.....	15	absent	absent
( » <i>lobiancoi</i> Carlgr.).....	1 (dt) I I I, I I I I,....	1 (dt) I I I, I I I I,....	16	present	absent
Family 3. Botrucnidiferidae.					
<i>Botrucnidifer norvegicus</i> Carlgr.....	1 (dt) 4 3 I, 3 2 3 I, 3 2 3 I,.... 1 (dt) 4 3 2, 3 I 3 2, 3 I 3 2....	0 (dt) 0 I I, I I I I,....	34	absent	present
<i>Botruanthus benedeni</i> (Torr. a. Kl.).....	3 cycles	?	90-100	?	?

Siphonoglyph. Number of the mesenteries, which are attached to the siphonoglyph	Hyposulcus	Hemisulci	Free part of the directive mesenteries	2nd Protomesenteries, <i>fl</i> : the ciliated tract, <i>nd</i> : the cnido-glandular tract, <i>c</i> : craspedonemes of the ciliated tract	Distribution of the me- senteries in the quar- tettes
rather broad; 6 mes.	narrow short	distinct, but filamentous	short	sterile, narrow short <i>fl</i> : narrow long <i>nd</i> well developed.	<i>M B m b</i>
exceedingly broad; 16 mes.	narrow long 1/3 of the length of the siphgl.	absent?	very short	sterile, very short; <i>fl</i> and <i>nd</i> ?	<i>M B m b</i>
rather broad; 8 mes.	>	distinct	absent?	sterile <i>fl</i> and <i>nd</i> ?	<i>M B m b</i>
rather broad; 8 mes.	very short	?	narrow long	sterile, narrow short; <i>nd</i> well developed.	<i>M B m b</i>
rather narrow; 6 mes.	>	distinct, filamentous	short	sterile, narrow short; well developed <i>nd</i> and with bunches of <i>c</i> .	<i>M B m b</i>
well developed	>	?	very short	sterile, narrow long; <i>fl</i> and <i>nd</i> ?	<i>M B m b</i>
?	?	?	?	sterile, short, <i>fl</i> and <i>nd</i> ?	?
rather narrow; 6 mes.	very short	not distinct, filamentous	very short	sterile, short, <i>c</i> in the aboral part, <i>nd</i> very short.	<i>M B m b</i>
rather narrow; 6 mes.	narrow short	distinct, flat, not filamentous	narrow long	fertile, very long; <i>c</i> very numerous, reach al- most to the aboral end; <i>nd</i> : thread-like.	<i>M B m b</i>
narrow; 4(-6) mes.	short	distinct, but filamentous	narrow short	fertile very long, reach about to the aboral end; distribution of the parts of the fila- ments as by <i>M</i> .	<i>M B m b</i>
narrow; 4 mes.	short	distinct, but filamentous	short	fertile very long, <i>fl</i> narrow long, <i>nd</i> feeble; craspedion region long.	<i>M B m b</i>
narrow; 4 mes.	short	short, but distinct, filamentous	very short	fertile, comparatively short, somewhat longer than <i>M</i> . Distribution of the parts of fila- ments compare <i>M</i> (Tab: 2).	<i>M B m b</i>
?	narrow short	very short	narrow long	fertile; reach to the aboral end. Distribution of the regions of filaments?	<i>M B m b</i>
?	short	distinct	narrow long	fertile; reach to the aboral end. Distribution of the regions of filaments?	<i>M B m b</i>
?	.	?	?	fertile? not reaching to the aboral end. Di- stribution of the regions of filaments?	?
?	absent?	?	short	fertile? very long, reach to the aboral end. Distribution of the regions of filaments?	<i>M B m b</i>
narrow; 4 mes.	short	distinct, but filamentous	narrow long	fertile, reach to the aboral end; <i>fl</i> rather short, <i>c</i> well developed. <i>nd</i> feeble, threadlike; long craspedion region with one threadlike cras- pedoneme.	<i>m B M b</i>
exceedingly broad 8-10 mes.	very long and broad with ciliated tract	absent	very short	sterile, a little longer than hyposulcus <i>fl</i> long, craspedia region shorter, <i>nd</i> absent.	<i>M B m b</i>
exceedingly broad 8-10 mes.	very long and broad with ciliated tract	absent	absent	almost of the length of the hyposulcus; for the rest as <i>A. oligopodus</i> .	<i>M B m b</i>
narrow; 4-6 mes.	very long and broad with ciliated tract	absent or very short	very short or absent	rather long, <i>fl</i> and <i>nd</i> about equally developed.	<i>M B m b</i>
very broad; 6-8 mes.	very long and broad with ciliated tract	absent	narrow long	sterile, somewhat longer than the directive mesenteries. <i>fl</i> long, <i>nd</i> rather well de- veloped.	<i>M B m b</i>
very narrow; 2 mes.	very short	very short	very short	fertile, reach to the aboral end, longer than <i>M</i> <sub>1</sub> ; <i>nd</i> developed as by <i>M</i> <sub>1</sub> .	<i>M B m b</i>
rather broad; 8 mes.	narrow short	distinct	narrow long	sterile? long, but somewhat shorter than <i>M</i> <sub>1</sub> .	<i>M b m B</i>

	The length of the metamesenteries in relation to each other and to the length of the column counted from the aboral end of the stomatodaeum to the aboral pole	The length of the ciliated tract on <i>M</i> and <i>m</i> .	The structure of the ciliated tract
Family 1. Cerianthidae.			
<i>Pachycerianthus solitarius</i> (Rapp.)	distinct difference between <i>M</i> and <i>m</i> and between <i>B</i> and <i>b</i> . The longest <i>M</i> reach almost to the aboral pole.	reach almost to the aboral ends of the mesenteries.	type 2 <sup>2)</sup>
» <i>aestuarii</i> (Torr. a. Kleeb.)	little difference between <i>M</i> and <i>m</i> which reach to the aboral pole. <i>B</i> and <i>b</i> very short.	?	?
» <i>johnsoni</i> (Torr. a. Kleeb.)	rather great difference between <i>M</i> and <i>m</i> ; <i>M</i> <sub>1</sub> reach to the aboral pole; most of <i>M</i> <sup>1</sup> / <sub>2</sub> of the length of the column <sup>1)</sup> .	long	?
» <i>fimbriatus</i> Mc. Murr.	<i>M</i> <sub>1</sub> reach to the aboral pole, the other <i>M</i> and <sup>2</sup> / <sub>3</sub> and on <sup>1</sup> / <sub>3</sub> of the length of the column <sup>1)</sup> . <i>B</i> and <i>b</i> short unequal in length.	<sup>1</sup> / <sub>4</sub> of the length of the column <sup>1)</sup> .	type 2
» <i>multiplicatus</i> Carlgr.	<i>M</i> reach to the aboral pole, <i>m</i> short about of the length of the <i>P</i> <sub>2</sub> ; <i>B</i> and <i>b</i> short.	reach about to the aboral ends of the mesenteries.	type 2
» <i>monostichus</i> Mc. Murr.	<i>M</i> reach to the aboral pole, the other mesenteries short.	?	?
» <i>benedeni</i> Roule	<i>M</i> <sub>1</sub> reach to the aboral pole. The others short.	?	?
» <i>maua</i> (Carlgr.)	<i>M</i> <sub>1</sub> , <i>M</i> <sub>2</sub> and <i>M</i> <sub>3</sub> on the right side and <i>M</i> <sub>1</sub> and <i>M</i> <sub>2</sub> on the left longer than the other <i>M</i> , which are <sup>1</sup> / <sub>2</sub> as long as the column <sup>1)</sup> . <i>m</i> much shorter than <i>M</i> .	reach on <i>M</i> to the aboral ends of the mesenteries, on <i>m</i> not as long.	type 2
<i>Cerianthus membranaceus</i> (Spall.)	<i>m</i> about as long as <i>M</i> . <i>M</i> <sup>1</sup> / <sub>3</sub> of the length of the column.	reach almost to the aboral ends of the mesenteries.	type 2
» <i>lloydii</i> Gosse	<i>m</i> and <i>M</i> about the same length, reach to the aboral pole.	rather long but short in comparison to the length of the mesenteries.	type 2
» <i>vogti</i> Dan.	as the former.	long almost as the former.	type 2
» <i>valdiviae</i> n. sp. Carlgr.	little difference in length between <i>m</i> and <i>M</i> . <i>M</i> <sup>1</sup> / <sub>3</sub> of the length of the column <sup>1)</sup> .	rather long but less than <sup>1</sup> / <sub>2</sub> of the length of the mesenteries <sup>1)</sup> .	type 2
» <i>ambonensis</i> Kwietn.	difference in length between <i>M</i> and <i>m</i> resp. <i>B</i> and <i>b</i> distinct but not great. <i>M</i> <sup>5</sup> / <sub>7</sub> , <i>B</i> <sup>1</sup> / <sub>7</sub> of the length of the column <sup>1)</sup> .	?	?
» <i>sulcatus</i> Kwietn.	like the former; the mesenteries though somewhat shorter	?	?
» <i>taedus</i> Mc. Murr.	do not reach to the aboral pole.	?	?
» <i>borealis</i> Verr.	great difference in length, <i>M</i> reach to the aboral end, <i>m</i> are half the length of the column <sup>1)</sup> .	?	type 2?
<i>Ceriantheopsis americanus</i> (Verr.)	great difference in length between <i>M</i> and <i>m</i> little difference between <i>B</i> and <i>b</i> , the longest <i>M</i> reach to the aboral pole. <i>M</i> increase in length towards the chamber of multiplication with many interruptions.	rather short	type 2
Family 2. Acontiferidae.			
<i>Arachnanthus oligopodus</i> (Cerf.)	fairly distinct difference in length between <i>M</i> and <i>m</i> .	on the longest mesenteries almost the same length as the hyposulcus	type 1
» <i>sarsi</i> Carlgr.	distinct difference in length between <i>M</i> and <i>m</i> .	almost the same as the former	type 1
( <i>Arachnactis albida</i> Sars)	like the former	like the former	type 1
( » <i>lobiancoi</i> Carlgr.)	fairly distinct difference in length between <i>M</i> and <i>m</i> .	long, reach almost to the aboral ends of the mesenteries	type 1
Family 3. Botrucnidiferidae.			
<i>Botrucnidifer norvegicus</i> Carlgr.	The longest <i>M</i> end some way from the aboral pole. Distinct difference between <i>M</i> and <i>m</i> and between <i>B</i> and <i>b</i> . <i>B</i> and <i>b</i> long.	on the longest mesenteries somewhat longer than the length of the stomatodaeum	type 3
<i>Botruanthus benedeni</i> (Torr. a. Kleeb.)	Distinct difference between <i>M</i> and <i>m</i> . <i>M</i> and <i>m</i> reach almost to the aboral pole ( <i>B</i> and <i>b</i> of different length, short).	?	?

<sup>1)</sup> The length of the mesenteries and of the column is always in these tables counted from the aboral end of the stomatodaeum to the

Craspedonemes of the ciliated tract	Bunches of craspedonemes in the ciliated tract	Cnido-glandular tract on <i>M</i> and <i>m</i>	Region of the craspedion (Filamentchen.)	"acontia"	botrucnidae
absent	absent	as a single craspedoneme at the aboral end of the mesenteries	absent	absent	absent
absent	absent	?	?	absent	absent
on <i>M</i> and <i>m</i> , on <i>m</i> concentrated somewhat just below the lower limit short, on the whole length of <i>M</i> and <i>m</i> , few on <i>B</i> and <i>b</i>	at the aboral ends of <i>B</i> and <i>b</i>	?	?	absent	absent
numerous, broad along almost the whole length of <i>M</i> and <i>m</i> .	very feeble on <i>M</i> and <i>m</i>	?	probably present	absent	absent
one <i>M</i> and <i>m</i> , not however in the region of the gonads.	on all mesenteries excepting the directives. The craspedonemes not closely packed	very short on <i>M</i> somewhat stronger on <i>m</i> , at the aboral end of the mesenteries	absent	absent	absent
on <i>B</i> and <i>b</i> ?	?	?	?	absent	absent
on all metamesenteries; well developed on <i>M</i> ; the most aboral craspedonemes of <i>M</i> only on the one side with filament	on <i>M</i> ; the craspedonemes not closely packed	absent on <i>M</i> , probably also on <i>m</i>	present on <i>m</i>	absent? absent	? absent
On the second and third <i>P</i> and on <i>B</i> ; on the other metamesenteries concentrated in bunches	on all metamesenteries and on <i>P</i> <sub>2</sub> , craspedonemes on <i>M</i> closely packed	very short on <i>M</i> , somewhat stronger on <i>m</i> at the aboral ends of the mesenteries	absent	absent	absent
absent	absent	as one well developed craspedoneme at the aboral parts of the mesenteries	very long on <i>M</i> and <i>m</i> and on <i>P</i> <sub>2</sub>	absent	absent
absent	absent	not strong development almost the same as on <i>B</i> and <i>b</i> in the oral parts of the mesenteries	long on <i>M</i> and <i>m</i> long more than 1/3 of the length of the mesenteries on <i>M</i> , <i>m</i> and <i>P</i> <sub>2</sub>	absent absent	absent absent
absent	absent?	?	?	?	absent
on the whole length of the <i>P</i> <sub>2</sub>	absent?	?	?	?	absent
?	?	?	?	?	?
?	?	?	?	?	?
On all metamesenteries	in the aboral end of the ciliated tract; the craspedonemes not closely packed	threadlike on <i>M</i> , somewhat stronger developed on <i>m</i> in the oral part of the mesenteries	very long on <i>M</i> , <i>m</i> and <i>P</i> <sub>2</sub> ; on the longest of these the craspedion forms one craspedoneme	absent	absent
absent	absent	absent	very long, in the oral part divided into 2 streaks	present on <i>M</i> <sub>1</sub> , sometimes on <i>m</i> <sub>1</sub> , endoderm without many nematoc.	absent
absent	absent	absent	very long, probably as the former	present on <i>M</i> <sub>1</sub> ; endoderm without numerous nematocysts	absent
absent	absent	absent	long, in the oral part divided into 2 streaks	present on <i>M</i> <sub>1</sub> endoderm without numerous nematocysts	absent
absent	absent	absent	on <i>M</i> and <i>m</i> but very short	present on <i>M</i> <sub>1</sub> endoderm with numerous nematoc.	absent
absent	absent	development almost the same as on <i>B</i> and <i>b</i>	very long on all mesenteries excepting the directives between <i>nd</i> and the botrucnids	absent	present on all mesenteries excepting the directives, on the aboral end of each mes. present, scattered on craspedonemes and on bunches of craspedonemes on <i>M</i> and <i>m</i> (also on <i>B</i> and <i>b</i> ?)
on all mesenteries except on the directive mesenteries	a compact bunch on each mesentery of <i>M</i> and <i>m</i> just below the aboral end of the coiled mesenterial filaments (cnido-glandular streaks?) of the shorter mesenteries	compare bunches!	?	absent	

aboral pole.

2) Concerning the types compare Section 4.

Finally I give p. 44—47 in tabular form a synopsis of those morphological facts in the adult Ceriantharia, which have been more thoroughly studied anatomically, and may now be grouped fairly correctly in their systematic relations. The species I have had occasion to examine are distinguished by spaced type. The species of *Arachnactis* of which I have given a detailed account are also included in the table subjoined. As appears from these, there is still a good deal to be added from an anatomical point of view before several of these species can be characterized quite satisfactorily. As the species I have myself investigated have been treated throughout in the same way, the anatomical account of them is more complete than in the case of the others, whose organisation I have built up from the accounts of publications, whose statements on the homology of the mesenterial appendages in particular, are often very obscure.

## Section IV.

### On the morphology of the Ceriantharia.

Since in my opinion the morphology of Ceriantharia, in spite of the researches of various investigators, is still inadequately worked out, I give here a general survey of the most important of the morphological facts found within this group of animals. In this survey I take account principally of such organs as shew more or less variation of structure and arrangement in the different species, and for that reason are of service for purposes of classification. In the following comparative view of the morphology I have chiefly taken into consideration such species as I have myself investigated. Above all I have treated in special detail the mesenterial filaments and their appendages, which in Ceriantharia present a very different appearance and structure in the different species.

#### I. Arrangement of the tentacles.

The tentacles in Ceriantharia are arranged, as is well known, not only marginal but also labial. The arrangement of these tentacles differs according to the size of the species and according to age. The simplest grouping is found in the small species *Arachnanthus oligopodus* (and *sarsi*?) and in *Botrucnidifer norvegicus*, where the labial tentacles are arranged in a single row, which is also the case with the marginal tentacles of the former. In larger species as in *C. membranaceus*, *lloydii*, *P. multiplicatus*, they are arranged in three or four cycles. As a typical arrangement in a larger species may be taken the grouping in *C. membranaceus*. That this arrangement only appears late in the course of the development, may be seen in *C. lloydii*, very young specimens of which only have the tentacles arranged in a row. In larger specimens on the other hand three, and in larger still, four cycles are found. It clearly follows from this, that the tentacle arrangement in the same species may alter and that rearrangements in the form of displacements take place during growth. In particular the zone about the directive chamber, where the tentacles as a rule shew a different arrangement from nearer the multiplication chamber, is remarkable for somewhat variable tentacle attachments. In the main however the grouping of the tentacles in the larger specimens is similar. Yet it is noticeable that certain labial tentacles

may occasionally be absent. This is often the case with the directive (median) labial tentacle, which is absent in *Cerianthus lloydii*, *valdiviae*, *Pachycerianthus multiplicatus*, *maua*, *Arachnanthus oligopodus*, *sarsi*?, *Arachnactis lobiancoi*, *Botrucnidifer norvegicus*, whilst it is found in *Cerianthus membranaceus* and *vogti*, *Pachycerianthus solitarius* and *Ceriantheopsis americanus*. In *Botrucnidifer norvegicus*, *Cerianthus vogti* and probably also in *Pachycerianthus multiplicatus* and *Arachnanthus sarsi*, the chamber contiguous to the directive chamber on either side of the animal is without a labial tentacle. Irregularities in the tentacle arrangement occur not infrequently, and this is specially true of *P. solitarius*. Probably we have here disturbances of growth, as they are accompanied by irregularities also in the arrangement of the mesenteries. Where to look for the cause of these disturbances, I cannot at present tell. Sometimes the tentacles are lacking in adult animals, as in *C. lloydii* and *A. sarsi*, or else are very small. In that case the animals are in a state of regeneration, the upper end of the animal having been torn off. Danielssen has not taken account of this in describing *C. borealis* (= *C. lloydii*), nor has Mc. Murrich (1893) in his description of *Cerianthus vas*.

The tentacle arrangement in Ceriantharia is related for the most part to the size of the animal. In no case however have more than 4 cycles been observed.

## 2. Stomatodaeum, siphonoglyph, hyposulcus and hemisulci.

The stomatodaeum shews a like structure in almost all the adult Ceriantharia which I have examined. The ectoderm forms high longitudinal ridges, which in the oral portion of the stomatodaeum are not supported by mesogloal ridges, but in the aboral portion are found covering such ridges. In the oral portion of the stomatodaeum, there is no great difference in structure between the ectoderm on the longitudinal ridges and that in the furrows; in the aboral portion where mesogloal ridges are found and where in consequence the ridges are considerably higher and the furrows deeper, the structure of the ectoderm in the ridges and in the furrows is different. The ectoderm lining the furrows consists chiefly of supporting cells, which at the point where the passage into the filaments occurs acquire very long cilia. On the other hand in the ectoderm of the ridges, in addition to supporting cells, are found numerous mucus cells and both spirocysts and thick-walled nematocysts, the last of the same appearance as in the cnido-glandular tract (for details see p. 15).

An exception to this rule is shewn by the two representatives of the genus *Arachnanthus*, *A. oligopodus* and *sarsi*. In this genus no mesogloal ridges are found in the stomatodaeum, in other words the longitudinal ridges of the stomatodaeum are formed exclusively of ectoderm, and the difference too in the histological structure of the furrows and ridges is insignificant.

The siphonoglyph in the Ceriantharia is more or less developed. It is characteristic of the Ceriantharia that almost always a number of mesenteries besides the directives are attached to the siphonoglyph. In *Botrucnidifer norvegicus* only the directive mesenteries are attached to the siphonoglyph. In all representatives of the genus *Cerianthus* and in *Ceriantheopsis* the siphonoglyph is not very broad though at least 4 mesenteries are attached to it. In the genus *Pachycerianthus* it is broader as a rule, and sometimes, in *P. aestuarii*, (according to Torrey and Kleeberger's account) may become quite broad, seeing that no less than 16 mesenteries are there found united with the siphonoglyph. In relation to the size of the body and the total number of mesenteries the siphono-

glyph is broadest in the genus *Arachnanthus*, in that almost half the total number of mesenteries (8—10) join on to the siphonoglyph.

The ectoderm of the siphonoglyph contains, besides strongly ciliated supporting cells, mucus cells in great abundance. As a rule these mucus cells are most numerous at its boundary with the stomatodaeum. Sometimes as in *Cerianthopsis americanus* the mucus cells are spread almost uniformly over the whole surface of the siphonoglyph. Here and there nematocysts occur, but always in small numbers.

The hyposulcus as a rule is rather short. In *Pachycerianthus aestuarii* it is however rather well developed (Torrey and Kleeberger 1909, fig. 1). It is still longer in the genus *Arachnanthus*, where it is longer than the stomatodaeum itself. The ectoderm of the hyposulcus is provided with fewer mucus cells than that of the siphonoglyph, which is the reason why more supporting cells occur in it than in the other. In other respects its structure agrees with that of the ectoderm of the siphonoglyph. In the genus *Arachnanthus* as also in the larval genus *Arachnactis*, the hyposulcus is provided along its free sides with filament differentiations (compare p. 36 and Carlgren 1912, p. 364, 371).

The hemisulci are unequally developed. Whilst they are absent in the genus *Arachnanthus* and rudimentary in *Botrucnidifer*, in the rest of the species examined by me they are more or less distinctly developed. In *P. solitarius* and *multiplicatus* and in *C. lloydii* they correspond in structure and in appearance. Their outline is rounded in transverse section and calls to mind a transverse section of an undivided median streak, though they are not so sharply distinguished from the mesenteries as these (compare fig. 4, Pl. 1). Their structure corresponds with that of a median streak, that is, there are mucus cells and for the most part numerous spirocysts also. In *C. membranaccus* the structure deviates to some extent from the above. Lengthwise the hemisulci are very elongated flattened, and are connected with one border of the directive mesenteries. They are strongly ciliated like the siphonoglyph and contain chiefly supporting cells, whilst the mucus cells, thick-walled nematocysts and spirocysts are sparse. The hemisulci in *Cerianthopsis americanus* (fig. 4, Pl. 5) occupy an intermediate position between those already mentioned. On the homology of the hemisulci and hyposulcus with the filaments I may refer to page 63.

### 3. Arrangement of the mesenteries and the reproductive organs.

The arrangement of the mesenteries varies a good deal in different species, though a definite scheme of their arrangement may always be discovered even if the regular arrangement is again and again interfered with. In *P. solitarius* especially such disturbances are very common and might almost obscure the typical arrangement (Carlgren 1912 text-figure 4 a, b) but in other species also, as in *P. multiplicatus* and *Botrucnidifer norvegicus*, irregularities in the arrangement present themselves. At any rate in *P. solitarius* the irregularities in the grouping of the mesenteries are connected with an irregular development of the tentacle cycles. As to the number of the primary mesenteries, the protomesenteries, my views coincide completely with van Beneden's. The first three mesenteries on either side of the directive plane are in my opinion protomesenteries; the metamesenteries therefore begin with the fourth couple. Below I give the precise grounds for this opinion of mine.

The length and structure of the different mesenteries vary considerably in Ceriantharia. The directive mesenteries are always sterile and as a rule without special differentiation of the filaments (see p. 50), the remaining mesenteries may be distinguished as fertile and sterile in regular alternation. A division into mesenteries bearing filaments and mesenteries bearing sexual organs, such as A. von Heider (1879) made, is absolutely untenable. O. and R. Hertwig maintained already, that the term "Filamentsepta" was not appropriate, as the fertile mesenteries also bear filaments. If this declaration was already justified at a time when knowledge of the filaments was so imperfect, such a division is still less defensible after my account of the filaments below has been made public, for we do not really find as a rule, with reference to the filaments on sterile and fertile mesenteries, any fundamental difference but merely one of degree. For both a ciliated tract region (spirocyst-glandular tract with ciliated tracts) and cnido-glandular tract region are found in general alike on the sterile and the fertile mesenteries. An exception however to this rule occurs in the genus *Arachnanthus* and also, it seems, in *P. maua*. O. and R. Hertwig further give expression to the conjecture that possibly the sterile<sup>1)</sup> mesenteries also become fertile later on. This is not the case however. Still the fact must be emphasised that the difference between the mesenteries is not so sharp, if irregularities occur in the arrangement of the mesenteries. Such is the case, for instance, in *P. solitarius*, in which small but fertile mesenteries bear very wavy cnido-glandular tract regions and so have a character approximating to the sterile mesenteries (Carlgren 1912 textfig. 4 a).

Protomesenteries 2, the second couple reckoning from the directive plane are either sterile or fertile; in the first case they resemble in point of length and structure the metamesenteries of the third and fourth cycles. If on the other hand they are fertile they agree with the metamesenteries of the first and second cycles. Fertile protomesenteries characterise the genera *Cerianthus*, *Ceriantheopsis* and *Botrucnidifer*, sterile the genera *Pachycerianthus*, *Arachnanthus* (and *Botruanthus*?)

Protomesenteries 3 which are immediately adjacent to the first metamesenteries, are always sterile and resemble structurally the metamesenteries of the third and fourth cycles.

The metamesenteries (= deuteromesenteries) as is already known are more or less clearly arranged in 4 cycles (Faurot). Reckoning from the directive chamber we find usually a mesentery of the 1st cycle (*M*), next comes one of the third (*B*) which together form a macrobimesentery (macrobisepium van Beneden): then comes a mesentery of the 2nd cycle (*m*) and one of the fourth (*b*) which together form a microbimesentery (microbisepium van Beneden). Exceptions to the rule are *Ceriantheopsis americanus* and *Botruanthus* (see below). These four metamesenteries form the first quartette (Faurot): then follows a second quartette, a third, and so on, which as a general rule become shorter the more they approach the multiplication chamber lying directly opposite the directive chamber.

As a type for the arrangement of the quartettes, it has been customary to take *C. membranaceus*, the species in which the quartette arrangement was first observed by Faurot (1891). A gradual

<sup>1)</sup> Mc. Murrich (1910 p. 28) mentions, that in *C. ambonensis* all metamesenteries are fertile. This would be a very singular thing, if such were really the fact, in which case it would surely be necessary to set up a new genus — although Mc. Murrich does not find it necessary. It must be noticed however, that both the specimens examined were in a very bad state of preservation, so that it is necessary to get this statement confirmed before removing the species from the genus *Cerianthus*. Possibly there may be only a question of such irregularities as are found in *P. solitarius*.

diminution in the length of the quartettes no doubt takes place, but this diminution is not regular as I have shewn in another paper (1912): here and there a break occurs, so that a quartette lying nearer the directive chamber may be less developed than one situated further away. Thus the fifth quartette is considerably longer than the fourth and provided with longer ciliated tracts, the 7th longer than the 6th. The 9th longer than the 8th. An indication that a similar relation also exists between the 2nd and 1st quartettes, appears from the fact that the metamesenteries of the 3rd cycle, in the 2nd quartette at least, are at least as long as and provided with longer ciliated tracts than the corresponding mesenteries in the first quartette. So great a departure<sup>1)</sup> as this of *C. membranaceus* from the normal decrease in length of these mesenteries as they approach the multiplication chamber, I have not discovered in any other Ceriantharium, although in several species (*C. lloydii*, *P. multiplicatus*, *solitarius*, *Botrucnidifer norvegicus*) the mesenteries of the third cycle in the second quartettes are better developed than the corresponding mesenteries in the first. That here the same relation is not met with in the case of the metamesenteries of the 6th, 7th and 8th quartettes is doubtless connected with the fact that several of the above species have a smaller number of mesenteries, and perhaps also with the fact that, as in *P. multiplicatus* for example, so little difference is found between the mesenteries in the first and second, or the third and fourth quartettes. In several species too such as *C. valdiviae* the arrangement of the mesenteries in quartettes is not clearly marked. Since this arrangement in quartettes is so indistinct in many species, it is quite probable that it is a later acquisition of the Ceriantharia and not an original character. Of like import too is the circumstance that the tentacle cycles and the mesenteries in younger individuals have a simpler arrangement than in the fully grown. In such circumstances the quartette arrangement would not prove to have any significance for the ascertainment of the affinities of Ceriantharia with other Anthozoa (see Faurot's paper 1891 p. 66 which compares the quartette arrangement in Ceriantharia with the arrangement of septa in Rugosa).

A peculiar arrangement of the mesenteries in *Ceriantheopsis americanus* has been described by Mc. Murrich (1910) — the results of whose researches I can confirm. (For some minor divergencies from Mc. Murrich's account I refer to the description of the species p. 24). It is not merely that the metamesenteries in every quartette have a different arrangement from the normal in Ceriantharia, since in every quartette we find first a mesentery of the 2nd cycle (*m*) followed by one of the third (*B*) then one of the first (*M*) and lastly one of the 4th (*b*) — but the metamesenteries of the first cycle increase in length towards the multiplication chamber though with several breaks as in *C. membranaceus*. The other cycles of mesenteries up to the fourth inclusive on the contrary diminish as they near the multiplication chamber, with the possible exception of the second cycle.

Finally we must mention a third kind of quartette arrangement based on Torrey and Kleeberger's figure of *Botruanthus benedeni*. Here in each quartette the metamesenteries occur in the following order. In the first place a mesentery of the first cycle, next one of the fourth, then one of the second, and lastly one of the third cycle. That is, the mesenteries of the third and fourth cycles have changed places, so to speak, provided that Torrey and Kleeberger's observations are correct.

<sup>1)</sup> According to Torrey and Kleeberger's figure of *C. johnsoni* a similar break appears to take place at the third quartette in this species also, and Mc. Murrich's figure of *Pachycerianthus jimbriatus* shews that a break occurs at the 7th quartette.

Reproductive organs: All the Ceriantharia which I have examined are hermaphrodite. This seems corroborated by the published accounts of other Cerianthida. It should be mentioned however, that Danielssen speaks of *C. borealis* (= *C. lloydii*) as being bi-sexual. Mc. Murrich (1891, 1910) also says that the ovaries and testes are allotted to separate individuals in the case of *C. americanus* and *Pachycerianthus fimbriatus*. I cannot confirm these statements in the case of *C. borealis* and *C. americanus*: both species are hermaphrodite. I have examined several individuals of both these species, and testes and ovaries were always found in the same specimen though not always in the same proportions. Lastly there is *Pachycerianthus fimbriatus*, apparently an exception to the rule. But most likely this species is also hermaphrodite. For I hold it probable that in certain species the different gonads are not mature at the same time, in other words that certain Ceriantharia at least are proterandrous hermaphrodites. The distribution of the sex-organs on the different mesenteries has been treated above.

#### 4. The mesenterial musculature.

It is well known that previous investigators of the mesenterial musculature of Ceriantharia, such as the brothers Hertwig, A. von Heider, Mc. Murrich, Boveri and others have expressed the most different opinions concerning the arrangement of this musculature (compare Carl-gren 1893 and van Beneden 1898). In a treatise published in 1893 I shewed however that in *Cerianthus lloydii*, *membranaceus* and *solitarius* and in an unnamed Cerianthid from Greenland (= *Cerianthus lloydii*) the mesenteries at the level of the oral portion of the stomatodaeum bore longitudinal muscles on the side looking away from the directive chamber, whilst the opposite side facing the directive chamber had transverse muscles. Only the directive mesenteries seemed to deviate from the rule, in as much as their very feebly developed muscles take a more slanting course, more transverse in the upper parts of the mesenteries, mostly longitudinal in the lower parts (p. 242 l.c.). Van Beneden (1898 p. 28) confirmed the arrangement of the musculature in this way in *C. lloydii*, and Cerfontaine (1909) in *Arachnanthus oligopodus*. The former however could not find any muscles on the directive mesenteries, whilst the latter was able to certify, in the species dealt with, the same arrangement of the musculature on the directive mesenteries as on the others. In the larval forms, on the contrary, van Beneden could not discover any definite arrangement of the mesenterial musculature; it varied so much, that v. Beneden came to the conclusion that there was nothing constant in the arrangement of the mesenterial musculature in Ceriantharia, unless it were the absence of a musculature on the directive mesenteries (p. 155). In the year 1900 I refuted van Beneden's contention that the directive mesenteries in this group of animals are without musculature and established the existence of the same arrangement of the mesenterial musculature in *C. maua* as in *C. lloydii* (I had not however investigated the directive mesenteries). Having now examined not only *A. oligopodus* but a number of other Ceriantharia here described (see tables) which are representative of Ceriantharia with "acontia", of those with botrucnidae and of those devoid both of "acontia" and botrucnidae, and having found a similar arrangement of the mesenterial musculature on all non-directive mesenteries, it seems to me in the highest degree probable that all adult Ceriantharia have the mesenterial muscles arranged in like manner. The longitudinal muscles are situated on the side of the mesenteries looking away from the directive chamber, the transverse muscles on the side facing it

As regards the directive mesenteries, it is no doubt true that their musculature is usually very indistinct, still I believe that there will be no danger of going very far wrong if we assume the same arrangement of musculature as original for these mesenteries also. Cerfontaine certainly states, that the muscles on the directive mesenteries in *A. oligopodus* have the same orientation as on the rest of the mesenteries. Further I have found the same arrangement in the well known Ceriantharian larval form *Arachnactis albida* (fig. 8, pl. 5). The same seems also to be the case in *C. valdiviac* and in the hemisulcus region of *P. solitarius*.

It still remains to be explained, why van Beneden in the case of larval forms of Ceriantharia<sup>1</sup>) found a different arrangement of the mesenterial musculature from that above described. It may possibly be, that with the growth of the larval forms the direction of the musculature shifts, and that the transverse muscles are relatively late in appearing. Though such an explanation is not excluded, still I think that we need not have recourse to such an hypothesis. It is more likely that van Beneden made a mistake, which is very easy, seeing that the mesenterial muscles are extremely faint in the larval forms. Has not the arrangement of the mesenterial musculature in adult Ceriantharia, whose musculature is many times better developed than in the larval forms, given rise to controversy, and that for the reason that most observers have taken contracted specimens, where it was a difficult matter to establish the direction of the muscles on mesenteries more or less folded!

### 5. Orientation of body.

In my above mentioned work (1893 a, p. 246) I urged that owing to the arrangement of the mesenterial musculature described above, which I compared with that of other Anthozoa, we must take the view that the directive mesenteries in Ceriantharia are dorsal directives, and that the siphonoglyph joining these is a dorsal siphonoglyph, whilst the Zoantharia in contrast to the Ceriantharia are provided with ventral directive mesenteries and a ventral siphonoglyph. I dwelt also on the fact that on this assumption not only the single multiplication zone of the mesenteries of Ceriantharia but also the two similar zones of Zoantharia will be situated in the ventral (posterior) portion of the body. Whilst some investigators such as Duerden (1902 p. 444) have accepted my terminology, others, like van Beneden (1898) and Mc. Murrich (1910), have not adopted it.

To begin with a criticism of van Beneden's view of the homology of the siphonoglyphs and directive mesenteries, I have to insist that van Beneden in the work cited — as far as I can see — forgets in one place what he has affirmed in another, with the result that he has involved

<sup>1</sup> Boveri (1889) in a young specimen described by him as a Cerianthid larval form at an 8-mesentery stage, found a mesenterial musculature arranged as in the genus *Edwardsia* — an observation which Mc. Murrich has made use of to support his view of the orientation of the body. Van Beneden has already questioned the ascription to the Cerianthidae of the larval form reproduced by Boveri in fig. 2, Plate 2, (1889). I can myself subscribe to the view of van Beneden the more heartily, for the reason that a transverse section of this globular form does not at all suggest a section of a Ceriantharian larval form but resembles an Actiniarian form, in as much as the filaments in this case are among other things about equally developed on all the mesenteries. As we know that the hemisulci answering to the filaments on the directive mesenteries are not so sharply marked off as the filaments and all filaments are alike, it follows indisputably that Boveri was mistaken in his identification of this larval form. On the other hand, the remaining larval forms described by Boveri with the exception of the young specimen reproduced in fig. 7, Plate 21 are Cerianthidae. As the arrangement of the musculature on the mesenteries and the presence of two couples of directive mesenteries are the characteristic marks of the *Edwardsia* stage of development, and not the order in which the mesenteries first appear, all ground disappears for holding that Ceriantharia pass through an *Edwardsia* stage of development.

himself in manifest contradictions. On page 12 (1908) he says "J'appelle (in Ceriantharia) antérieure l'extrémité de l'actinostome que les actinologistes ont appelée ventrale; elle est caractérisée par la présence du tentacule marginal médian, de la loge directrice et du sillon actinopharyngien, que je désigne, avec Haddon sous le nom de sulcus. J'appelle postérieure la commissure buccale qui répond à la loge de multiplication, toujours dépourvue de tout tentacule, appelée dorsale par les auteurs récents". On page 196 speaking of Zoanthidae he calls the directive chamber by which the siphonoglyph is situated, the anterior: "Dans les deux larves l'incurvation est telle que la concavité de la courbe répond à la face antérieure, c'est à dire à la loge directrice". He thus makes homologous to each other the siphonoglyph and directive mesenteries which are disparate in Ceriantharia and Zoantharia, and considers them to be ventral or anterior. On page 165 van Beneden maintains another view. After insisting that the mesenterial musculature in Ceriantharian larval forms is by no means uniformly arranged (see mesenterial musculature) he continues "Rien ne prouve donc que l'hypothèse de Carlgrèn soit fondée et il n'existe actuellement aucune donnée qui nous permette d'affirmer l'homologie du sulcus des Cérianthides avec la rainure actinopharyngienne, dite ventrale, des Zoanthes et des Hexactiniens". Here then all homology is denied between the siphonoglyph of Ceriantharia and that of Zoantharia. With the latter statement the following remark of van Beneden is also in conflict (p. 164). "Il en résulte que la partie du corps qui prend naissance (in Zoantharia) dans la seconde période se forme par opposition, non pas d'arrière en avant, comme chez les Cérianthides, mais d'avant en arrière".

It is clear that we cannot call the siphonoglyph of the Cerianthidae, sulcus, if we maintain the view, that no homology exists between the siphonoglyph of the Cerianthidae and that of Zoanthidae or the ventral one of Actiniaria (Hexactiniae), for by denominating the siphonoglyph of Cerianthidae sulcus and not sulculus, we ipso facto make the siphonoglyph of Cerianthidae homologous with the siphonoglyph of Zoanthidae and with the ventral one of Actiniaria. For we must remember that the actinologist who introduced the designation sulcus into the terminology of the Anthozoa, namely Haddon, applied the term sulcus to the so-called ventral siphonoglyph of Actiniaria (Hexactiniae), and the term sulculus to the so-called dorsal one of that group. If then we deny all homology between the siphonoglyph of Cerianthidae and either of the siphonoglyphs of Actiniaria, we naturally cannot call the siphonoglyph of Cerianthidae either sulcus or sulculus.

Now it is very probable that the directive plane is similarly situated in all Anthozoa, because the Anthozoa, as far as our knowledge goes, are a very homogeneous group. If then we take the directive plane as the basis of orientation, we have to determine how far the directive mesenteries in Ceriantharia are ventral or dorsal, or, in other words, how far the single siphonoglyph in this case is ventral, and therefore a sulcus, or how far it is dorsal, and therefore a sulculus. To answer this question, we can only make use — as far as I can make out — of the anatomy and the development of the mesenteries, for the physiological orientation of the siphonoglyph to the bottom gives us no fixed standpoint for judging of the homology.

To take first the morphology of the mesenteries, the disposition of the mesenterial musculature plays, as is well known, an essential part in the orientation of the mesenteries of Actiniaria and other Anthozoa, as in the 8-mesentery stage the longitudinal musculature of the mesenteries on either side

of the directive mesenteries is turned away from the directive couple, named dorsal but turned towards the ventral directives. If then we find the orientation of the Ceriantharia from the mesenterial musculature (see above, mesenterial musculature) everything tells in favour of the view that the directive mesenteries of the Cerianthidae — as I have already urged (1893) — are dorsal directives and that the siphonoglyph is a dorsal siphonoglyph, in other words, a sulculus. If on the other hand we suppose the siphonoglyph here to be a sulcus, the disposition of the musculature of the non-directive mesenteries would prove to be quite the reverse of that of all the other Anthozoa.

Granted that the arrangement of the musculature is distinctly in favour of the view which I defend, the case is not so clear at first sight with the arguments from embryology. It is well known that different investigators such as Mc. Murrich, Boveri, and in recent years Kingsley<sup>1)</sup> (1904, p. 349—351) have endeavoured to determine the homology of the mesenteries in the different groups of Anthozoa by the order in which they first appear. That is, by examination of various but usually only isolated stages of development, and very largely by means of the order in which the filaments appear, they have believed they could prove, that the appearance of the first 8 mesenteries in Actiniaria (Hexactiniae) and Madreporaria follows a fixed rule. Mc. Murrich (1891) also, from the difference in size of the mesenteries in a Ceriantharian larval form, *Arachnactis*, in the 8-mesentery stage, drew the conclusion that the first 8 mesenteries in Ceriantharia, Actiniaria and Madreporaria alike were developed in the same order and that the first 8 mesenteries occupy the same position in all three groups, if the orientation of Ceriantharia is such that the siphonoglyph answers to the ventral siphonoglyph of the other two groups. This view seemed soon after to gain confirmation, when van Beneden (1891) shewed in a series of stages of development of *Arachnactis*, that the development of the first 8 mesenteries in this larval form took place in the same order as in Actiniaria as a rule, though some differences in the first formation of the chambers (loges) could be shewn to occur, differences conditioned in part by the form of the stomatodaeum in the earliest stages. According to this then, if we were to base the orientation of the body on the order of appearance of the first 8 mesenteries, the directive mesenteries of Ceriantharia would be ventral.

But more recent and thorough investigators of the development of Actiniaria can lend Mc. Murrich and Boveri's views no stronger support than the discovery of a great variability in the order of appearance of the earliest mesenteries in this group. Even earlier some investigators (Lacaze-Duthiers 1872 and Wilson 1888) had pointed out various irregularities in the development of the mesenteries, such as the occurrence of mesenteries 2 in the place where mesenteries 4 should appear and more recently Götte (1897) Appellöf (1900) and Faurot (1903) have met with so many irregularities in the development of the first 8 mesenteries in this group, that it is impossible, now-a-days at least, to set up a fixed rule for the order in which the first 8 mesenteries appear.

As it is very probable that the mode of life may have an influence on the course of development of the mesenteries — in crawling forms, as is well known, mesenteries are often suppressed in

<sup>1)</sup> Kingsley remarks that *Halcampa* has only one siphonoglyph. As I had previously (*Zool. Anzeiger* Bd. 27, 1904 p. 536) pointed out, the larval form described by Haddon as belonging to the genus *Halcampa* is nothing of the sort but a *Peachia*. It is likewise misleading to state that *Cerianthus* has a second siphonoglyph in the multiplication zone (Kingsley p. 348).

their development — we may even assume a priori that the order of successive appearance of the first 8 mesenteries in the different Anthozoa may many times have undergone modification.

Besides, it may be questioned, whether any difference in the time of development of the second and third mesentery couple, both of which form at the corners of the mouth in the 6-mesentery stage of Ceriantharia, really takes place at all: from all we know it must be very slight, if it exists at all. In any case we must very cautious in making use of the order of succession of the first 8 mesenteries for the orientation of the body in Anthozoa, because the smallest difference of time, whether it means the anticipation or retardation of the appearance of a couple, may completely upset the whole order of development of the mesenteries or else bring the originally different orders of mesenterial development shewn by two groups, into harmony with each other. In such circumstances we run the risk of making serious mistakes if we make use of the order of development of the 8 primary mesenteries as evidence for the orientation of the body in Anthozoa.

In the order of appearance of the subsequently formed mesenteries in Ceriantharia, Zoantharia, Actiniaria and Madreporaria a certain agreement is found, which certainly is not very obvious at first sight in all groups, but still does occur according to the results arrived at by several investigators, even in biradial Anthozoa; this consists in the tendency of the mesenteries to develop from the one couple of directive mesenteries towards the other. The Ceriantharia from the 6-mesentery stage develop their new mesenteries in a zone lying just opposite the siphonoglyph, and the formation of the new mesenteries takes place from the siphonoglyph towards the opposite side. The Zoantharia from the 12-mesentery stage perhaps even from the 8-mesentery stage develop the mesenteries from the dorsal side towards the region of the siphonoglyph, that is from the 12-mesentery stage in two zones, one on each side of the large ventral couple of directive mesenteries. In the development of mesenteries 8 to 12 in Actiniaria and Madreporaria, as also in some cases in the appearance of the mesenteries of the second and third cycles, we may trace a development of the mesenteries from the dorsal side towards the ventral, in the fact that the mesenteries of the different cycles form earlier in the dorsally situated exocoels than in the ventral. [Carlgren (1893, 1897) Faurot (1903), Duerden (1902)]. Whether this phenomenon in the biradial forms is the rule, it is no doubt too early to make sure, since hitherto comparatively few forms have been examined, but even if it were not the case the fact would not signify much, because we must of course assume that in many cases the rearrangement of the mesenteries from a bilateral to a biradial symmetry has obscured the course of development.

Thus we can plainly trace in the development of the mesenteries in the above mentioned Anthozoa a formation of the mesenteries from the one side towards the other. Now if we fix the orientation of Ceriantharia as the mesenterial musculature requires, we obtain also a development of the mesenteries from the dorsal towards the ventral side, and consequently a general conformity of which we may always expect to find indications in all Anthozoa that have numerous mesenteries.

We have thus two factors, the mesenterial musculature and the order of development of the mesenteries after the (6) 8-mesentery stage, which tell in favour of the view that the directive couple of mesenteries in Ceriantharia are dorsal (anterior) and that the single siphonoglyph is here a sulculus. Of these the first factor is probably sufficient to determine the orientation of the body in Anthozoa

and indeed we have no other factor of service, if we try to find the homology of the varying arrangements of mesenteries in Anthozoa.

On the other hand, for the contention that the siphonoglyph and the directive mesenteries in Ceriantharia are ventral, the only argument to be adduced is, as we have urged, the hypothetical agreement in the order of succession of the first (6) 8 mesenteries, but after the proof of the irregularity in the development of these mesenteries, such alleged agreement cannot weigh heavily in balancing the arguments for the ventral or dorsal character of the directive mesenteries and siphonoglyph in Ceriantharia. On the supposition that the directive mesenteries in Ceriantharia are ventral, the mesenterial musculature of this group in the 6 (8) mesentery stage, will, as I have urged above, face exactly the opposite way to that seen in the other Anthozoa, and further new formations of mesenteries after the protomesentery stage would take place in the direction of the dorsal instead of the ventral side as is the case in Zoantharia and, in a way, in Actiniaria and Madreporaria also — a state of things which is quite inexplicable.

On the other hand, by making use of my terminology and regarding the directive mesenteries of Ceriantharia as dorsal, we have no difficulty in eliminating the diversity thus occasioned in the order of development of the first mesenteries, for a merely trifling divergence in the time of formation of the directive mesenteries, by which they appear as second in the series of mesenterial development instead of third, brings the formation of the first 6 mesenteries in Ceriantharia into harmony with the series of development which is assumed at least on phylogenetic grounds for the first six mesenteries in Actiniaria. We need not compare more than the first 6 mesenteries in Ceriantharia with the like number of mesenteries in Actiniaria, because the protomesentery stage in the former group is completed with the appearance of the first 6 mesenteries.

I range myself then, as I declared before, on the side of van Beneden, when he maintains in opposition to Boveri and Mc. Murrich, that Ceriantharia do not pass through an *Edwardsia* stage. For the first, it must be noted that during the period of development Ceriantharia have no definitely marked off 8-mesentery larval stage, whilst the larval forms of Actiniaria, Madreporaria, and in all probability Zoantharia also, remain in that stage a good while. For the second, there appears after the 6-mesentery stage a zone of new mesentery formation, on the directive plane produced, directly opposite the directive mesenteries. This enables us to distinguish two periods in the development of the mesenteries in Ceriantharia, the first period, during which the first 6 mesenteries make their appearance — first a couple vertical to the directive plane, then a second couple at the corner of the mouth opposite the directive chamber which is later to appear and lastly, immediately after the forming of the second couple, the directive mesenteries, at the other corner of the mouth — and a second period, during which a new formation of mesenteries takes place in a multiplication zone in the chamber bounded by the second couple. The demarcation between the protomesenterial and the mesenterial stage in Ceriantharia thus occurs after the formation of the first six mesenteries, from which point of time a distinct zone of mesenterial formation presents itself, and not after the 8-mesentery stage, which is not a distinctly marked off stage at all of the development in this group. No doubt it may be objected, that neither does the 6-mesentery stage itself, as far as we know at present, mean a pause in the development of the Ceriantharia, seeing that so far the development

of a single species only, *Arachnactis bournei*, has been closely studied by van Beneden. That is quite true, yet if we draw a distinction between protomesenteries and metamesenteries (protocnemes and deuteroconemes Mc. Murrich) it seems to me the only possible course to draw the line dividing them immediately after the 6-mesentery stage. There are other circumstances in favour of this besides the appearance of a multiplication zone from this stage onward. For we must remember, that the fourth couple of mesenteries (according to the series of development in the mesenteries maintained by Mc. Murrich) in Actiniaria, Madreporaria and Zoantharia is a couple of directive mesenteries, whilst in Ceriantharia it is nothing of the sort. The obvious assumption is, that there has been a differentiation of Ceriantharia from the other Anthozoa with the exception of Antipatharia previous to the 8-mesentery stage. The likeness too of the young Cerianthid larval form to a primitive Antipatharian form, as regards mesenteries, stomatodaeum, chambers and presence of an ectodermal musculature of the column, though not at once decisive, is still very striking.

In view of the facts above adduced I must give my adhesion to van Beneden's view that Ceriantharia have only 6 protomesenteries. Mc. Murrich's contention that in this group 8 protomesenteries would be found, based as it is solely on the order of sequence in the appearance of the first 8 mesenteries, seems untenable for the simple reason, that the order in which the mesenteries in Actiniaria<sup>1)</sup> occur, is very inconstant.

### 6. The mesenterial filaments, acontia and botrucnidae.

Although several investigators, above all A. von Heider (1879), the brothers Hertwig (1879) and in particular van Beneden (1898) have studied the free border of the mesenteries with its appendages, several points of structure are not yet made clear both in the case of the mesenterial filaments and of the so-called acontia and botrucnidae discovered by van Beneden. As I have had for examination adult representatives of Cerianthidae both with "acontia" and with botrucnidae, as well as specimens without "acontia" and botrucnidae, I state here my conception of these organs, referring at the same time to my description of certain Cerianthidae in *Mittheilungen aus der zoologischen Station zu Neapel* 1912. Since I touch several times below on the different authors' views of the mesenterial appendages, I take it to be unnecessary to give a chronological sketch of the history of opinion on the supposed structure of these organs.

To begin with the mesenterial filaments; it is already known, thanks to v. Heider and Hertwig, that at their commencement immediately below the stomatodaeum they consist of a middle portion, a so-called cnido-glandular tract, and of 2 lateral portions, ciliated tracts, also that the cnido-glandular tract is continued aborally in a wavy single portion, "la portion terminale ou simple, qui se prolonge jusqu'à l'extrémité aborale du filament" (van Beneden 1898, p. 34), but as far as I can

<sup>1)</sup> Unfortunately the order of sequence of the mesenteries in Actiniaria and Madreporaria rests for the most part only on observations of disconnected stages and not of complete sequences of development. Whilst Mc. Murrich in his work on the phylogeny of Antinozoa (1891) thinks that Ceriantharia pass through an Edwardsia stage, he does not affirm this so distinctly in his recently published work (1910). There he urges merely that Ceriantharia pass through an 8-mesentery stage which is common to the other Anthozoa with the possible exception of Antipatharia. Ceriantharia certainly pass through an 8-10-12 mesentery stage and so on, but from grounds stated above it is very improbable that a larval form with 8 mesenteries can be the primitive form for all Anthozoa with the exception of Antipatharia.

discover, no investigator has brought out the difference between the structure of the cnido-glandular tract in the ciliated tract region and in the single portion below the ciliated tracts. In order to recognise the homologies between the different filament portions of the sterile and fertile mesenteries in the various Ceriantharia, it is necessary however to distinguish as I have already done above, these cnido-glandular tracts from each other. The middle tract in the ciliated tract region I have also called above the median streak or perhaps better the spirocyst-glandular tract<sup>1)</sup>, characterised by the presence of numerous thin-walled nematocysts and very numerous mucus cells. For the wavy filament on the sterile mesenteries of the third and fourth cycles and also for its analogue on the fertile mesenteries, I have retained however the old designation cnido-glandular tract. It is characterised by the presence of numerous, large and broad, thick-walled nematocysts, and of closely packed granular gland cells, whilst spirocysts are either absent or very rare. The first tract, as A. von Heider long ago (1879) and later van Beneden (1898) pointed out, forms a direct continuation of the ectoderm of the stomatodaeum and in certain species such as *Cerianthus lloydii*, *Botrucnidifer norvegicus* is prolonged on certain mesenteries below the cnido-glandular tract as a craspedion region. The cnido-glandular tract on the other hand and van Beneden's "acontia" and botrucnidae are to be regarded as special differentiations of the filament.

The ciliated tract region of the filament is composed of the following parts:

- 1) a median streak or spirocyst-glandular tract, which is a direct continuation of the ridges of the stomatodaeum.
- 2) two ciliated tracts one on either side of the median streak, which are a direct continuation of the ectoderm and mesogloea in the furrows of the stomatodaeum.

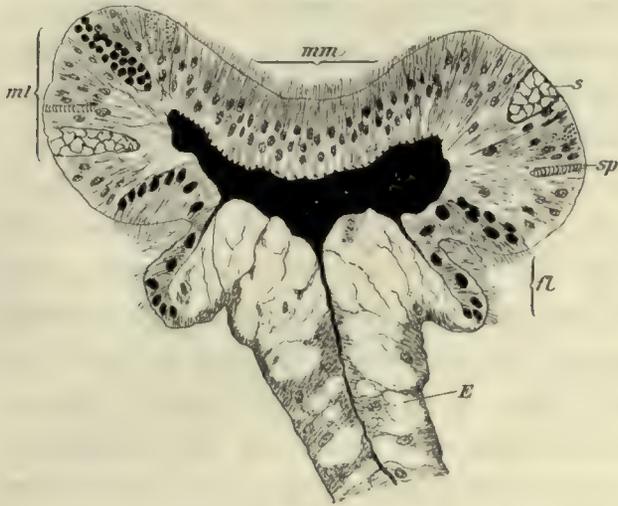
The ectodermal origin of the filament is adopted by v. Heider (1879) and Boveri (1889) but denied by O. and R. Hertwig (1879). Later van Beneden (1898) gave several grounds for an ectodermal origin of the filaments, and shewed the connection between the filaments and the stomatodaeum. I subscribe unreservedly to the opinions expressed by van Beneden on the genetic origin of the ciliated tract region. Of its relation to the cnido-glandular tract, the "acontia" and botrucnidae, I shall say more further on.

As van Beneden has described, the attachment of the mesenteries is shifted in the most aboral part of the stomatodaeum. Instead of the junction of the mesenteries taking place in the longitudinal furrows, as it does over the greatest part of the stomatodaeum, the line of mesenterial attachment gradually creeps up to the ridges, so that where the stomatodaeum passes over into the filaments, the longitudinal furrows come to lie between the attachments of the mesenteries.

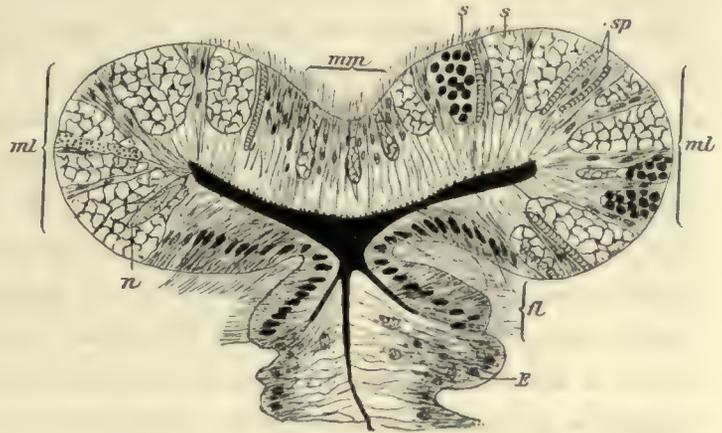
Let us first consider a median streak. The ridge, more or less tongue-like in transverse section, in the most aboral parts of the stomatodaeum has become considerably shortened in all species with the exception of *Botrucnidifer norvegicus*, so that the ridges soon get broader than they are high. Both the ectoderm and the mesogloea partake in this flattening so that the latter forms a process more or less T-shaped in transverse section. The nerve layer and the longitudinal muscle layer at

<sup>1)</sup> When speaking of nematocysts in the filaments, writers hardly ever make any distinction between thick-walled and thin-walled nematocysts. The latter I call briefly spirocysts, without taking any decided attitude on the question whether the two forms do or do not shew any difference in their intimate structure or function (compare Will. 1909, Moroff 1909).

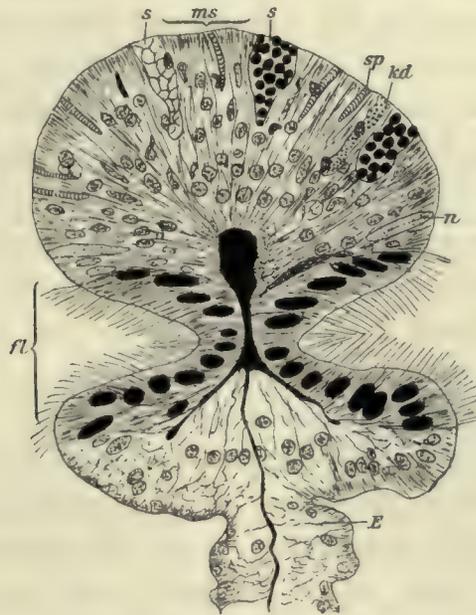
the apex of the ridge broaden out, so that they come to cover the whole side of the mesogloea facing the centre of the body. In the thick ectoderm which covers these layers as well as the sides of the ridges are found the thin-walled nematocysts, spirocysts, which are characteristic of the median streak as contrasted with the cnido-glandular tract, and also homogeneous mucus and more sparsely granular



Textfigure 8.



Textfigure 9.



Textfigure 10.

Textfigure 8—10. Section of the ciliated tract region of the filaments some way below the stomatodaeum. Fig. 8 of *Arachnactis albida* (Type 1), Fig. 9 of *Cerianthus lloydii* (Type 2) and Fig. 10 of *Botrucnidifer norvegicus* (Type 3).

gland cells together with covering cells. The gland cells and spirocysts however are not uniformly distributed over the above surface. For, as far as I have been able to discover, these cells in all the species examined by me except *Botrucnidifer norvegicus* are aggregated at some distance from the stomatodaeum into two groups, forming two streaks one on either side of the mid-plane of the mesentery, whilst the great mass of the covering cells lie in the mid-plane of the mesentery. This arrangement is seen most clearly in *Arachnactis lobiancoi*, as the median streak is here subdivided

as shewn also in its shape into two spirocyst-glandular portions, separated from each other by a deep groove. This groove here consists exclusively of covering cells which are considerably lower than the other ectoderm cells in the median streak, but bear longer cilia than they, in short this depression is a ciliated groove. In *Arachnanthus oligopodus* and *sarsi* as also in *Arachnactis albida* the groove between the two portions of the median streak is also strongly marked, but its ectoderm is higher than in *A. lobiancoi* (Textfigure 8). In *C. membranaceus*, *lloydii*, *valdiviae*, *P. solitarius*, *multiplicatus*, *maua*, *C. americanus* we may also trace this subdivision of the median streak, in the fact that in these cases also a depression, though not so deep as in the cases previously mentioned, runs down the middle of the median streak (the depression is plainer in *C. lloydii*, *valdiviae*, *P. multiplicatus*, *maua* and *C. americanus* than in *C. membranaceus* and *P. solitarius*). In this depression, and consequently in the mid-plane of the mesentery, the ectoderm cells consist chiefly of covering cells with strong cilia; it is noticeable however that between the supporting cells especially in *C. membranaceus*<sup>2)</sup> and *C. lloydii* scattered gland cells and nematocysts are interposed (Textfigure 9). In *Botrucnidifer norvegicus* on the other hand (Textfigure 10, Pl. 5, fig. 9) no trace is found of such a differentiation of the median streak. It has in transverse section a tongue-like appearance and in outline is suggestive of a cnido-glandular tract. This applies also to the mesogloea, which is not in this species divided into two lamellae, as is the case with the species mentioned above. The median streaks thus shew in Ceriantharia grades of transition from a simple undivided structure (in *Botrucnidifer norvegicus*) to a separation into two well marked portions running parallel and divided by a differentiated ciliated groove (in *Arachnanthus oligopodus* and *Arachnactis albida* and *lobiancoi*).

In the aboral part of the ciliated tract region there is a gradual disappearance of this subdivision of the median streak in the series *C. membranaceus*—*C. americanus*, so that the median streak here assumes the same appearance as the median streak in *Botrucnidifer*. In *Arachnactis lobiancoi* and *albida* and also in *Arachnanthus* the median streak shews on the contrary a bi-partition throughout the whole course of the ciliated tract region, so that a well marked ciliated groove is always found between the two portions of the median streak.

We now pass on to consider the ciliated tracts which consist only of ciliated supporting cells.

Just before the stomatodaeum terminates, we have seen that its longitudinal furrows acquire longer cilia than higher up. When the ridges of the stomatodaeum at the transition into the filaments divide in the middle of the longitudinal furrows, the ectoderm in the bottom and a portion of the sides of the furrow on either side of the ridges passes over into the ciliated tracts. The ciliated cells in the sides of the furrows, through the flattening out of the ridges, come to lie on the underside of the median streak, whilst the ciliated cells at the bottom form a process, supported by a

<sup>1)</sup> Where the stomatodaeum passes over into the filament the median streak has often not retained this flattening and differentiation. Thus in the case of *C. lloydii*, in the median streak on the mesenteries of the third and fourth cycles immediately below the stomatodaeum, not a trace is to be seen of a partition into streaks, though further down these median streaks also assume the same appearance as on the other mesenteries.

<sup>2)</sup> Mc. Murrich (1910) mentions the same arrangement in *Pachycerianthus fimbriatus* and *Ceriantheopsis americanus*. Mc. Murrich distinguishes five streaks, one median (my median ciliated groove), two lateral distal streaks (my two portions of the median streak) and two lateral proximal streaks (the ciliated streaks of other writers). It seems to me hardly fitting to designate Mc. Murrich's first three streaks as separate streaks, as the whole transition from a single median streak to a separation of the median streak into two distinct portions divided by a well marked ciliated groove takes place in the Ceriantharia. Topographically of course Mc. Murrich's terms may be made use of.

mesogloal lamella, which forms a continuation of the mesogloea that connects the ridges of the stomatodaeum. The ciliated region of the side and bottom portions which pass continuously one into the other without break thus forms a ciliated groove. This is well marked for the most part and always in the oral portions of the ciliated tract (for example in protomesenteries 2 and the metamesenteries in *C. membranaceus*) throughout the whole course of the ciliated region, more rarely, as in *Arachnanthus oligopodus* on the proximal portions of protomesenteries 2 and the metamesenteries of the first and second cycles, it disappears through a reduction in the number of the ciliated cells and is indicated only by a feeble ciliated streak, though that too very soon disappears and blends with the craspedion region.

The part of the ciliated tract adjoining the endoderm of the mesenteries is supported by a mesogloal lamella, which in *A. lobiancoi*, *albida*, *Arachnanthus oligopodus* and *sarsi* issues from the median streak's mesogloal lamella (Type 1), but in the others from the undivided mesogloal lamella of the mesentery<sup>1)</sup> (Type 2) — a characteristic difference probably connected with the fact that in the first named species the grooves of the ciliated tract are very shallow whilst in the others they are considerably deeper.

The ciliated tract region of the filaments, as several investigators already have repeatedly remarked, is developed on all mesenteries, if the mesenteries are old enough to have acquired filament at all. An exception is found however in the directive mesenteries, which mostly lack a differentiated ciliated region; only in species with well developed hyposulcus (in *Arachnactis lobiancoi*, *albida* and *Arachnanthus* and also in many of van Beneden's Ceriantharia larval forms) is a distinct ciliated tract region found on the free border of the hyposulcus, but this filament region is made up of half only of a filament, in as much as only one spirocyst-glandular tract<sup>2)</sup> with the ciliated tract going with it is developed, as may easily be seen by comparing this part with the ciliated tracts on another mesentery, for example, of *Arachnactis lobiancoi*. This circumstance singular at first sight is easily explained however, if with van Beneden we regard the hemisulci together with the hyposulcus as homologous with the mesenterial filaments on the other mesenteries. For on the side facing the directive chamber, the hyposulcus is common to both directive mesenteries and is not divided between them separately, and consequently there cannot be in this case a distinct ciliated tract region for each mesentery, and on the continuation of the hyposulcus, the hemisulci, no differentiations of the ciliated tract are found on the same side facing the directive chamber. Thus it is only the half of the filaments remote from the directive chamber that may sometimes (in the species mentioned) be differentiated on the directive mesenteries, whilst the parts lying towards the directive chamber have not divided into distinct filament parts different for each directive mesentery.

The ciliated tract region of the filaments is straight for the most part as in *A. oligopodus*, *C. lloydii*, *P. solitarius*, and the most oral parts in *C. membranaceus*. Sometimes even in these cases it may be folded, but possibly except in *P. solitarius* this may be due exclusively to a strong con-

<sup>1)</sup> To this group also plainly belong, according to Mc. Murrich's investigations, *Pachycerianthus fimbriatus* and *Ceriantheopsis americanus*. I can corroborate this statement with regard to the latter.

<sup>2)</sup> The second spirocyst-glandular portion and the ciliated groove running between the two divisions of the median streak are indicated in *A. lobiancoi* and *Arachnanthus oligopodus*.

traction of the mesenteries. In some species (*C. membranaceus*, *P. multiplicatus*, *maua* and *C. americanus*) the ciliated tract region forms craspedonemes, which below the straight ciliated region issue one after the other from the free border of the mesentery, and finally terminate, at least in the first three species, in a more or less compressed bunch<sup>1</sup>). A typical example of this successive outgrowth of craspedonemes is seen in protomesenteries 2, the so-called continuous mesenteries, of *C. membranaceus*, as also in *P. multiplicatus* in which the craspedonemes shew most ramification, and in which they occur on all metamesenteries of the first and second cycles. The bunches of the craspedonemes are seen most finely developed on the metamesenteries of the first cycle in *C. membranaceus*. The structure of these formations has been elucidated by O. and R. Hertwig (1879). They have shewn that the craspedoneme consists of a thread-like or a flattened process of the mesogloea and entoderm, over which passes a descending and an ascending limb of the ciliated tract region of the filament. The ciliated tract region of the filament passes from one craspedoneme to another and forms a continuous covering of all craspedonemes. In a transverse section therefore of the craspedoneme a ciliated tract region of the filament is seen at the two poles and in the middle an entoderm part supported by the mesogloea (Textfigure 12). My investigation of the structure of the craspedoneme, whether the craspedoneme is simple or with bunches attached, is in complete accord with the statements of the brothers Hertwig.

Before concluding the description of the craspedonemes of the region of the ciliated tracts I may mention a peculiar structure of a craspedoneme in the ciliated tract region of *P. maua*. Whilst as a rule the craspedonemes in the ciliated tract region shew a typical structure, and externally a flat ribbon-like form, on the two sides of which runs a layer of filament, there was found on several metamesenteries in the most aboral part, a craspedoneme which in transverse section had a more rounded shape and externally suggested an "acontium". The anatomical investigation of these craspedonemes proved that the craspedoneme consisted of a relatively slight endoderm part which bore on one side, the oral, only a mesenterial filament of the ciliated tract region (Textfigure 13). So much was quite clear, but the constitution of the extremity of the craspedoneme I could not determine in all points with certainty, as the specimen was in a poor state of preservation. The part of the ciliated tract attached to the different mesogloea processes certainly disappears in this case, as also the mesogloea processes, and the entoderm part is reduced in size, but apparently the portion of the ciliated tracts that lies close to the median streak and bounds the inside portion of the ciliated groove is still left. If, as I think probable, these details are correctly observed, a ciliated tract region would not occur in its entirety in the most distal portion of the craspedoneme, but merely an undifferentiated median streak with half only of the ciliated grooves. These acontium-like craspedonemes are therefore constituted — and the same is the case with the craspedonemes of the craspedia in *C. americanus*, as we shall see below — quite differently from the acontia in the genus *Arachnanthus* and in *Arachnactis*, though they have the same external appearance and correspond in situation. [Compare Carlgren (1912)].

The ciliated tract region is best developed on the metamesenteries of the first and second cycles, and on protomesenteries 2, since protomesenteries 3 and the metamesenteries of the 3rd and

<sup>1</sup>) The bunches of the craspedonemes are not therefore van Beneden's "acontia", as this investigator considers possible (1898 p. 33), but doubtless Mc. Murrich's "acontia" in *C. americanus* (1890 p. 138, fig. 1, Pl 7).

4th cycles have much shorter ciliated tracts. This being so, the length of the ciliated tract region stands in inverse proportion to that of the cnido-glandular tract region, as we shall see. The length of the ciliated tracts varies considerably on the analogous mesenteries of the different species.

The region of the cnido-glandular tract is always devoid of ciliated streaks. The cnido-glandular tract is distinguished from the median streak in the ciliated tract region by the fact that the epithelium contains numerous large thick-walled nematocysts<sup>1)</sup> and numerous elongated, granular gland cells, in addition to which supporting cells occur, and more sparsely, homogeneous mucus cells. The configuration of this tract in transverse section is always more or less tongue-like, never flattened, and the mesogloea of the mesenteries terminates in the filament without ramification. The muscles consequently, having no means of attachment to the slight mesogloea lamella, are either absent or extremely feebly developed.

The region of the cnido-glandular tract, which answers to the single wavy coiled cnido-glandular tract in Actiniaria, is best formed on protomesenteries 3 and on the metamesenteries of the third and fourth cycles, where it forms more or less folded (in *A. oligopodus*, *sarsi*, *C. valdiviae*, *lloydii*, *B. norvegicus*) or very wavy bands. A close examination of the metamesenteries of the first and second cycles and of protomesenteries 2 teaches us, however, that these mesenteries also for the most part bear cnido-glandular tracts, though more feebly developed. This is the case at least with all the Ceriantharia studied by me with the exception of the forms provided with van Beneden's "acontia", that is to say, the genus *Arachnanthus*, and also the metamesenteries of the first cycle in *P. maua*. Least developed are those on protomesenteries 2 and the metamesenteries of the first cycle in *C. membranaceus* and *C. americanus* and on the metamesenteries of the first and second cycles in *P. solitarius*. Better developed are those of the metamesenteries of the second cycle in *C. membranaceus* and of the metamesenteries of the first and second cycles in *C. lloydii*. Yet how easily they escape observation, may be inferred from the fact that no investigator has called attention to the presence of these subdivisions of the filament on the above-mentioned mesenteries of the first and second cycles, and on protomesenteries 2 in adult individuals. Van Beneden for instance did not see this tract on the metamesenteries of the 1st and 2nd cycles or on protomesenteries 2 in *C. lloydii*, as appears from his not marking it in the diagram of his work (1898 fig. A, p. 25), nor mentioning it in discussing (1898 p. 22) von Heider's "Filamentsepten" (cloisons à pelotons). On the other hand, van Beneden did observe them in some larval forms (1898). It is probable enough that other investigators have also noticed the cnido-glandular tract on these mesenteries — as Mc. Murrich in *C. americanus* — but in view of the very complicated and conflicting nomenclature of the divisions of the filament and the usually imperfect descriptions of the filaments, this cannot be positively settled.

The cnido-glandular tract, as has been said, is feebly developed in some species on the metamesenteries of the first and second cycles, where it has the form of a straight or more or less winding thread. The simplest case is found in *P. solitarius*, where the cnido-glandular tract on the meta-

<sup>1)</sup> So-called spirocysts, thin-walled nematocysts, may occur here, but very sparsely if they do, just as, conversely, thick-walled nematocysts may occur in the median streak on the boundary of the cnido-glandular tract. In rare cases thick-walled nematocysts seem to occur in greater numbers in the median streak. This is the case in *P. maua*, where the cnido-glandular tract is absent on the better developed metamesenteries.

mesenteries of the 1st and 2nd cycles is just a simple thread which exactly answers to the craspedonemes of the ciliated tracts, but with this difference naturally, that no ciliated streaks are developed on it and that the ascending and descending limbs of the filament consist of a cnido-glandular tract and not of a median streak. The descending and ascending limbs of the cnido-glandular tract are separated by an endoderm portion. The cnido-glandular tract on the metamesenteries of the first and second cycles in *P. solitarius* consists then, we may say, simply of a craspedoneme. From this starting point a number of intermediate stages are found, leading up to the very wavy cnido-glandular tract of the metamesenteries of the 3rd and 4th cycles. For no more than between the craspedonemes of the ciliated tract region and its bunches of craspedonemes, is there any essential difference between the simple craspedoneme of the cnido-glandular tract and the much coiled filament of that region. The simple craspedoneme of the ciliated tract region has its counterpart in the simple craspedoneme of the cnido-glandular tract, the bunches of tightly compressed craspedonemes in the ciliated tract region are represented in the cnido-glandular tract by the very wavy coils on the metamesenteries of the third and fourth cycles in a number of species.

The Craspedion region (Filamentchenregion Carlgren 1912).

The Craspedion is the name I have given above to that part of the filament, where the course of the median streak (spirocyst-glandular tract) is simple without ciliated tracts. They occur on the one hand in species with "acontia" (consequently in *Arachnactis lobiancoi*, *albida*, *Arachnanthus oligopodus* and *sarsi*) on mesenteries of the first and second cycles in an oral direction from the "acontia", between these and the ciliated tract region, and on the other hand they are found on mesenteries, which are very long, have cnido-glandular tracts running to no great distance from the stomatodaeum, which is the case with protomesenteries 2 and the metamesenteries of the first and second cycles in *C. lloydii*, *vogti* and *C. americanus*, with the metamesenteries of the 2nd cycle in *P. maua*, and with all mesenteries but the directive in *Botrucnidifer norvegicus*. In *C. lloydii* and *vogti* they take up the greatest part of the length of the mesenteries below the cnido-glandular tract, and the same thing happens on the metamesenteries of the first cycle in *Ceriantheopsis americanus*. In *B. norvegicus* they stretch between the cnido-glandular tract and the botrucnidae at the aboral extremity of the mesenteries. But the craspedion region is very rudimentary in *B. norvegicus* on the metamesenteries of the third and fourth cycles.

Form and structure of this region alike vary to some extent among the different Ceriantharia. As regards form at least, this is connected with the varying appearance of the filaments. In structure the craspedion mostly corresponds with the median streak; but in *C. lloydii*, *C. americanus* and *A. oligopodus*, the most aboral portion has a more composite character, in as much as thick-walled nematocysts become more common in this part. In *Arachnactis lobiancoi* the craspedion region remains of exactly the same structure as the median streak of the ciliated tract region; also the craspedia are very short here and form a very inconsiderable section between the ciliated tract region and the "acontia".

In *Arachnanthus oligopodus* the craspedia form the longest part of the filament. On the disappearance of the groove of the ciliated tracts by the coalescence of the borders of the groove the ciliated tract passes on towards the aboral side as a small streak on either side of the mesentery, but

very soon disappears, so that only the median streak remains, in the form of a craspedion. The craspedia are to begin with and for the greatest part of their course of the same structure as the median streak, save that the ectoderm of the craspedion region is lower, less prominent and that the groove between the parallel bands of the spirocyst-glandular tract is not so deep. In the most aboral portion these bands gradually coalesce. The ciliated groove between them disappears, so that the craspedium now presents itself as a uniform structure with epithelium of the same height, which in transverse section shews as a broad flat layer. Here in particular the craspedia are smaller in cross-section than the median streak in the ciliated tract region. In the most aboral portion of the craspedion we now find in addition to spirocysts very large thick-walled nematocysts especially near the limit of the ectoderm. These nematocysts have the same appearance as in the entoderm of the mesenteries. They present much the same appearance in *Arachnactis albida*.

In *C. lloydii* the craspedia are fairly broad aborally, but taper off in the aboral direction and sink more and more into the entoderm, so that in transverse section they present a small oval with the longer axis in the mid-plane of the mesentery. The craspedia contain in the aboral part very numerous large thick-walled nematocysts, which gives the craspedia a more mixed character.

In *Botrucnidifer norvegicus* the craspedia are broad and consist chiefly of gland cells, whilst nematocysts are more sparse.

In *P. maua* the craspedia are narrow and contain a very thin sprinkling of nematocysts, if any at all.

The craspedia in *Ceriantheopsis americanus* are very broad throughout their whole course and except in the lower part they contain, in addition to supporting cells, principally thin-walled nematocysts and homogeneous gland cells. The muscular layer is quite well developed. In the most aboral part is found on the metamesenteries of the first cycle a thread-shaped craspedoneme (compare p. 26). This shews a different structure. Whilst the homogeneous glands cells are still to be found, numerous granular gland cells now present themselves. The thin-walled nematocysts disappear almost entirely, and in their place thick-walled nematocysts are now met with in very large numbers. The muscular layer too is distinctly feebler than in the upper part of the craspedion.

As we have seen, not only the ciliated tract region and the cnido-glandular tract but also the craspedion region may thus form craspedonemes, though in the latter case they are more diminutive and consist of a single thread only. The craspedoneme in the craspedion region of *C. americanus* is no doubt suggestive of the structure of the cnido-glandular tract, by the presence of thick-walled nematocysts though the accordance is not complete: still as in *C. lloydii* and *Arachnanthus oligopodus* thick-walled nematocysts also occur in the under (aboral) portions of the craspedia. We shall hardly be going too far in regarding the single craspedoneme in the most aboral part of the mesenteries of *C. americanus* as a differentiation of the craspedion. For if we regard this craspedoneme as a differentiation of the cnido-glandular tract, we should have in *C. americanus* on protomesenteries 2 and on the longer more developed metamesenteries of the first cycle two portions of the gnido-glandular tract, separated from each other by a very long craspedion region, a circumstance very hard to explain.

As we shall see, the position and structure of these craspedonemes in *C. americanus* throws some light on the real nature of the organs which van Beneden has called acontia and made homologous with the acontia of Actiniaria.

"Acontia".

Van Beneden has described as acontia certain thread-shaped, single or slightly branched organs at the aboral end of various Ceriantharian larval forms. Van Beneden gives the following account of the structure of the acontia in general. Around the central mesogloal axis of the thread spreads an entodermal longitudinal musculature. The epithelium that covers the mesogloea, contains principally nematocysts and gland cells in large numbers, and in addition to these, supporting cells. He has in some cases observed that the acontia do not issue from the border of the mesentery, but that their attachments are somewhat lateral. This fact, as also the circumstance that the nematocysts are so numerous in the acontia, tells, he thinks, in favour of the view that the acontia are practically stinging batteries and that they are homologous with the acontia of Actiniaria. At the same time he finds a few, though trifling differences in the acontia of Ceriantharia, namely (p. 31) "forme de l'axe mésenchymatique, uniformité de structure de l'épithélium sur tout le pourtour de l'axe, caractères de l'épithélium". In point of origin van Beneden considers the acontia to be endodermal formations in distinction from the ectodermal filaments, a view which is supported by the fact that the large nematocysts found in the acontia are exactly like those which occur in the entoderm of the mesenteries. Lastly he holds the acontia to be homologous with the botrucnidae.

These views of the structure and homology of the acontia were probably formed by van Beneden in consequence of an imperfect examination of the acontia. As the bent form of the acontia makes it often difficult to prepare satisfactory transverse sections from any point in the acontium's length, I surmise that van Beneden's cross sections were as a rule taken from the distal portion of the acontium only, whilst of the proximal portion they were usually longitudinal or oblique. And in fact the study of sections so taken really does suggest such a theory of the structure of the acontia. But a closer investigation of the acontia shews in my opinion that, in the matter of the structure and homology of the acontia, van Beneden has been mistaken in several important points. The acontia are practically a continuation and differentiation of the filaments and consequently — assuming as is probable that the filaments are ectodermal — are themselves ectodermal; only a part of the acontia, that, namely, in which the large thick-walled nematocysts are numerous, is endodermal.

I have examined "acontia" both in the Ceriantharian larval forms *Arachnactis lobiancoi* and *albida* and in the Ceriantharium adult forms *Arachnanthus oligopodus* and *sarsi*. The acontia of *Arachnactis albida*, *Arachnanthus oligopodus* and *sarsi* correspond almost exactly in structure, whilst the acontia of *A. lobiancoi* look more like the acontia of *Ovactis*, a larval genus described by van Beneden, in that they contain very numerous nematocysts in the entoderm part, whilst these are infrequent in the other species examined. Before I describe the structure of the acontia, I wish to lay stress on the fact, that the formations I have examined are the identical ones to which van Beneden applied the name. In as much as van Beneden examined in the first place the threadlike processes at the aboral pole of the longest mesenteries of *Arachnactis albida* and designated them as acontia, it is quite

out of the question that I can have had before me any other formations than van Beneden's acontia.<sup>1)</sup> Nor do I think it probable that van Beneden meant to denote by the term "acontia" threads of unlike structure, that is to say, that van Beneden's acontia are heterogeneous formations — but that is a point which cannot be definitely cleared up until van Beneden's Ceriantharian larval forms have been examined afresh.

In *Arachnanthus oligopodus*, as I shew in another work (Mittheilungen z. Stat. Neapel 1912) the acontia are in the form of a thread, which in transverse section is oval in shape. The craspedion region is continued in the acontium, forming a stronger ascending limb and a slighter descending one. In the most distal portion of the thread the two limbs of the filament run so close together, that no boundary can be detected. Towards the base the descending limb gets thinner, so that on both sides of it an endoderm part becomes visible and divides one limb from the other. At the base of the "acontium" in *Arachnanthus oligopodus* the descending limb has disappeared, so that the thread consists here merely of an ectodermal part, the ascending limb of the filament, and an endoderm part going with it.

In *Arachnactis albida* the descending limb lasts longer on the free border of the mesenterial thread, so that both limbs are met with at the base of the "acontium". The histological structure of the acontium filament is rather different from that of the craspedion region. Supporting cells occur, but the great bulk of the ectoderm is made up of mucus cells, and there is found only a thin sprinkling of spirocysts and thick-walled nematocysts. The longitudinal muscles which are restricted solely to the ectodermal part, are found in the distal portion of the acontium, where the filaments enclose the whole mesogloea, to run in a continuous layer all round the mesogloea: on the other hand towards the base of the acontium the longitudinal muscles are differentiated into two groups, one for each limb of the filament, or else (in *A. oligopodus*) only one group is found at the descending limb. The mesogloea in *A. oligopodus* shews signs of breaking up about each limb of the filament. The endoderm cells are almost exclusively supporting cells, only very rarely do we find a large thick-walled nematocyst. In *Arachnanthus oligopodus*, *sarsi* and *Arachnactis albida*, all whose acontia agree in structure, the function of the "acontium" therefore is not that of a sting battery.

Regarding the structure of the acontia in *Arachnactis lobiancoi*, the account I have elsewhere (1912) given on another page is not so complete as that of *Arachnactis albida* and *Arachnanthus oligopodus*, as the sections of the basal portion were taken lengthwise, of the distal portion transversely or obliquely, still I have obtained transverse sections approaching so nearly the basal portion that there also the nature of the acontia is made clear. For, in the first place, it plainly appears that the "acontium" consists of an ascending and a descending limb of the filaments, containing principally gland cells. In the second place I have succeeded in ascertaining the important fact, that the large nema-

<sup>1)</sup> Mc. Murrich (1910) seems in contrast to Cerfontaine (1909, p. 686–87) to regard the "prolongements filamenteux" in *Arachnanthus oligopodus* as acontia. At the same time Mc. Murrich, who has examined a number of larval forms with acontia, states that he has nothing to add to the description of the acontia given by van Beneden. Cerfontaine's description of these organs however, which according to my investigations fully agree with van Beneden's acontia in *Arachnactis albida*, differ materially from van Beneden's description. Cerfontaine's account of the "prolongements filamenteux" in *A. oligopodus* agrees substantially with mine of the acontia.

tocysts which occur in great numbers, are situated between the two limbs of the filament, that is to say, they are set in the endoderm. The entodermal part of the acontium thread is slightly larger here than in the species mentioned previously.

The threads which van Beneden called "acontia" are thus in my view composed in the main in the same way as the craspedonemes of the ciliated tract region in *Cerianthus membranaceus* or a craspedoneme of the cnido-glandular tract in *P. solitarius*, in the respect, that is, that they are composed of an ascending and a descending limb of the filament, which encloses an endodermal process of the mesentery. The only difference is, that here the endodermal part is reduced in size much more than in the craspedonemes alluded to, and to such an extent that the endoderm in the distal portion of the acontium completely or all but disappears, so that the two limbs of the filament become completely or all but contiguous (textfigure 14).

If we may thus assimilate the "acontium" to a craspedoneme, the question arises whether the principal part of the acontium, namely the filament part, is a differentiation of the median streak and in that case of the craspedion, or whether it is to be regarded as a modification of the cnido-glandular tract. To answer this question, the only sure data for our guidance are to be found in the structure and situation of the "acontia". To take first the situation of the "acontium" and of the cnido-glandular tract, it would seem at first sight to be of no use in establishing an homology, because the cnido-glandular tract of the metamesenteries of the first and second cycles as well as of protomesenteries 2 does not occupy the same position in the different Cerianthidae. If, for instance, we look at *Pachycerianthus multiplicatus* and *Cerianthus lloydii*, both of which have very long metamesenteries, and at protomesenteries 2 of *Cerianthus membranaceus*, we find that on the mesenteries in question the cnido-glandular tract is situated not far from the stomatodaeum in *C. lloydii*, but in the other two cases in the most aboral part of the mesentery. We find however on closer examination, that this difference depends on the varying length of the ciliated tract region in the different species. For, if we examine the disposition of the different parts of the filament, we find that in immediate proximity to the aboral border of the stomatodaeum a ciliated tract region is developed, next comes a cnido-glandular tract in the aboral direction, and lastly in many species a craspedion region which at its aboral end may form a craspedoneme (in *C. americanus*). In other words, the cnido-glandular tract lies between the ciliated tract region and the craspedion region. Now, as on the mesenteries that bear "acontia" in *Arachnanthus* and *Arachnactis* s. str. — the ciliated tract region passes immediately into the craspedion region without forming a cnido-glandular tract region, and the "acontia" are situated at the aboral end of the craspedion the situation of the "acontia" tells in favour of the hypothesis that they are differentiations of the craspedion.

Secondly, the anatomical structure of the "acontia" in *Arachnanthus* and *Arachnactis albida* leads us to a similar conclusion. For, if we exclude supporting cells, the great bulk of the filament part of the acontia is composed, as we have seen, of gland cells and these mucus cells, whilst nematocysts are so rare as scarcely to count as a special feature at all. A longitudinal muscle layer is also developed, which, like the filament part itself, is ectodermal.

The presence in the acontia of the numerous homogeneous gland cells and the extremely well developed longitudinal muscles, which are very rare in the cnido-glandular tract if not entirely

absent, whilst they are characteristic of the median streak in the species bearing acontia, thus tends to shew that the acontia in *A. oligopodus* and *sarsi* and in the typical species of the larval genus *Arachnactis* are differentiations of the median streak, that is, of its continuation, the craspedion<sup>1)</sup> whilst there is nothing essential to their structure that suggests the cnido-glandular streak.

If then the acontia in question are differentiations at the aboral end of the craspedion they ought to be homologous with the craspedonemes of the craspedia in *Ceriantheopsis americanus*, though the development of these two organs would have taken a different course. In that case the "acontia" have retained the mucus cells of the median streak and augmented them, and the muscle layer of the streak has not been lost, but on the other hand the descending and ascending limbs of the acontium filament have drawn close together through the reduction of the endoderm part, the acontium becoming rounded and presenting an oval form in transverse section. The said craspedoneme from the craspedia, on the contrary, has reduced the number of mucus cells and spirocysts and lost the muscle layer almost entirely, but on the other hand granular gland cells and thick-walled nematocysts have arisen in greater numbers — just as thick-walled nematocysts have been developed in the most aboral portion of the craspedion in several of the species not provided with acontia (as in *C. lloydii*) — though the form of the craspedoneme has undergone no change but corresponds with that of a craspedoneme from the ciliated tract region.

My study of the "acontia" in Ceriantharia has thus led me to a different conception of their structure and origin from van Beneden's. It is now clear, I think, that van Beneden's views on this point must be considerably modified. Above all we must insist that the principal parts of the "acontia" are ectodermal (granted that the filaments themselves are ectodermal formations<sup>2)</sup>, which seems highly probable), further that the "acontia" are not sting batteries in the same sense as the "acontia" in Actiniaria, for either the large thick-walled nematocysts are very sparse or if they are found in larger numbers it is in the endoderm part of the "acontium" only. Mucus cells on the contrary are to be found in great numbers. Under these circumstances the propriety may well be questioned of homologizing, as van Beneden does, the "acontia" of Ceriantharia and the acontia of Actiniaria, the latter of which probably have no nematocysts in the endoderm. In my view the "acontia" of Ceriantharia have nothing in common with those of Actiniaria, and it would be more correct to give the "acontia" of Ceriantharia another name, such as muco-craspedonemes. At the most we can only speak of acontium-like threads in Ceriantharia, and that mainly with reference to their outward form. I ought to mention besides, before leaving the subject of the acontia in Ceriantharia and Actiniaria, that van Beneden's statement, that their attachment with the mesenteries corresponds in the two groups, does not hold good. Van Beneden says that he has many times noticed that the acontia run laterally in Ceriantharia at the point of junction. I have thought I noticed myself an attachment of this kind, but this circumstance depends in my opinion on an irregular con-

<sup>1)</sup> As the median streak and the craspedion correspond in structure, and the first is continuous with the ectoderm of the stomatodaeum, they are doubtless to be regarded as primary filaments from which the cnido-glandular tract has been developed.

<sup>2)</sup> Independently of the morphological support given above for the ectodermal origin of the filament we may adduce the fact that the mesenteries in the development zone do not acquire filaments until they have reached the lower border of the stomatodaeum.

traction of the two sides of the mesenteries, and this is confirmed by the fact that the filaments also sometimes appear to take a lateral course. The resemblance in the attachment of the acontia in the two groups is thus quite superficial.

Although I cannot therefore concur with van Beneden's view of the acontia in several points, I am nevertheless at one with him provisionally (pending a closer investigation of the botrucnidae of *Botruanthus*) in regarding the "acontia" as homologous organs with the botrucnidae.

#### Cnidorages and Botrucnidae.

As is well known, van Beneden (1898) has given a description of some peculiar organs, to which he has given the name botrucnidae. They were aggregations resembling clusters of grapes formed at the aboral end of the mesenteries and on their free edge. Each grape, which when isolated van Beneden called a cnidorage, was attached to the mesentery by a stalk. The cnidorages were exclusively epithelial and entodermal globular formations, which contained two kinds of cells besides supporting cells, namely nematocysts and mucus cells, the latter always in very small numbers. The nematocysts were partly large thick-walled ones, partly thin-walled (spirocysts) larger or smaller. The clustered botrucnid-grapes were in no wise distinguishable (l. c., p. 127) from the isolated ones, save that the former possessed a stalk. Van Beneden then equally considered the Botrucnidae to be exclusively epithelial and entodermal organs and to be homologous with the acontia, on the ground that they occupy the same position as the acontia in the larval forms that bear acontia.

Adult forms of Ceriantharia bearing botrucnidae have not however been described by van Beneden, though he mentions that he has found such organs<sup>1)</sup> in *C. oligopodus*. Two years ago Torrey and Kleeberger (1909) found cnidorages in one of the Ceriantharia described by them, *Cerianthus benedeni*. If I rightly understand Torrey and Kleeberger's descriptions they are to be found on the mesenteries of the first and second cycle partly and principally on the craspedoneme bunches that are on about the same level as the cnido-glandular tract ("the coiled mesenterial filaments") in the third and fourth cycle, partly on more dispersed craspedonemes issuing from the border of the mesentery nearer the aboral side<sup>2)</sup>. As regards the homology of the cnidorages Torrey and Kleeberger come to the conclusion, that since the cnidorages have appeared only on filaments that "correspond perfectly to the filaments figured by van Heider for *C. membranaceus*", they cannot be homologous with the acontia, which according to van Beneden "differ totally — in position, morphological value, structure and function — from these filaments in *C. membranaceus*".

<sup>1)</sup> Cerfontaine the author of the name *C. oligopodus*, in his exhaustive account of this Cerianthid (1909) does not mention the occurrence of botrucnidae. I myself, in examining a species, which was unquestionably the same as Cerfontaine's, failed to see any botrucnidae either. Consequently van Beneden's *C. oligopodus* must be a different species.

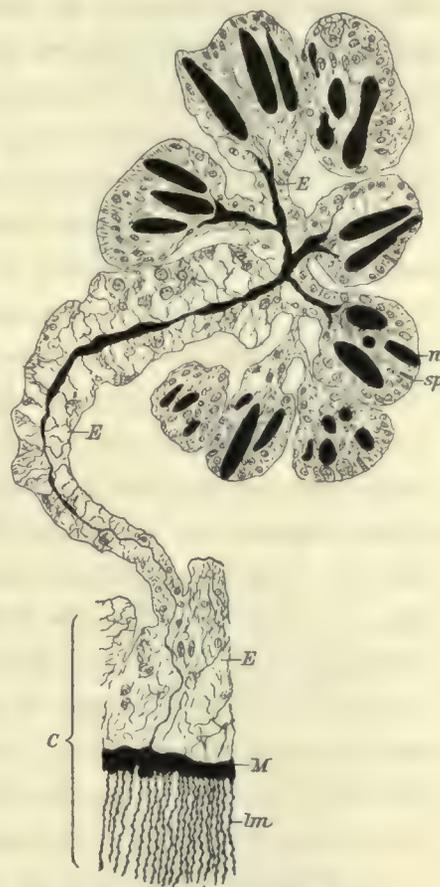
<sup>2)</sup> Unfortunately Torrey and Kleeberger have apparently not made a close anatomical study either of filaments or cnidorages, at any rate they give neither an anatomical description nor figures of anatomical details concerning the filaments — for which reason it is very difficult to determine the orientation of the different parts of the filaments. The question is whether the "compact bunches on the mesenteries of the first and second orders" are really craspedonemes or, as seems more likely, cnido-glandular tracts as in Botrucnidifer. If these "compact bunches" are really craspedonemes, then these bunches are quite differently situated from those in *Cerianthus membranaceus* and *Pachycerianthus multiplicatus*, where they are found at the aboral end of the mesenteries. Further, I don't understand what Torrey and Kleeberger mean, when they draw a distinction between "cycles" and "orders". On p. 122 they inform us that cnidorages appear on the mesenteries of the third and fourth cycles, on p. 123 that they are found on the mesenteries of the first and second orders.

I have described above a Cerianthid with botrucnidae, *Botrucnidifer norvegicus*. Botrucnidae occur in this species on protomesenteries 2 and 3, on the first quartette of metamesenteries, and on the longest mesenteries of the second. Their position is the most aboral part of the mesenteries, that is to say, they occupy exactly the same position as in the larval forms described by van Beneden.

In the first place as to the histological structure of the isolated cnidorages, it is possible that in certain cases van Beneden may be right in his statement that they consist only of epithelium, in certain isolated cnidorages however I have succeeded in ascertaining beyond all doubt the presence of a mesogloea portion (figs. 7, 8, Pl. IV.). The stalked botrucnid-grapes also are otherwise constituted, according to my investigations, than as van Beneden describes. They are not simply an epithelial formation, the mesogloea enters into the composition of these grape-like organs. That is, the mesogloea of the mesentery is continued into the botrucnidae, ramifying like a tree and giving off a branch to each botrucnid-grape (Textfig. 11). The mesogloea process passes through the grape-stalk and broadens out at the base of the berry forming a sort of cup or funnel. From this cavity thin threads apparently proceed in the direction of the unattached side of the grape, though the course of such extremely fine threads is hard to follow. In any case the mesogloea processes sustain the usual supporting cells, which cover the outside of the basal portion of the grape, and within the cavity lie the bases of the very large thick-walled nematocysts, which are set close together and project outwards towards the periphery of the grape. Between the thick-walled nematocysts lie the thin-walled ones, the smallest of which are just below the free surface of the supporting cells.

It holds good therefore that the botrucnidae and cnidorages contain not merely epithelial but also mesogloea parts.

Van Beneden, as already said, regards both the acontia and the botrucnidae as endodermal organs. I cannot endorse this view: everything points rather to the ectodermal origin of both acontia and botrucnidae. As I have said above, they issue from the most aboral portion of the craspedion and come into immediate contact with the filaments. Whilst the acontia are continuous with the craspedion the botrucnidae are separated from the craspedion; the latter circumstance however is a consequence of the structure of the botrucnidae, in as much as in them the filament part is broken up into a number of lobes. Moreover the presence of numerous spirocysts is a point in favour of the comparison of the botrucnidae to the craspedion. And the statement of Torrey and Kleeberger that the cnidorages in *Botruanthus* occur on craspedonemes points the same way. If the filaments are ectodermal in the first place, and this van Beneden himself assumes, then the botrucnidae are ectodermal also. Only the



Textfigure 11. *Botrucnidifer norvegicus*. Section of the column and a mesentery with botrucnidae. On some of the botrucnid-grapes only the epithelial elements are sectioned.

stalk of the botrucnidae will be entodermal. It is difficult however to draw a hard and fast line between ectoderm and endoderm. And probably some cells at the base of the botrucnid-berry on the outside of the cup are endodermal.

Lastly as regards the homology of the botrucnidae, my view at the present time, as I have said before, coincides with van Beneden's, that they are homologous with the acontia, amongst other reasons because both in van Beneden's larval forms and in *Botrucnidifer norvegicus* they form like the acontia the most aboral part of the craspedion region. It is true that the botrucnidae of *Botruanthus benedeni* appear to have a different position on the mesenteries, but as it is very hard to determine the precise distribution of these botrucnidae, of which I may add, judging solely by the account of Torrey and Kleeberger, we have no very exact description, and as such distribution is totally at variance with that in the remaining Ceriantharia provided with botrucnidae, I am unable at present to pay much heed to these investigations. Nor is it beyond the bounds of possibility that the botrucnidae of these writers are not identical with the organs so named by van Beneden. In their inner structure it is important to notice that the botrucnidae occupy an intermediate position between the acontia and the craspedonemes of the craspedion. It is true that they are quite different in shape, for instead of presenting the thread-like appearance of the acontia and the craspedonemes, they are split up into a large number of grape-like organs. But such a circumstance need not preclude the essential homology of these organs, and the less so as an interruption of the filaments may occur also in other Anthozoa. In *Scytophorus antarcticus* for instance and in some other soleless Actiniarian forms I have found a discontinuity of the ciliated tracts, and in *Calliactis (Sagartia) parasitica* the filaments on the least developed mesenteries shew interruptions in several places in the ciliated tract region. Now if we imagine that a strongly coiled filament part has parted in a large number of places and that each section so formed has rolled itself up, we shall have an organ corresponding in form to a botrucnid. As to their anatomical structure, they have reduced the number of mucus cells, and augmented the spirocysts and the thick-walled nematocysts, but without developing any granular gland cells.

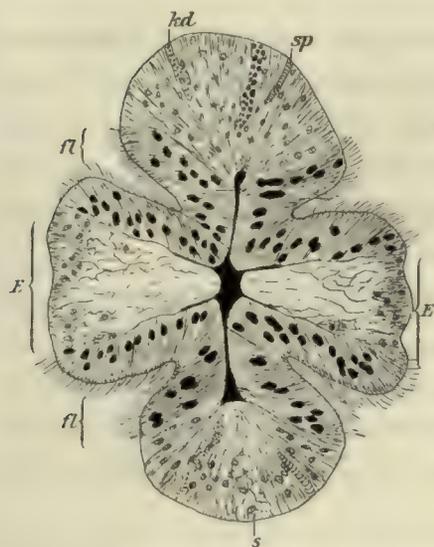
Bringing into relation all the morphological data given above, I think that we are bound, at least until further light is thrown upon the matter, to admit the homology of the botrucnidae of *Botrucnidifer* and of van Beneden's larval forms with the acontia of the genera *Arachmanthus* and *Arachnactis* and with the craspedonemes of the craspedion region in *Ceriantheopsis americanus*.

Before I conclude, it may be convenient to give a short summary of the different kinds of craspedonemes found in Ceriantharia, with some diagrams.

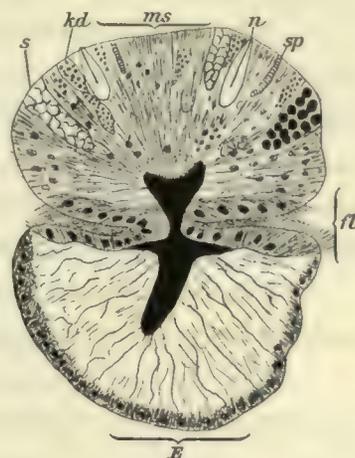
As we have seen, craspedonemes may be developed as well — or rather more — from the ciliated tract region of the filaments as from the cnido-glandular tract and from the craspedion region, though in a more or less modified form. All these craspedonemes, — I disregard the botrucnidae — are flat or show themselves in transverse section as slightly rounded processes, in the middle of which is an entodermal and a mesogloal axis, and whose free edge is covered, for the most part at least, with a filament part. There is thus found as a rule a from the oral side ascending limb of the filament and a descending limb. Only in the most aboral craspedoneme in the terminal portion of the filament in *P. maua* does the descending limb appear to be absent. A transverse section of the cras-

pedoneme or "acontium" thus intersects as a rule both the ascending and the descending limb; only at the base of those craspedonemes in which the filaments come to an end, is there no descending limb to be found.

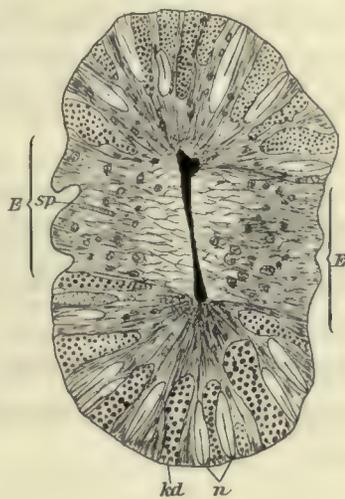
The craspedonemes of the ciliated tract region are of two kinds.



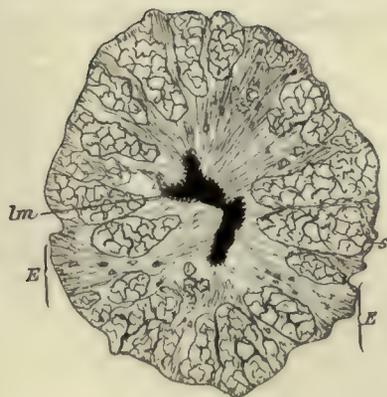
Textfigure 12.



Textfigure 13.



Textfigure 14.



Textfigure 15.



Textfigure 16.

Textfigures 12--16.

Fig. 12. Section of a craspedoneme in the ciliated tract region of *Ceriantheopsis americanus*. Fig. 13. Section of the most aboral craspedoneme in the ciliated tract region of *Pachycerianthus maua*. Fig. 14. Section of the craspedoneme-like cnidoglandular tract of *Pachycerianthus solitarius*. Fig. 15. Section of a so-called "acontium" (mucus-thread) of *Arachnanthus oligopodus*. Fig. 16. Section of a craspedoneme in the craspedion region of *Ceriantheopsis americanus*. — All sections from about the middle of the respective processes.

1) Craspedonemes of the normal type which occur in many species usually in great numbers, and have a filament limb on each side. They are found for example in *C. membranaceus*, *P. multiplicatus*, *maua*, *C. americanus* (Textfig. 12). Often, as in *C. membranaceus*, *P. multiplicatus* they are

found aggregated at the aboral end of the ciliated tract region, forming bunches. These bunches answer to the wavy coils of the cnido-glandular tract.

2) Craspedonemes which possess only an ascending limb of the filament (Textfig. 13). This is the case in *P. maua*. Here evidently the filament has not yet reached the aboral side of the craspedoneme in the course of its growth.

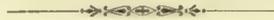
The cnido-glandular tract more rarely forms a craspedoneme and only on mesenteries whose cnido-glandular tract region is extremely slight. This is so with certain mesenteries of *Pachycerianthus solitarius* (Textfig. 14) and sometimes in *Cerianthus lloydii*. Still the wavy coils of the cnido-glandular tract correspond, as already mentioned, to the bunches in the ciliated tract, though they may not display such thread-like formations as the ciliated tract, but even so the cnido-glandular tract traverses processes of mesenterial entoderm and mesogloea.

The craspedonemes of the craspedion region are met with partly in the form of acontia partly in the form of craspedonemes undifferentiated in outward appearance.

The "acontia" are rounded in transverse section. The filamentous part consists mainly of mucus cells: they are provided with an ectodermal muscle layer. In the endoderm numerous nematocysts may sometimes (often?) be developed. Typical "acontia" are found in *Arachnanthus* and in *Arachnactis albida* (Textfigure 15).

The more undifferentiated craspedonemes of the craspedion region retain partially the mucus cells and spirocysts, but have developed in addition granular gland cells and thick-walled nematocysts. Such craspedonemes have hitherto been met with only in *Cerianthopsis americanus* (Textfigure 16).

Finally, as modified craspedonemes of the craspedion region may be regarded the Botrucnidae. Typical botrucnidae are found in *Botrucnidifer norvegicus* and in many of van Beneden's Ceriantharia-larval forms (Textfigure 11).



## Bibliography.

1859. Agassiz, L. On some new Actinoid polyps of the United States. Proc. Boston Soc. Nat. Hist. 7, 1851—61.
1862. — A. On *Arachnactis brachiolata* Proc. Boston Soc. Nat. Hist. 9. 1862.
1863. — A. On *Arachnactis brachiolata* a species of floating Actinia found at Nahaut, Massachusetts. Journ. Boston Soc. Nat. hist. 7, 1863.
1883. Andres, A. Le Attinie. Fauna und Flora des Golfes von Neapel 9, 1883.
1900. Appellöf, A. Studien über Actinien Entwicklung. Bergens Mus. Aarb. 1900, No. 1.
1891. Beneden, E. van. Recherches sur le développement des *Arachnactis*. Archiv de Biol. 9, 1891.
1898. — Die Anthozoa. Ergeb. Plankton Expedition der Humboldt Stiftung 2. 1898.
1889. Boveri, Th. Über Entwicklung and Verwandtschaftsbeziehungen der Aktinien. Zeits. für wiss. Zool. 49, 1889.
1904. Breitung, L. L. Expedition für wissenschaftlich-praktische Untersuchungen an der Murmanküste. Liste der Fauna des Barent-Meer. Comité für Unterstützung der Küstenbewölkerung des russischen Nordens. St. Pétersburg.
- 1893 a Carlgren, O. Zur Kenntnis der Septenmuskulatur bei Ceriantheen und der Schlundrinnen bei Anthozoen Öfvers. K. Vet. Akad. Förhandl. Stockholm 1893, No. 4.
- 1893 b. — Studien über nordische Actinien I. K. Svenska Vet. Akad. Handlingar No. 3.
1897. — Zur Mesenterienentwicklung der Actinien. Öfvers. K. Vet.-Akad. Förhandl. Stockholm.
1900. — Ostafrikanische Actinien gesammelt von Herrn Dr. F. Stuhlmann. Mitth. a d. Naturh. Mus. Hamburg 17.
1906. — Die Actinienlarven in Nordisches Plankton 5. XI, Kiel and Leipzig.
1912. — Über Ceriantharien des Mittelmeers. Mitt. Zool. Stat. Neapel Bd. 20, p. 1.
1891. Cerfontaine, P. Sur l'organisation et le développement de différentes formes d'Anthozoaires. Bull. Acad. Roy. Belgique. Ser. 3, 22, 1891.
1909. — Contributions a l'étude des Cerianthides. Nouvelles recherches sur le *Cerianthus oligopodus* (Cerf.) Arch. de Biol. 26.
1877. Danielssen, D. C. Fauna littoralis Norvegiae H. 3.
1888. — *Cerianthus borealis*. Bergens Mus. Aarb. 1888, Bergen 1889.
1890. — Actinida. Den Norske Nordhavsexpedition 19. Zool. Christiania 1890.
1902. Duerden, J. E. Westt Indian Madreporarian Polyps. Mem. Nat. Acad. Sc. Washington 8, 1902.
1891. Faurot, I. Sur le *Cerianthus membranaceus* Gmelin. Mém. Soc. Zool. de France 4. 1891.
1895. — Etudes sur l'anatomie..... des Actinies. Arch. Zool. Expér. et Gén. Sér 3., 3.
1903. — Développement du pharynx, des couples et des paires des cloisons chez les Hexactinies. Arch. de zool. Expér. et Gén. (4) Vol 1.
1843. Forbes, E. On the Genus *Edwardsia* with description of new species. Ann. and Mag. Nat. hist. Ser 1., 12. 1843.
1847. — in Johnston History of the British Zoophytes London 1847. Edit. 2.
1897. Fowler, G. H. The later development of *Arachnactis albida* (M. Sars) with notes on *Arachnactis bournei* (n. sp.). Proc. Zool. Soc. London.
1856. Gosse, P. H. *Edwardsia vestita* (Forbes) Ann. Mag. Nat. Hist. (2) 18.
1858. — Synopsis of the Families, Genera and Species of the British Actiniae. Ann. Mag. Nat. Hist. (3) 1.
1858. — Characters and description of some new British Sea-Anemones. Ann. and Mag. Nat. Hist. (3) 3.
1860. — Actinologia britannica London 1860.
1897. Goette, A. Einiges über die Entwicklung der Scyphopolypen. Zeits. f. wiss. Zool. 63. 2.
1889. Haddon, A. C. A revision of the British Actiniae P. I. Trans. Roy. Dublin Soc. Ser. 2, Vol. 4.
1894. Hartlaub. Beiträge zur Meeresfauna von Helgoland. Die Coelenteraten Helgolands. Wiss. Meeresunters. Kiel.... Neue Folge Band 1. Kiel und Leipzig 1894.
1879. Heider, A. R. von. *Cerianthus membranaceus*. Ein Beitrag zur Anatomie der Actinien. Sitzber. k. k. Acad. Wien Mat. Nat. Classe 79.
1879. Hertwig, O. and R. Die Actinien Jena 1879.
1882. Hertwig R. Report on the Actinaria. Reports Sci. Res. Voya. Challenger. Zool. 6.
1904. Kingsley, J. S. Description of *Cerianthus borealis* Verr. Tafts College Studies No. 8.
1872. Lacaze Duthiers A. de. Développement des Coralliaires. Arch. de zool. Expér. et Gén. 1. 1872.

1893. **Levinsen, G. M. R.** Anthozoen. Det videnskabelige Udbytte af Kanonbaaden "Hauch's Togter 5. Kjøbenhavn 1893
1860. **Lütken, C.** Nogle Bemærkninger om de ved de danske kyster iagttagne Arter af Actiniernes gruppe. Videnskab. Meddel. naturh. Forening. Kjøbenhavn f. 1860.
1889. — Nogle temmelig uventede Forøgelse af den norske havfauna. Vid. Medd. Nat. Hist. Foren. Kjøbenhavn.
1909. **Moroff, Th.** Entwicklung der Nesselzellen bei Anemonia. Arch. für Zellenforschung, Bd. 4. p. 142.
1890. **Mc. Murrich J. P.** Contributions on the Morphology of the Actinozoa 1. The structure of *Cerianthus americanus*. Journ. of Morph. 4.
1891. — Contributions on the morphology etc. 3. The Phylogeny of the Actinozoa. Journ. of Morphology 5. No. 1.
1893. — Report on the Actiniae collected by the United States Fish Commission Steamer Albatross . . . Proc. U. S. Nat. Mus. 16.
1910. — The Actiniaria of the Siboga Expedition. P. 1. Ceriantharia. Siboga-Expeditie 15 a. Leyden.
1900. **Parker, G. H.** Synopsis of North-American Invertebrates 13. The Actiniaria. The Americ. Naturalist 34. No. 405.
1910. **Pax, P.** Studien an westindischen Actinien. Zoologische Jahrbücher Abt. Syst. Suppl. 2. H. 2. 1910.
1904. **Roule, L.** Sur un Cerianthaire nouveau. Comptes Rendus Ac. Sc. Paris 138. 1904.
1905. — Description des Antipathaires et Cerianthaires recueillis par S. A. S. le Prince de Monaco dans l'Atlantique nord 1896—1902. Res. des Campagnes — de Monaco Fasc. 30.
1846. **Sars, M.** Über *Arachnactis albida*, einen schwimmenden Polypen. Fauna littoralis Norvegiae 1. 1846.
1861. — Beretning om en i Sommeren 1859 foretagen zoologisk reise ved kysten af Romsdals amt. Nyt Mag. for Naturv. 11. Christiania.
1909. **Torrey, H. B. and Kleeberger, F. L.** Three Species of *Cerianthus* from southern California. University of California Publications in Zoology 6. No. 5.
1895. **Vanhöffen, E.** Untersuchungen über Anatomie und Entwicklungsgeschichte von *Arachnactis albida* Sars. Bibliotheca Zool. 20.
1862. **Verrill, A. E.** Revision of the Polypi of the eastern coast of the United States. Mem. Soc. Nat. hist. 1. Boston.
1863. — List of Polyps and Corals . . . . Bull. Mus. zool. Harvard College in Cambridge Mass. I.
- 1873 a. — Brief contributions to zoology, dredging on coast of New England. *Cerianthus borealis*. Americ. Journ. Sc. V.
- 1873 b. — Exploration of Casco Bay by the U. S. Fish Commission in 1873. Proc. Americ. Assoc. 32. P. 2.
1888. **Vogt, C.** Des genres *Arachnactis* et *Cerianthus*. Arch. de Biol. 8.
1888. **Wilson, H. V.** On the development of *Manicina areolata*. Journ. of Morph. 2. 1888.
1909. **Will, L.** Die Klebkapseln der Actinien und der Mechanismus ihrer Entladung. Sitzungsber. Nat. Gesellsch. Rostock (2) Bd. 1. p. 1.

## Explanation of the Plates.

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Explanation of letters.

<i>a.</i> acontium.	<i>m</i> <sub>1</sub> , <i>m</i> <sub>2</sub> , <i>m</i> <sub>3</sub> , <i>m</i> <sub>4</sub> . metamesenteries of the 1, 2, 3 4 cycles.
<i>b.</i> botrucnidae.	<i>mf.</i> craspedoneme of the craspedia.
<i>bm.</i> bunches of craspedonemes in the ciliated tract.	<i>ml.</i> lateral portions of the median streak.
<i>c.</i> craspedonemes of the ciliated tract.	<i>mm.</i> median portion of the median streak.
<i>C.</i> column.	<i>mn.</i> craspedoneme of the cnido-glandular tract.
<i>cn.</i> cnidorages.	<i>ms.</i> median streak of the filaments.
<i>dl.</i> directive loge.	<i>mt.</i> marginal tentacles.
<i>dm.</i> directive mesenteries.	<i>mz.</i> multiplication zone.
<i>E.</i> endoderm.	<i>n.</i> nematocysts (dickwandige Nesselkapseln).
<i>Ek.</i> ectoderm.	<i>nd.</i> cnido-glandular tract.
<i>ff.</i> Craspedia (Filamentchen).	<i>o.</i> ovarium.
<i>f.</i> ciliated streaks.	<i>P</i> <sub>1</sub> , <i>P</i> <sub>2</sub> , <i>P</i> <sub>3</sub> . 1. 2. 3. Protomesenterium.
<i>fp.</i> maeandric bands of the cnido-glandular tract (Nesseldrüsenstreifen s. str., le filament pelotonné).	<i>s.</i> mucus cells (homogene Drüsenzellen).
<i>g.</i> gonads.	<i>sd.</i> ridges supported by the mesogloea in the aboral part of the stomatodaeum.
<i>h.</i> hyposulcus.	<i>si.</i> siphonoglyph.
<i>kd.</i> granular gland cells.	<i>sp.</i> spirocysts.
<i>lm.</i> longitudinal muscles.	<i>st.</i> stomatodaeum.
<i>lt.</i> labial tentacles.	<i>t.</i> testes.
<i>M.</i> mesogloea.	<i>tm.</i> transversal muscles.

Plate I.

## Plate I.

*Pachycerianthus multiplicatus.*

Fig. 1. Natural size.

- 2. Section of three mesenteries with the adjacent parts of the stomatodaeum and column. Ectoderm of column not shewn.
  - 3. Section of a portion of a marginal tentacle.
  - 4. Section of a hemisulcus with adjacent portion of directive mesentery.
  - 5. Section of craspedoneme (Mesenterialfaden der Flimmerstreifenregion).
  - 6. Section of cnido-glandular tract ("the simple portion of the mesenterial filament" — "Nessel-drüsenstreifen", "le filament pelotonné").
-

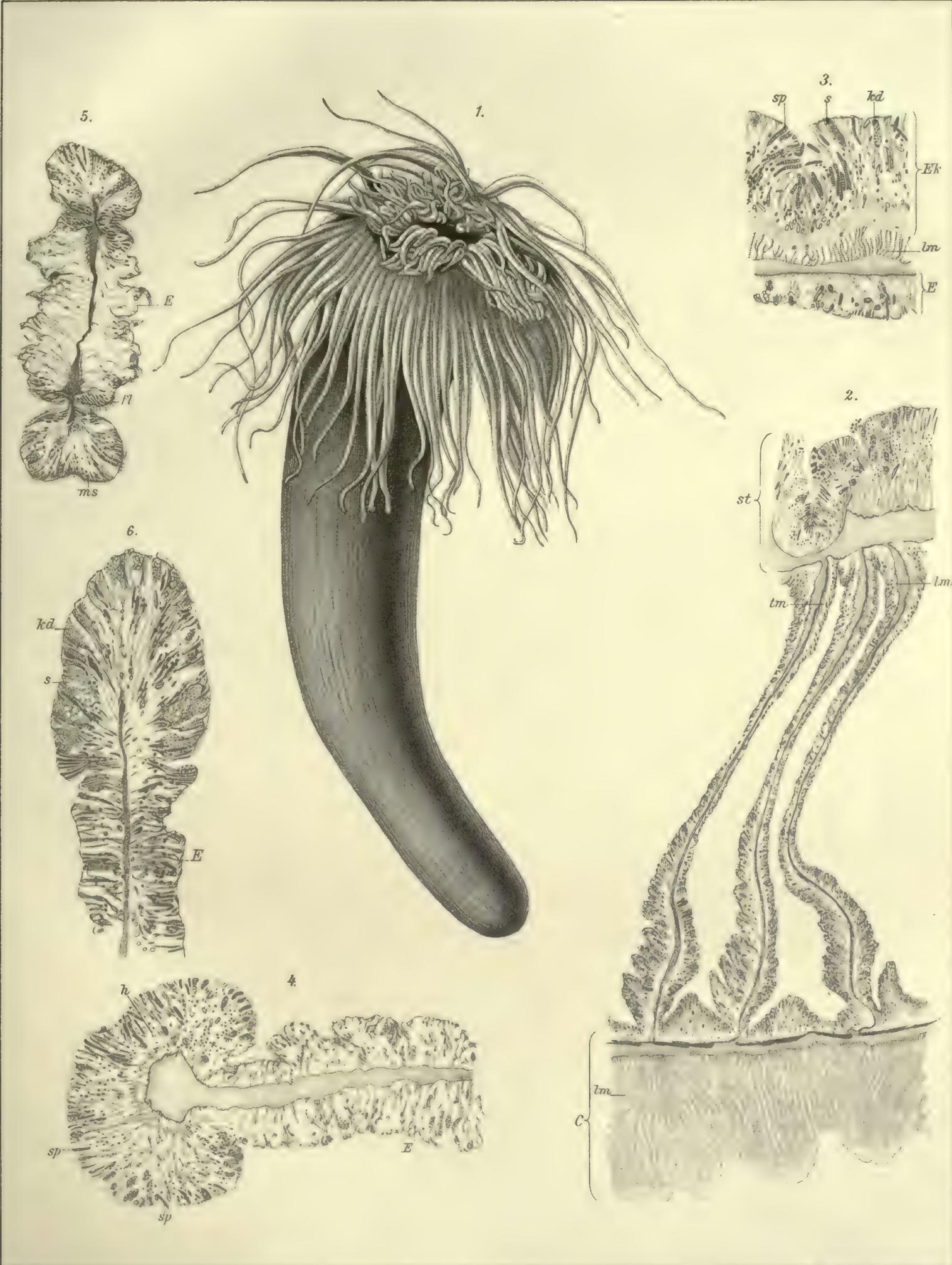




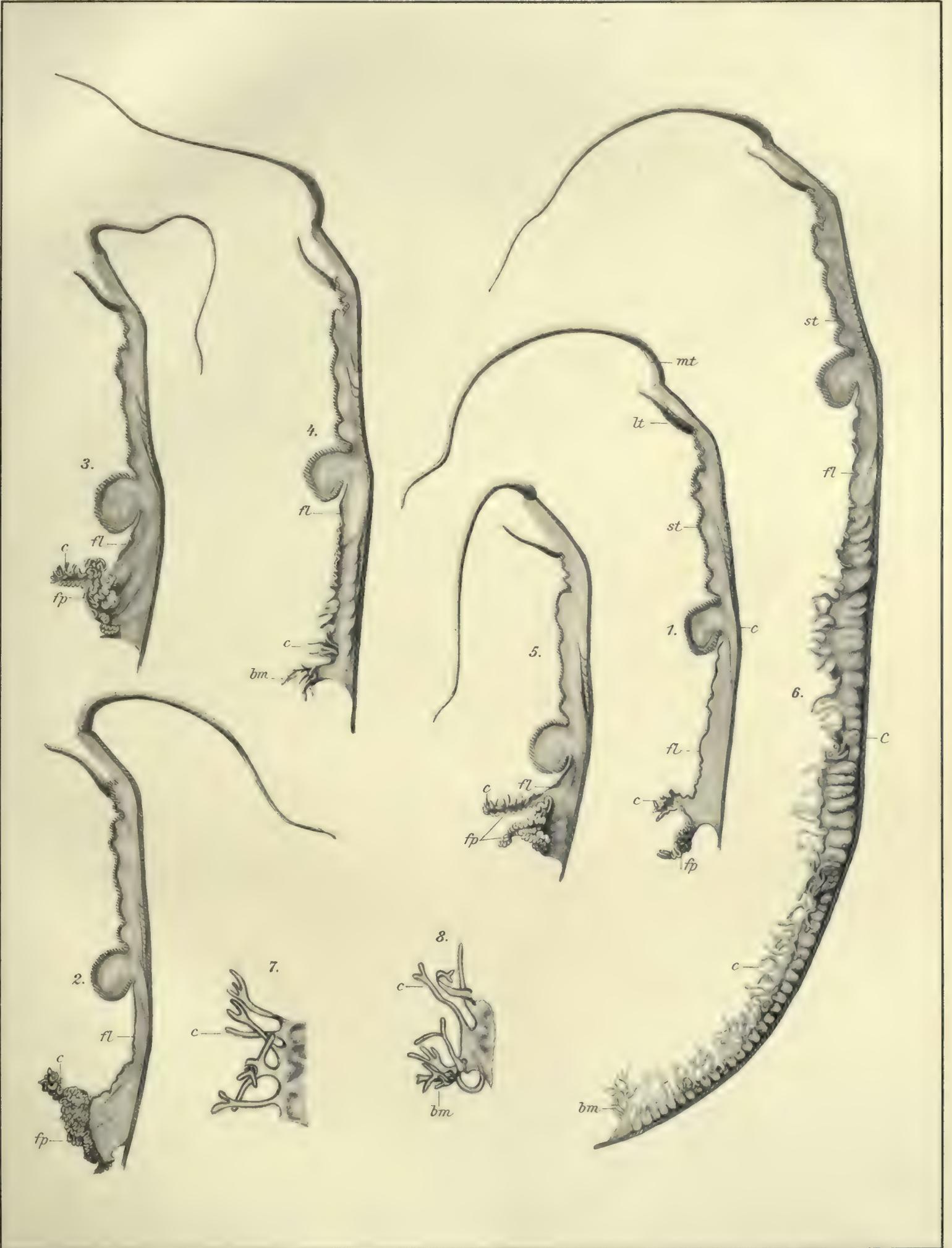
Plate II.

## Plate II.

*Pachycerianthus multiplicatus.*

- Fig. 1. The second protomesentery (P. 2)  $\times 1^{1/2}$ .  
— 2. The third protomesentery (P. 3)  $\times 1^{1/2}$ .  
— 3. The second (sterile) metamesentery  $\times 1^{1/2}$ .  
— 4. The third (fertile) metamesentery  $\times 1^{1/2}$ .  
— 5. the fourth (sterile) metamesentery  $\times 1^{1/2}$ .  
— 6. The fifth (fertile) metamesentery (first metamesentery in the second quartette)  $\times 1^{1/2}$ .  
— 7. Part of a mesentery with craspedonemes.  
— 8. » » » » » at their lowest extremity.

The very slight cnido-glandular tracts on the metamesenteries of the first and second cycles (figs. 4, 6) are not shewn in those figures, nor in fig. 8.



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Plate III.

## Plate III.

*Cerianthus lloydii.*

- Fig. 1. Section of a portion of the column and siphonoglyph in the upper part of the latter.
- 2. Section of the same parts in the lower part of the stomatodaeum.
  - 3. Section of a portion of the stomatodaeum and mesenteries at the point where the stomatodaeum passes into the filaments.
  - 4. Section of two of the processes supported by mesogloea, from the lower part of the stomatodaeum.
  - 5. Section of a part of the siphonoglyph.
  - 6. Section of a part of a mesentery with a craspedion (Filamentchen).
-

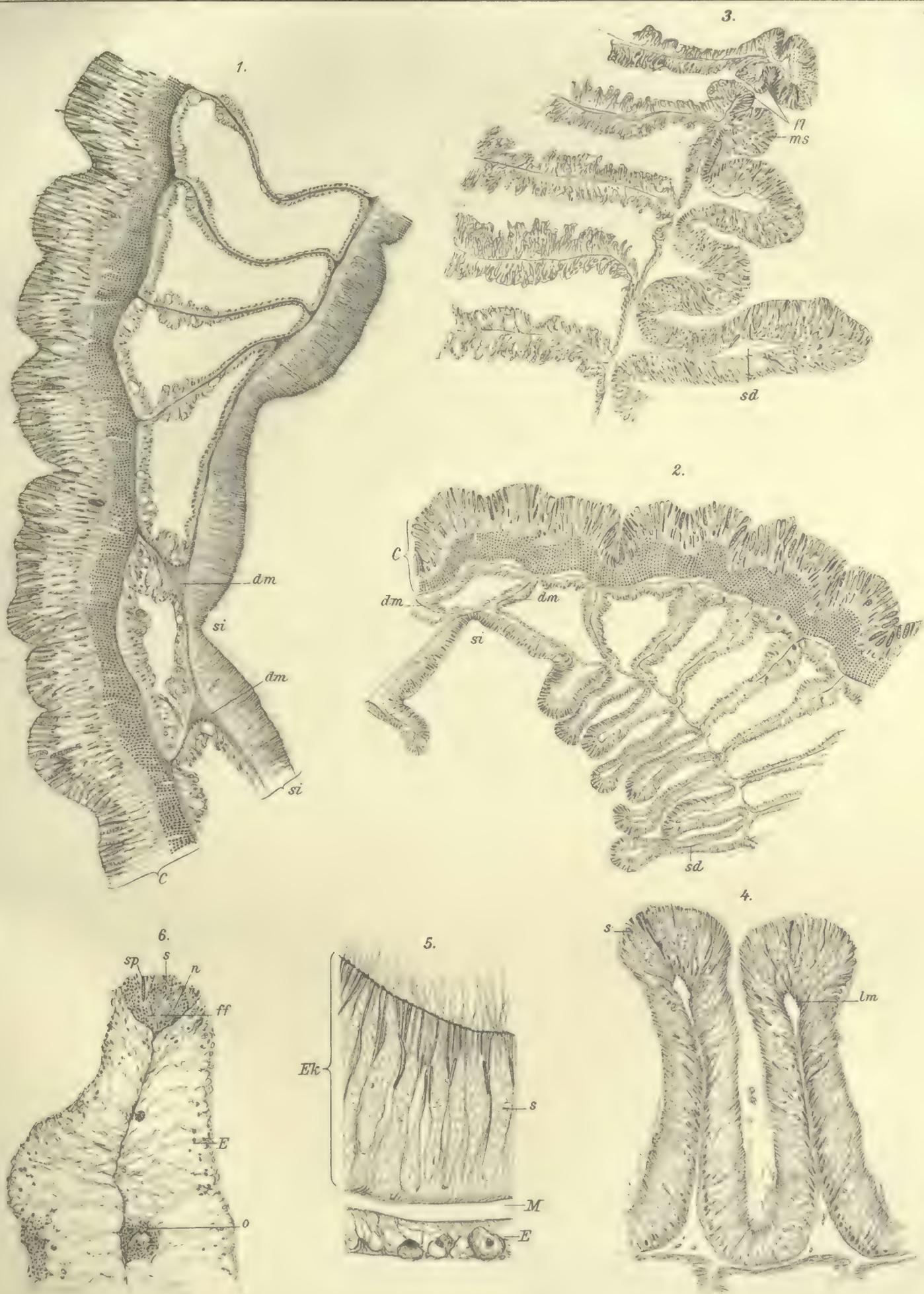




Plate IV.

## Plate IV.

Figs. 1—3. *Arachnactis albida*. Figs. 4, 5. *Cerianthus loydii*. Figs. 6—8. *Botrucnidifer norvegicus*.

Fig. 1. Section of two mesenteries at the extreme aboral border of the stomatodaeum.

— 2. Similar section  $10\mu$  below that of fig. 1.

— 3. » »  $160\mu$  » » » »

— 4. Section of a craspedoneme of the cnido-glandular tract on a mesentery of the second cycle.

— 5. Section of about half a young specimen a little before the stomatodaeum.

— 6. Section of the column and a mesentery with botrucnidae.

— 7, 8. Sections of cnidorages. In fig. 8 is seen the mesogloea stalk which connects the cnidorage with the mesentery.



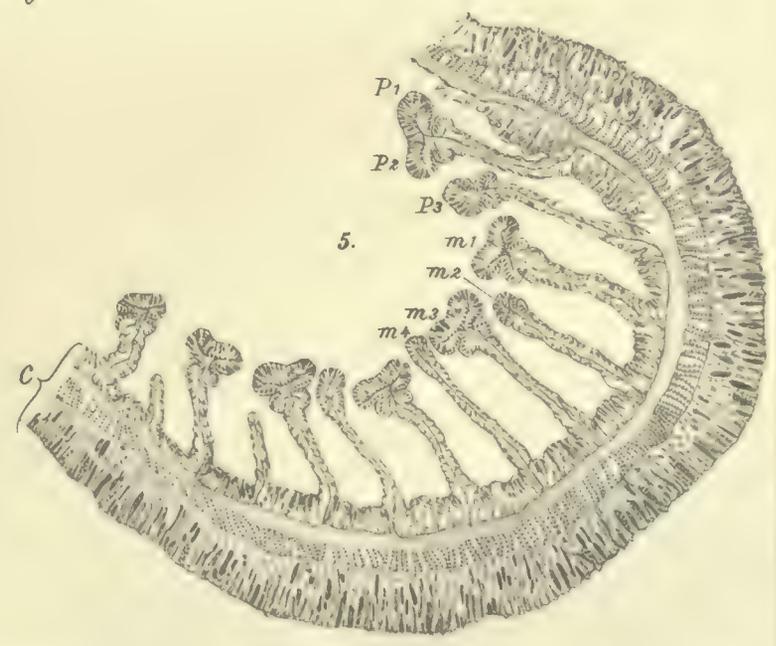
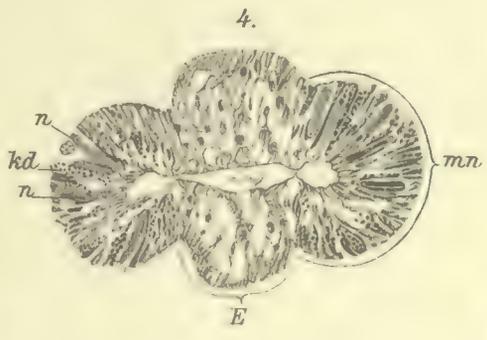
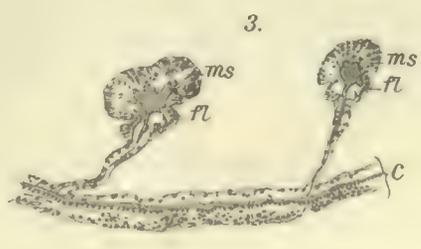




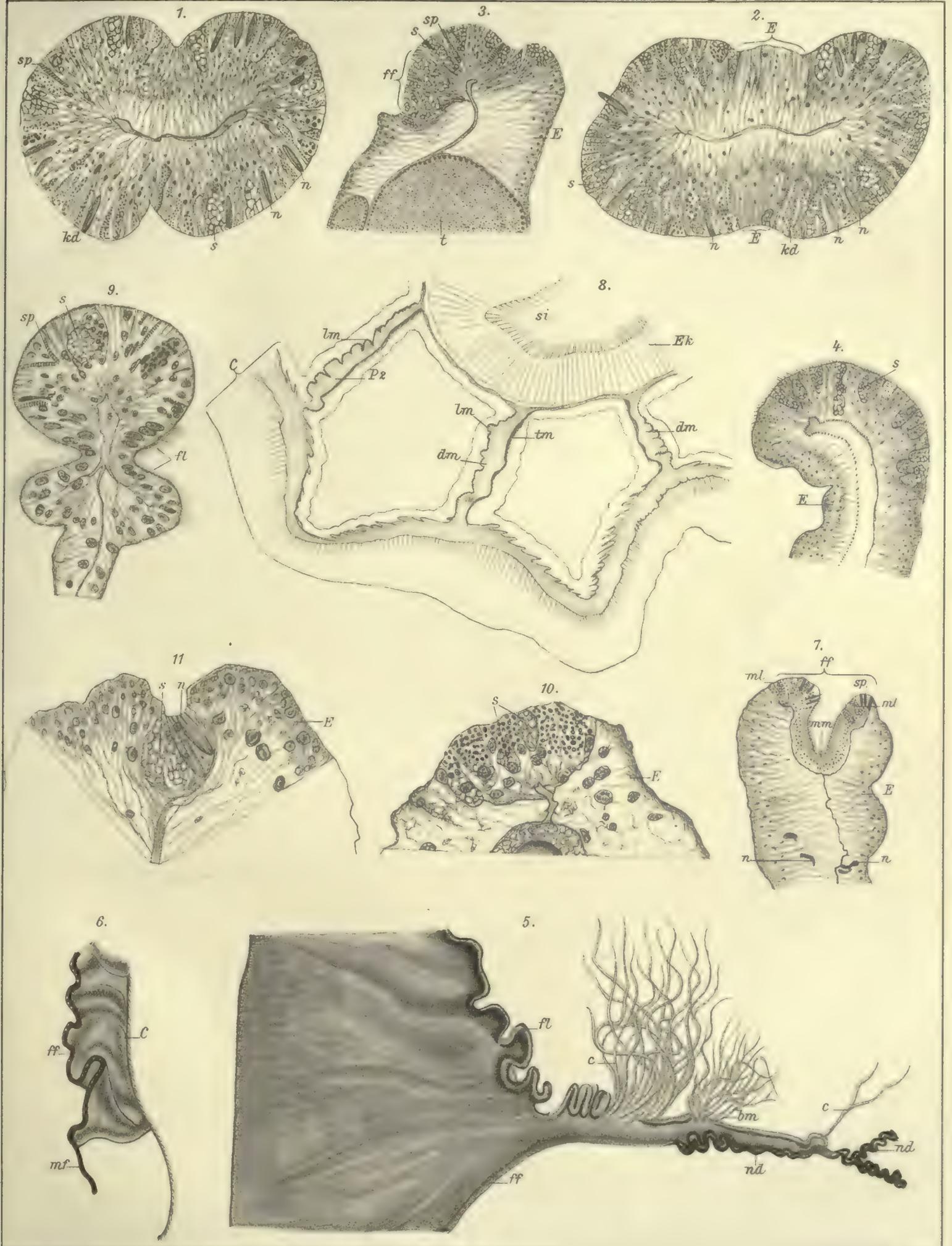
Plate V.

## Plate V.

Fig. 1—6. *Ceriantheopsis americanus*. Figs. 7, 8. *Arachnactis albida*.

Figs. 9, 10. *Botrucnidifer norvegicus*. Fig. 11. *Cerianthus lloydii*.

- Fig. 1. Section of a craspedoneme of a craspedion some way from the extremity.
- 2. Similar section nearer the base of the craspedoneme.
  - 3. Section of a portion of a fertile mesentery in the region of the sexual organs, together with craspedion.
  - 4. Section of the aboral portion of an hemisulcus. The hemisulcus is the part shewing cilia.
  - 5. Part of the second protomesentery in the craspedoneme and cnido-glandular tract region.
  - 6. Part of a mesentery with a craspedoneme of the craspedion region.
  - 7. Section of a portion of a mesentery with a craspedion in the oral portion of the latter.
  - 8. Section of a portion of a young specimen in the upper part of the hyposulcus, to shew that the directive mesenteries exhibit the same arrangement of the musculature as the rest of the mesenteries.
  - 9. Section of filament in the ciliated tract region a little below the stomatodaeum.
  - 10. Part of a mesentery with a craspedion.
  - 11. » » » » » at the aboral end of the animal.
-





# THE INGOLF-EXPEDITION

1895—1896.

## THE LOCALITIES, DEPTHS, AND BOTTOMTEMPERATURES OF THE STATIONS.

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
1	62° 30'	8° 21'	132	7°2	24	63° 06'	56° 00'	1199	2°4	45	61° 32'	9° 43'	643	4°17
2	63° 04'	9° 22'	262	5°3	25	63° 30'	54° 25'	582	3°3	46	61° 32'	11° 36'	720	2°40
3	63° 35'	10° 24'	272	0°5		63° 51'	53° 03'	136		47	61° 32'	13° 40'	950	3°23
4	64° 07'	11° 12'	237	2°5	26	63° 57'	52° 41'	34	0°6	48	61° 32'	15° 11'	1150	3°17
5	64° 40'	12° 09'	155			64° 37'	54° 24'	109		49	62° 07'	15° 07'	1120	2°91
6	63° 43'	14° 34'	90	7°0	27	64° 54'	55° 10'	393	3°8	50	62° 43'	15° 07'	1020	3°13
7	63° 13'	15° 41'	600	4°5	28	65° 14'	55° 42'	420	3°5	51	64° 15'	14° 22'	68	7°32
8	63° 56'	24° 40'	136	6°0	29	65° 34'	54° 31'	68	0°2	52	63° 57'	13° 32'	420	7°87
9	64° 18'	27° 00'	295	5°8	30	66° 50'	54° 28'	22	1°05	53	63° 15'	15° 07'	795	3°08
10	64° 24'	28° 50'	788	3°5	31	66° 35'	55° 54'	88	1°6	54	63° 08'	15° 40'	691	3°9
11	64° 34'	31° 12'	1300	1°6	32	66° 35'	56° 38'	318	3°9	55	63° 33'	15° 02'	316	5°9
12	64° 38'	32° 37'	1040	0°3	33	67° 57'	55° 30'	35	0°8	56	64° 00'	15° 09'	68	7°57
13	64° 47'	34° 33'	622	3°0	34	65° 17'	54° 17'	55		57	63° 37'	13° 02'	350	3°4
14	64° 45'	35° 05'	176	4°4	35	65° 16'	55° 05'	362	3°6	58	64° 25'	12° 09'	211	0°8
15	66° 18'	25° 59'	330	-0°75	36	61° 50'	56° 21'	1435	1°5	59	65° 00'	11° 16'	310	-0°1
16	65° 43'	26° 58'	250	6°1	37	60° 17'	54° 05'	1715	1°4	60	65° 09'	12° 27'	124	0°9
17	62° 49'	26° 55'	745	3°4	38	59° 12'	51° 05'	1870	1°3	61	65° 03'	13° 06'	55	0°4
18	61° 44'	30° 29'	1135	3°0	39	62° 00'	22° 38'	865	2°9	62	63° 18'	19° 12'	72	7°92
19	60° 29'	34° 14'	1566	2°4	40	62° 00'	21° 36'	845	3°3	63	62° 40'	19° 05'	800	4°0
20	58° 20'	40° 48'	1695	1°5	41	61° 39'	17° 10'	1245	2°0	64	62° 06'	19° 00'	1041	3°1
21	58° 01'	44° 45'	1330	2°4	42	61° 41'	10° 17'	625	0°4	65	61° 33'	19° 00'	1089	3°0
22	58° 10'	48° 25'	1845	1°4	43	61° 42'	10° 11'	645	0°05	66	61° 33'	20° 43'	1128	3°3
23	60° 43'	56° 00'	Only the Plankton-Net used		44	61° 42'	9° 36'	545	4°8	67	61° 30'	22° 30'	975	3°0

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
68	62° 06'	22° 30'	843	3°4	92	64° 44'	32° 52'	976	1°4	118	68° 27'	8° 20'	1060	-1°0
69	62° 40'	22° 17'	589	3°9	93	64° 24'	35° 14'	767	1°46	119	67° 53'	10° 19'	1010	-1°0
70	63° 09'	22° 05'	134	7°0	94	64° 56'	36° 19'	204	4°1	120	67° 29'	11° 32'	885	-1°0
71	63° 46'	22° 03'	46			65° 31'	30° 45'	213		121	66° 59'	13° 11'	529	-0°7
72	63° 12'	23° 04'	197	6°7	95	65° 14'	30° 39'	752	2°1	122	66° 42'	14° 44'	115	1°8
73	62° 58'	23° 28'	486	5°5	96	65° 24'	29° 00'	735	1°2	123	66° 52'	15° 40'	145	2°0
74	62° 17'	24° 36'	695	4°2	97	65° 28'	27° 39'	450	5°5	124	67° 40'	15° 40'	495	-0°6
	61° 57'	25° 35'	761		98	65° 38'	26° 27'	138	5°9	125	68° 08'	16° 02'	729	-0°8
	61° 28'	25° 06'	829		99	66° 13'	25° 53'	187	6°1	126	67° 19'	15° 52'	293	-0°5
75	61° 28'	26° 25'	780	4°3	100	66° 23'	14° 02'	59	0°4	127	66° 33'	20° 05'	44	5°6
76	60° 50'	26° 50'	806	4°1	101	66° 23'	12° 05'	537	-0°7	128	66° 50'	20° 02'	194	0°6
77	60° 10'	26° 59'	951	3°6	102	66° 23'	10° 26'	750	-0°9	129	66° 35'	23° 47'	117	6°5
78	60° 37'	27° 52'	799	4°5	103	66° 23'	8° 52'	579	-0°6	130	63° 00'	20° 40'	338	6°55
79	60° 52'	28° 58'	653	4°4	104	66° 23'	7° 25'	957	-1°1	131	63° 00'	19° 09'	698	4°7
80	61° 02'	29° 32'	935	4°0	105	65° 34'	7° 31'	762	-0°8	132	63° 00'	17° 04'	747	4°6
81	61° 44'	27° 00'	485	6°1	106	65° 34'	8° 54'	447	-0°6	133	63° 14'	11° 24'	230	2°2
82	61° 55'	27° 28'	824	4°1		65° 29'	8° 40'	466		134	62° 34'	10° 26'	299	4°1
83	62° 25'	28° 30'	912	3°5	107	65° 33'	10° 28'	492	-0°3	135	62° 48'	9° 48'	270	0°4
	62° 36'	26° 01'	472		108	65° 30'	12° 00'	97	1°1	136	63° 01'	9° 11'	256	4°8
	62° 36'	25° 30'	401		109	65° 29'	13° 25'	38	1°5	137	63° 14'	8° 31'	297	-0°6
84	62° 58'	25° 24'	633	4°8	110	66° 44'	11° 33'	781	-0°8	138	63° 26'	7° 56'	471	-0°6
85	63° 21'	25° 21'	170		111	67° 14'	8° 48'	860	-0°9	139	63° 36'	7° 30'	702	-0°6
86	65° 03'6	23° 47'6	76		112	67° 57'	6° 44'	1267	-1°1	140	63° 29'	6° 57'	780	-0°9
87	65° 02'3	23° 56'2	110		113	69° 31'	7° 06'	1309	-1°0	141	63° 22'	6° 58'	679	-0°6
88	64° 58'	24° 25'	76	6°9	114	70° 36'	7° 29'	773	-1°0	142	63° 07'	7° 05'	587	-0°6
89	64° 45'	27° 20'	310	8°4	115	70° 50'	8° 29'	86	0°1	143	62° 58'	7° 09'	388	-0°4
90	64° 45'	29° 06'	568	4°4	116	70° 05'	8° 26'	371	-0°4	144	62° 49'	7° 12'	276	1°6
91	64° 44'	31° 00'	1236	3°1	117	69° 13'	8° 23'	1003	-1°0					





# THE DANISH INGOLF-EXPEDITION.

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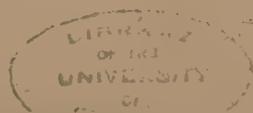
CONTENTS:

*OSKAR CARLGREN: ZOANTHARIA.*

PUBLISHED AT THE COST OF THE GOVERNMENT

BY

THE DIRECTION OF THE ZOOLOGICAL MUSEUM OF THE UNIVERSITY.



COPENHAGEN.

H. HAGERUP.

PRINTED BY BIANCO LUNO.

1913.



# THE DANISH INGOLF-EXPEDITION.

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VOLUME V.

4.

## ZOANTHARIA.

BY

OSKAR CARLGREN.

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WITH 7 PLATES AND 6 FIGURES IN THE TEXT.



COPENHAGEN.

PRINTED BY BIANCO LUNO.

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THE present paper on the Zoantharia (Zoanthidae) has been drawn up according to the same plan as my report on the Ceriantharia of the Ingolf-Expedition. Thus, it comprises not only the Zoantharia collected during the Ingolf-Expedition but also all the other northern and arctic forms of this group of animals which have been sent to me for examination, especially from the Riksmuseum in Stockholm but also from the museums in Copenhagen, Upsala, Bergen, Trondhjem and Tromsø. Besides, I have had the opportunity of examining some forms from the museums in Vienna and Berlin. To the chiefs of the Invertebrate departments or the custodians of the Coelenterata at these museums I would offer my best thanks for having lent me the material required. I am also greatly indebted to my colleague Docent Nils Holmgren in Stockholm for helping me to photograph the originals for the figures reproduced on Pl. 2.

The paper is divided into three parts:

1. Literature and summary of the northern and arctic Zoantharia.
2. Contribution to the systematic classification of Zoantharia (Zoanthidae).
3. Description of the species.



## Section I.

### Literature and summary of the northern and arctic Zoantharia.

THE first species of Zoantharia (Zoanthidae) described from northern waters was *Epizoanthus incrustatus*, which forms colonies and lives symbiotically with Eupaguridae. This easily known species was found on the Norwegian coast by Dübén and Koren, who in 1847 called it *Mamillifera incrustata*. M. Sars (1851, 1860) and Danielssen (1859) also observed this species from other localities on the same coast. In the year 1860 Sars mentioned a new species from Finmarken, which he named *Zoanthus arcticus* and in 1868 Norman described from the Shetland Islands *Z. incrustatus* and *Z. anguicomus*, the latter for the first time. A fourth species found in the Trondhjem Fjord was described by Koren and Danielssen in 1877 under the name of *Zoanthus norvegicus*. In the year 1877 Marenzeller mentioned *Zoanthus arcticus* from the regions round Smith Sound, which however is identical with *Epizoanthus lindahli* described later in this paper, and in 1886 (p. 16) the same author stated, that *Palythoa norvegica* had been dredged near Jan Mayen, a statement however which proved to be incorrect, as the specimens on closer examination were found to be identical with or at any rate closely related to *Epizoanthus glacialis*, a species described later by Danielssen. The same year (1886, p. 52) C. Aurivillius put forward a new species *E. couchii* unknown in the Norwegian fauna, a statement however that could not be maintained, as the species in question is closely related to *Epizoanthus erdmanni* of the present work and may possibly even be considered a variety of the latter species. Thus, up to 1890 4 species of Zoanthidae living at the Norwegian coasts or in the northern seas, namely, *Epizoanthus incrustatus*, *E. arcticus*, *E. norvegicus* and *Parazoanthus anguicomus*, had been described in some detail, though very incompletely.

During the period from 1860—1880 the well-known naturalist Verrill provided us with information regarding some Zoanthidae from the coasts of North America. In the year 1864 he described from New Jersey *Zoanthus* (*Epizoanthus*) *americanus*, which has later been met with very often in the arctic regions, as far as Cape Cod and also in the region Cape Cod to Cape Hatteras (Parker 1900, p. 757). In 1891 Haddon and Shackleton proved, however, that this species is identical with Sars' *E. incrustatus*. In the year 1882 another species of the North American Zoanthid fauna became known, namely, *Epizoanthus paguriphilus*, first observed in deep water off the Nova Scotian coast; like *E. incrustatus* this species forms carcinoecia. Further, Verrill mentions an incrusting variety of *E. americanus* (1882, p. 316, 1883, p. 6), which he considers to be identical with Koren and

Danielssen's *E. norvegicus*. In his paper of 1883, Pl. 8, fig. 6, an illustration of this variety is given. Though it is, of course, very difficult to settle the question without being in possession of the original specimens, if they exist, the variety undoubtedly belongs to a Parazoanthus species. Verrill's figure has, namely, a fairly strong resemblance to the colony figured by me on Pl. I, fig. 19, collected at St. 2245 U. S. F. C. together with the typical *E. americanus* (incrustatus) and determined as such, but which on closer examination proved to be a Parazoanthus species and in my opinion no other than *P. anguicomus*. Lastly, in the year 1885 Verrill described another carcinom-forming species, *Epizoanthus abyssorum*, dredged during the Albatross Expedition in 1884, and mentioned at the same time a free variety of this species (probably a new species). Though *Epizoanthus abyssorum* has evidently a more southerly distribution than the other North American species mentioned, I prefer to deal with it here for comparison between *E. incrustatus* and *E. paguriphilus*. I would point out, however, that I have had very little material of the North American species at my disposal, this being the reason why these are not dealt with in greater detail here, as also because a further criticism of the species based on the literature is fairly unremunerative. A revision of the collected material of the Zoanthidae forms will certainly prove, that the number of Zoanthid species is also on this coast not so small as seems to appear from the literature. I have not thought it necessary to give a complete list of the literature of these three species here. Up to 1891 such a list has in any case been given for both of the first-named species in Haddon and Shackleton's paper (1891).

In the year 1890 the number of known northern and arctic Zoanthidae species was almost doubled by Danielssen's description of the material collected during the Norwegian North Atlantic Expedition. The new species occurring are *Epizoanthus roseus*, *E. arborescens*, *E. glacialis* and *Mardöl erdmanni*, the last of which was proved by Haddon and Shackleton's investigations (1891) to belong to the genus *Epizoanthus*. In 1887 (p. 316) Mortensen was of opinion, that he had found *Zoanthus sulcatus* and *couchii* in the Limfjord, a determination however which must be erroneous at least as regards the latter, as this species according to Haddon and Shackleton is an *Epizoanthus* species, whereas Mortensen's form appeared to belong to a genus *Isozoanthus* founded by me. Lastly, in 1905 Carlgren mentions from Finmarken, besides *E. erdmanni*, also *Isozoanthus arborescens*, for which he later set up the above-named genus, *Isozoanthus*, forming a link between the genera *Epizoanthus* and *Parazoanthus*.

Thus, when I began my paper on the northern and arctic Zoanthidae, altogether some ten species of these had been described previously, many of them, however, very incompletely and mainly according to the external features. In 1890 Danielssen certainly gives anatomical descriptions of his new species, but in many respects these are not to be trusted and are of small use for the identification of the species. Of far greater importance is Haddon and Shackleton's paper on the British species of Zoanthidae. We find here a good anatomical description, which however in some respects might have been somewhat more comprehensive. As this is the only efficient work dealing with the Zoanthidae of the North European coasts, I may refer to it specially, as it also contains an account of the most important literature on the Zoanthidae up to 1891. Of the species dealt with in the sequel, however, only *E. incrustatus*, *E. paguriphilus* and *Parazoanthus anguicomus* are described in detail in the above-named paper.

Of the species already known the following are described in the present paper.

*Epizoanthus* *incrustatus*, *paguriphilus*, *abyssorum*, *glacialis*, *roseus*, *norvegicus* and *erdmanni*.

*Isozoanthus* *arborescens* and

*Parazoanthus* *anguicomus*.

Further, some anatomical details of *Parazoanthus dixonii* are also given here.

The new species are:

*Epizoanthus* *danielsseni*, *lindahli*, *beerenislandicus*, *koreni*.

*Isozoanthus* *bulbosus*, *danicus*, *magninsulosus*, *multinsulosus*, *davisi*, *ingolfi*, *dubius*, *islandicus*.

*Parazoanthus* *haddoni*.

All told the descriptions thus comprise 22 species, showing that the northern and arctic Zoanthid fauna is not so poor as was formerly thought.

In the present paper I do not occupy myself very much with the geographical distribution, as I shall return to this subject later on when dealing with the Ceriantharia and Actinaria of the same regions. Along with this I propose to make a more detailed comparison between the Actinian fauna of the arctic and antarctic waters. It is worth noting, that though the number of known species from these regions has increased considerably, no representatives of the microcnemic Zoanthidae have been found there. The occurrence of the new genus *Isozoanthus* in both of these zones is also worthy of note, though it is not impossible, that this genus like the genera *Epizoanthus* and *Parazoanthus* also occurs in the intermediate regions. There seems to be a great difference in the distribution towards the north between the genera *Epizoanthus* and *Isozoanthus* on the one side and *Parazoanthus* on the other, the latter not being represented in the true arctic fauna, in which both the first-named occur. Towards the north the genus *Parazoanthus* seems to be replaced by *Isozoanthus*, of which a decidedly arctic species, *I. bulbosus*, has been met with so high up as north of Spitzbergen at 81° N. Lat., this being the northernmost place of occurrence of any Zoanthid species. It is as yet too early to foretell, what the conditions are in the antarctic region, but I am of opinion, that they are similar there. The material at my disposal from this region is, however, too limited to allow of any certain decision. The Zoanthid fauna seems to be poorer and to decrease more quickly towards the south, than is the case in the northern waters towards the north.

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## Section II.

### Contribution to the systematic classification of the Zoanthidae.

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Among the Anthozoa, at least among the forms generally comprised under the name sea-anemones, there is hardly a group which is so uniform in its morphological characteristics as the Zoantharia (Zoanthidae). The few genera are generally easily distinguished from each other, whereas it is more difficult to separate the species within the different genera. A number of Zoantharia species have been described especially in the older literature and almost exclusively from outer

characteristics, which however are often so little distinct, that an identification is only possible in exceptional cases. This is all the more difficult as the group of Zoantharia evidently comprises many species that are probably in process of differentiation. An attempt to bring some order into the classification was tried in 1891 by Haddon and Shackleton, who quite reasonably founded their classification on anatomical characters. Other scientists, as Duerden and several others, have followed in their footsteps but we are still without sufficiently good characteristics for the separation of quite a number of species.

Thus, many of the characteristics on which the classification of the species has been founded are found to be of small importance. Regarding the appearance of the cœnenchyme, firstly, it may sometimes give us good hints but we still know too little of its variations, which are caused by the object on which the cœnenchyme is fixed. That a variation takes place is almost certain, but its limits cannot be determined as yet. That the cœnenchyme may have a different appearance in the same species is seen in *Epizoanthus incrustatus*, which may have both a carcinoecium-forming cœnenchyme and a slightly tube-shaped cœnenchyme, on the supposition that the free variety *barlesi* of *E. incrustatus* belongs to this species. Pax' investigations of West Indian species of *Palythoa* seem to indicate, that a variation occurs, even though it seems possible here that separate species have been dealt with. The canal-system in the cœnenchyme might also be of use for the separation of the species, though but very little information thereon has been published as yet.

The outer appearance of the polyp may sometimes show very good characteristics for identification, but the species are often so little distinguished from each other that two polyps alike in outer appearance may nevertheless belong to 2 different genera (cf. e. g. figs. 13, 19, Pl. I). The relation between height and breadth has been used for differentiation of species, but is such a weak character that the different degrees of contraction in different polyps may change the proportion between height and breadth. Even the capitular region and the distal contours of the polyp are always somewhat different in appearance according to the amount of contraction. Thus, the greatly distended polyps of one species cannot be summarily compared with the greatly contracted ones of another. The furrows on the capitulum, which generally correspond to half the number of mesenteries, are also a much used, specific character, but this method has the fault, that the character is variable, as furrows are not always found corresponding to the youngest mesenteries and the number of mesenteries and thus also the number of capitular furrows change according to the age of the polyps, the older ones having more mesenteries and consequently more capitular furrows than the younger, and even in the former a variation also occurs though within certain limits. In characterising the species according to the capitular furrows, it is thus necessary to pay attention to well-developed polyps, which often necessitates having large material.

Most of the Zoanthidae are, as already known, incrustated with foreign bodies, foraminifera, sand-grains and sponge needles. Regarding the incrustation generally, it seems in each separate species to consist of the same material, as shown by Haddon and Shackleton, though small variations naturally always occur; but I know more than one case, especially in *I. bulbosus*, where two different specimens of the same species have had quite different incrustations, for which reason I think it possible that similar conditions may be observed among other species. Though, in my

opinion, a different incrustation in two otherwise similar forms does not entitle us to set up two different species, and the incrustation thus theoretically is of no great value for the characterization, yet in practice, owing to what has been said above, it may be used to help in the characterization of a species.

Regarding the arrangement and appearance of the tentacles, they give at least in preserved specimens no assistance in the identification of the species, the appearance and arrangement being almost the same in all species of Zoanthidae. The number varies in different species but as it is dependent on the number of mesenteries, it is of no practical importance for the classification.

Even the structure of the œsophagus provides no basis for the identification of the species, as it is fairly uniform. Whether it is elongated or not, whether the diameter is small or large, is generally dependent on its more or less contracted state. The appearance of the siphonoglyphe is only exceptionally of importance for the classification, especially as in the Zoanthidae, in contrast to what we find in the Ceriantharia, it is only the directive mesenteries which are always attached to it. The same applies to the prolongation of the siphonoglyphe (hyposulcus) which, at any rate in all species examined by me, showed almost the same degree of development.

As to the finer anatomical structure, the body-wall, especially the structure of the mesoglœa, provides one of the best characters for the separation of the species, even though variations may sometimes occur within the same species. The different sizes of the ectoderm, endoderm and mesoglœa in relation to each other should be fairly constant in the different species, whereas the size of the germ-layers varies with the state of contraction. The ectoderm may vary greatly in appearance in the different species but above all the appearance of the mesoglœa is of importance for the classification, as it either contains but few cells, or is provided with numerous cells, cell-islets or lacunae arranged in a manner often very characteristic for the species.

The appearance and structure of the sphincter help to characterize the genera but are not always of such great importance for the separation of the species, though in a few cases very characteristic sphincters occur. It must also be observed that there is a variation in the appearance of the muscle, which at least in many cases may be connected with the state of contraction of the sphincter.

The number of the mesenteries gives a very good character for the separation of the species, but the variations are not so unimportant, even in full-grown polyps. Furthermore, it has to be mentioned, though already pointed out previously in discussing the capitular furrows, that the mesenteries increase in number with age, so that only full-grown specimens of different species can be compared with certainty. The breadth of the micro-mesenteries may vary in different species, though this is fairly seldom, as it is generally of importance for the separation of species. It must specially be pointed out, that in different species the breadth is compared at the same part of the body, as for example the lower part of the œsophagus, the micro-mesenteries in the different parts of the body being of extremely varying breadth, in the distal part well developed but tapering quickly downwards. But even if we consider this, we run the risk of making mistakes in classifying, as the state of contraction of the pylop changes the position of this zone very considerably. The appearance of the longitudinal muscles in the mesenteries may often be very characteristic, but even here we

must notice, that a specimen expanded broadwise gives quite a different appearance from a specimen with mesenteries contracted broadwise. The parieto-basilar muscles seem generally to be weak, sometimes they may be more differentiated, but are on the whole of small importance for classification. The distribution of the longitudinal and the parieto-basilar muscles on the body-wall is sometimes small, sometimes greater and is sometimes of use for the separation of the species. The macro-mesenteries project more or less into the gastrovascular cavity, so that it would seem as if this might be a fairly useful character. It must be pointed out, however, that the appearance of the mesenteries is quite different in contracted and expanded specimens of the same species and it is also of importance in the same respect whether the sexual organs are developed or not. If the sexual organs are much developed, namely, the mesenteries are considerably broader than is otherwise the case.

The structure of the filaments is of no great use for the classification of the species, as it is mainly the same in all forms.

As has been pointed out, there is great uniformity in structure and appearance in most of the species within the genera, for which reason the identification of many species is distinctly difficult. As most of the Zoanthidae are besides incrustated so much, that in many cases it is quite impossible to get moderately good sections, it is obvious that the identification of Zoanthidae-species and the setting up of new species is in most cases a matter of considerable difficulty. It was of great importance, therefore, to find some more peculiarities of organisation, which showed such great differences in the different species, that they could be used for their identification. As I have found regarding the Actiniaria, that the structure, size and arrangement of the nematocysts provide good characters for identification, I have investigated if the same was the case in the Zoantharia. Even if this is not so much the case in the Zoantharia as in the Actiniaria — as the first-named show great uniformity probably even in the nematocysts, the structure, size and arrangement of the nematocysts in the Zoantharia may nevertheless contribute to the identification of the species. As in the Actinaria there may certainly be some species of a genus which have almost the same distribution, structure and size of the nematocysts, whereas other species may show great differences in this respect. As the length and breadth of the nematocysts seem to be constant — of course with a certain amount of variation — the measurements of the nematocysts are in my opinion more suited to the determination of a species than most of the measurements of Zoanthidae, even more suited than most of the other structural characters, though of course with certain exceptions. In the following I have also taken account of the nematocysts as far as possible in the description of the species. Especially the large nematocysts with much coiled spiral threads, which are found in the body wall and filaments, sometimes in the tentacles and the oesophagus, appear to be of varying size in the different species. It must be observed that the range of variation seems great in certain cases. It is possible, however, that this condition is only apparent. I cannot set aside the possibility, namely, that some of the large nematocysts with greatly twisted threads, which have a thinner wall than the other capsules, may to some extent change their dimensions in different liquids of preservation, i. e. not be quite resistant. The relation between length and breadth would thus be different in varying degrees of contraction. I cannot however express my opinion on this point with certainty, as none of the experimental proofs in this respect could be made by me. Without denying the possibility that the large

nematocysts may change their form a little in the different liquids of preservation, these capsules may nevertheless be considered resistant on the whole. This is also indicated by the agreement in numbers I obtained in species where a large material was examined. It seems to me at any rate, that data regarding the structure, size and distribution of the nematocysts must be taken into consideration in the characterisation of the different forms of Zoanthidae. Such data may often give reliable information as to whether we have a constant species before us and are at any rate for the sake of control of great value.

The arrangement, size and structure of the nematocysts have been examined in preparations embedded in glycerine diluted with water. As to the filaments it is generally very difficult to separate them from other parts of the mesentery. Parts of these break loose when the filaments are removed. We might imagine, therefore, that the nematocysts are not always lying in the filament but in other parts of the mesentery. This does not seem however — at any rate not as a rule — to be the case, as I have found none of the capsules characteristic of the species in sections of the non-filamentous part of the mesenteries. There are exception to this rule however, to be mentioned later in the present paper. In a bottle with 6 colonies of *Epizoanthus incrustatus* from the neighbourhood of Iceland I found that two of the colonies had some peculiar, egg-shaped nematocysts in the mesenteries, which were not present in the other colonies from the same locality. At first sight I thought I had another species before me or at any rate a variety, but as I could find no other characters separating these colonies from the normal ones, I had to look for another explanation. This was soon obtained, all the sooner because it struck me in the first examination that these nematocysts closely resembled the nematocysts of Hydrozoa. In this case they should not lie in the filament itself but inside this in the entoderm. On closer examination of the section this was found to be correct. The egg-shaped capsules have thus undoubtedly been taken in together with the food. I have found the same kind of nematocysts in a colony of *Epizoanthus erdmanni* also from Iceland. Even in this colony the capsules seemed to be lying in the entodermal part of the mesentery, though the fixing was hardly so good here that they could be said with absolute certainty to be found in the entoderm only. If this kind of unusual capsule occurs in the filament, especially if only in certain specimens of a species, there is reason to suspect that we are dealing with capsules that have penetrated into the animal from without and not a normal component. I think it necessary to point this out specially for the sake of future investigations.

In all the specimens examined by me the nematocysts are almost always arranged in the same way. In the ectoderm of the cœnenchyme and of the body-wall only nematocysts with greatly twisted thread are found. Regarding the distribution of the nematocysts in the body wall, they are most numerous in the proximal part, in the capitular region they are scarce or absent. Yet sometimes the nematocyst-capsules there are more numerous and of a different size and appearance than in the other parts of the body-wall. In the ectoderm of the tentacles there are always extremely numerous spirocysts (thin-walled capsules), less numerous typical, thick-walled capsules, sometimes similar capsules as in the body-wall, though never abundantly.

The oral disc shows, in the few cases I have examined this, the same distribution of the capsules as occurs in the tentacles. In the œsophagus there is mostly thick-walled capsules, in some

of which the basal part of the spiral thread is fairly distinct; more seldom and more scattered we also find some nematocysts of the same kind as in the body-wall. In the filaments we find the same sort of capsules as in the body-wall, sometimes in two different sizes, and also some thick-walled capsules through which the basal part of the spiral thread can be seen and often, further, typical, transparent thick-walled capsules.

Though I hope that the nematocysts of the Zoantharia species may be of use in the identification of these species and make this to some extent easy, I am however fully aware that we are still far from having discovered the special characters of many species. The large number of Zoanthidae described in this paper may appear surprisingly great to many Actiniae specialists. But I would remark, that the material investigated from northern and arctic seas is undoubtedly the largest that any scientist has had for examination. It is of course quite possible, that later investigations may show, that some of the species described here are varieties of other species or that what is considered a variety here may come to be regarded as a separate species. Taken on the whole, I feel convinced, however, that the number of species will not be much reduced, as most of the species, of which I have had a rich material, are certainly good species.

As already pointed out in 1900, the distribution, size and structure of the nematocysts are in the Actiniae of no small importance for the identification of the species, a theory that has been confirmed by my later investigations on the Actiniae. Pax doubts their importance, but so far as I can find, he has not made any extensive investigations on a large number of species to clear up the question. He admits, however, that in a few cases the capsules may serve as good characters. As evidence for his view he refers to some measurements made by me on 3 species belonging to the genus *Actinioides* and finds them to be almost the same, from which he draws the conclusion that the nematocysts are of no great importance for the classification. I do not agree with him here, for the same might be said about any organs of the species, if we agreed with Pax's standpoint. How often do we not find, that the sphincters, the arrangement of the mesenteries and a great many other organs show agreement in many species of a genus of Actinaria, yet nobody would deny their great importance for the classification of this group. The occurrence of certain kinds of nematocysts, their size and arrangement, is a character as good as any, even if it is not always of importance for the separation of closely-related species. For the separation of many genera of Actinaria they may also be used with advantage, for, so far as I have found in the abundant material investigated, many genera have nematocysts of a certain nature and arranged in a certain manner. It is at any rate a fact, that the nematocysts are found to be indispensable for the separation of the species, as soon as the expert has recognized their utility. In some cases, I may say, it is only a closer study of the nematocysts, which has given a starting point for the separation of the species belonging to two nearly allied genera — species which showed so great a resemblance that it would hardly have been possible to separate them, had not the different size of the nematocysts in certain parts of the body opened up the possibility for a grouping of the species. In another paper I shall deal further with these features. I would therefore recommend those who write on the Actinaria, to pay particular attention to the arrangement and structure of the nematocysts, being convinced that many systematic errors would be avoided if the capsules were only subjected to a proper examination.

## Section III.

### Description of the species.

Family *Macrocneminae* Haddon & Shackleton 1891.

Genus *Epizoanthus*. Gray 1867.

Macronemic Zoantharia with a single mesogloæal sphincter muscle. The body wall is incrustated. The ectoderm is usually continuous but may be discontinuous; cell-islets and lacunae often in the mesogloæa. Dioecious polyps connected by cœenchyme, which may be band-like, incrusting or greatly reduced, as in the free forms.

As Haddon and Shackleton have given a good diagnosis of the genus, I have used it in the main here. Of the 11 *Epizoanthus* species described here 4 are new: *lindahli*, *danielsseni*, *beerenislandicus* and *koreni*. *E. incrustatus* and *paguriphilus* have previously been described in detail by Haddon and Shackleton (1891) but their description needs supplementing on several points. Regarding *E. norvegicus* these authors also give some anatomical information and show that *Mardøel erdmanni* Dan. is an *Epizoanthus*-species. The other species are described entirely from outer appearance or the anatomical description is so bad, that it cannot be used for a characterization of the species.

Four of the species *E. incrustatus*, *paguriphilus*, *lindahli* and *koreni* have been dredged by the Ingolf-Expedition.

#### Synopsis of the *Epizoanthus*-species described here

- A. Species with carcinoecium
- a. Without ventral polyp. Ectoderm of the body wall continuous.
    - b. The capitular region of the polyps in the contracted state truncate, disc-like, number of mesenteries 32—42 ..... *incrustatus*.
    - bb. The capitular region of the polyps in the contracted state not truncate, not disc-like, number of mesenteries about 46 ..... *abyssorum*.
  - aa. With ventral polyp. The ectoderm of the body wall discontinuous, except in the capitular region; number of mesenteries 64—80 ..... *paguriphilus*.
- B. Species without carcinoecium
- a. The ectoderm of the body wall in the polyp discontinuous ..... *norvegicus*.
  - aa. The ectoderm of the body wall in the polyp continuous.
    - b. Single unattached polyps or free colonies.

- c. The large nematocysts of the filaments and of the capitular region have the same structure, narrow and long (4 times longer than broad), unlike those in the other parts of the body wall ..... *lindahli*.
- cc. The large nematocysts of the filaments are of moderate length (length being at most as 3.5 times breadth). The capsules of the capitular region, if any, resemble those in the other parts of the body wall..... *erdmanni*.
- bb. Polyps and colonies attached. The cœnenchyme more or less developed.
- d. The large nematocysts of the filaments are narrow and long (the length being more than 4 times the breadth). The capsules of the capitular region of the same kind, but unlike those in the other parts of the body wall ..... *danielsseni*.
- dd. The large capsules of the filaments are of moderate length (the proportion between length and breadth being at most as 3.5 to 1). The capsules of the capitular region, if any, resemble those in the other parts of the body wall.
- e. The sphincter comparatively feeble, number of mesenteries about 32. The large nematocysts of the filament 22—31  $\mu$  long, 12  $\mu$  broad ..... *roseus*.
- ee. Sphincter strong
- f. The large nematocysts of the filaments 34—41  $\mu$  long and 10—12  $\mu$  broad. Cell-islets and lacunae often found at the base of the insertion of the mesenteries, number of mesenteries 38—42..... *beerenislandicus*.
- ff. The large nematocysts of the filaments 26—36  $\mu$  long and 10—12  $\mu$  broad. Cells numerous, cell-islets more scarce in the mesogloea of the body wall, but not present near the base of the mesenteries; number of mesenteries 36—52 .... *glacialis*.
- fff. The large nematocysts of the filaments 26—29  $\mu$  long and 10  $\mu$  broad. Numerous oval or round and separate, large cell-islets, further, large lacunae containing cells in the mesogloea of the body-wall; number of mesenteries about 36.. *koreni*.

Species **Epizoanthus incrustatus** Düb. & Koren.

Pl. 2, fig. 26.

*Mammillifera incrustata* n. sp. Düben & Koren 1847. Förhandl. Skand. naturf. Möde p. 268. Isis 1848 p. 536. Sars 1851. Nyt Mag. Naturv. 6 (2), p. 142, Danielssen 1859. Nyt Mag. Naturv. 11, p. 45.

*Zoanthus incrustatus* Düb. & Koren, Sars 1860. Förhandl. Vidensk. Christiania, p. 141. Förh. Skand. Naturf. København 8, p. 691.

*Polythoa arenacea* d. Ch. p. p. Andres 1883 Le Attinie, p. 522.

*Epizoanthus incrustatus* (Düb. & Koren) Haddon & Shackleton, Sc. Trans. R. Dublin Soc. 1891, p. 636, Pl. 58, figs. 1—22, Pl. 59, fig. 2, Pl. 60, fig. 1 (contains a complete synonymy and list of literature of this species up to 1891).

*Epizoanthus americanus* n. sp. Verrill. 1867. Mem. Boston. Soc. Nat. Hist. 1, p. 34, 45.

*Palythoa incrustata* Roule 1900. C. R. Acad. Sc. Paris. 131 1900 p. 279.

*Sidisia incrustata* Düb. & Koren Arndt Jahr. Schl. Gesells. vat. Cultur 1912, p. 123.

Occurrence. Jutland Reef 60—130 fathoms, M. Uddström 1873, R. M.

Jæderen 100—150 fathoms, M. Olsson 1877, R. M.

Bergen Koren, R. M.

N. W. of Bergen 100—200 fathoms, M. Olsson 1877, R. M.

Finmarken Karlsø N. of Tromsø 70 fathoms, Goës & Malmgren, R. M.

— — 90 fathoms, Malmgren 1864, R. M.

— Foldenfjord, 530 m. 64, Nordgaard.

— Vestfjord, clay 11·8 1877, St. 252 N. N. Atlantic. Ex., Bergen M.

61° 16' N., 1° 18' E. 150 m. Sand, mud, shells. Greenland Ex. 21/5 1899, R. M. St. 58 Michael Sars Ex. 1900 30/8 Bergen M.

66° 35' N., 23° 47' W. 117 Danish fm., bottom temperature 6·5°. Ingolf-Exp., St. 29, Cop. M.

50° 57' N., 10° 46' W. 184 m. St. 96, 27/7. 1910 Michael Sars Exp., Bergen M.

(75 miles S. off Marthas Vineyard 86 fm., from U. S. N. M., R. M.)

- — off Marthas Vineyard U. S. Fish. Comm. Cop. M.)

40° 40' N., 69° 30' W. 23/5. 1888, R. M.

(40° 01' 15" N., 70° 22' W. 98 fm., U. S. Fish. Comm. Albatross, R. M.).

Sandy Hook Shinnicock Bay, 18 fm. Josephine Exp., R. M.

N. America, Bank of New Jersey, R. M.

Size: The largest colony I have examined — the colony had no less than 18 polyps — had a length of 2·5 cm. and a breadth of 1·3 cm. not comprising the polyps. The largest polyp when contracted had a length of 1·1 cm.

Colour: Light sandy-coloured or dark-gray in alcohol.

External appearance: As the outer appearance of the colonies has been described in detail by Haddon & Shackleton (1891), I shall here only give a short description of the carcinoecium-forming typical forms. The cœnenchyme is well developed, forming the carcinoecia originally on gastropod-shells, which are inhabited by hermit crabs. In older specimens the polyps are arranged irregularly on the dorsal side of the carcinoecium. In the largest specimen I counted no less than 18 polyps, thus a larger number than observed by Haddon and Shackleton. No ventral single polyp is found as is the case in *E. abyssorum*. Haddon and Shackleton state, that in younger colonies the polyps are arranged in three series and describe their arrangement. Even if the development seems in many cases to proceed as described by Haddon & Shackleton, there is undoubtedly a great number of exceptions from the rule laid down by them. The only thing I have been able to determine with certainty is, that during the 2-polyp stage, one of the polyps lies nearer the apex of the gastropod, the other near the entrance to the carcinoecium, to begin with over the opening or even laterally, and that the third polyp is formed between these two. For my part I think it most probable, that the places where the polyps are formed are to a great extent dependent on the shape of the gastropod. Be this as it may, practically, the arrangement of the polyps in three series in the young specimens has hardly any importance for the classification. The polyps are cylindrical, the larger double the height of the smaller. On the contracted specimens with retracted tentacles the distal part of the polyp is broader than the other part and forms "a flattened disc-like

termination" (H. & S.), so that seen from the side the distal part is sharply truncate. The capitular furrows are well-marked, in smaller polyps the number is 15, in larger about 18, sometimes even 22. In dark specimens these furrows seem to be more distinct. The polyps show a slight bending at the entrance of the carcinœcium, i. e. forwards. The polyps as well as the carcinœcium are strongly incrustated with sand-grains. As opposed to what we find in *E. paguriphilus* I have seen no trace of the cuticle in this species.

The œsophagus is short, the siphonoglyphe distinct with a well developed hyposulcus of almost the same length as the œsophagus. Haddon & Shackleton state that the siphonoglyphe is "somewhat" indistinct. It may be, that they have come to this result, owing to their sections passing through the uppermost part of the œsophagus, where the siphonoglyphe is not distinctly developed as yet.

Anatomical description: Haddon and Shackleton have described the anatomy of this species. On several points I am able to supplement their description. The ectoderm of the body-wall is continuous and fairly low. It contains a large number of nematocysts with strongly twisted thread (length 22—24  $\mu$ , breadth 8—10  $\mu$ ). Owing to the strong incrustation it is difficult to judge of their distribution on the different parts of the body. The mesogloea is several times broader than the ectoderm. It is generally fairly homogenous, but contains here and there some scattered small cells and in the inner part very few cell-islets and lacunae. The ectoderm is thinner than the ectoderm. The incrustations are rather strong and consist almost exclusively of fairly coarse sand-grains, which fill the whole of the body-wall and may sometimes, as mentioned by Haddon and Shackleton, even penetrate into the coelenteron.

The sphincter is short but strong, the muscle-fibres are large and separated by narrow bands of connective tissue. In contracted specimens the sphincter is broad in the upper part, often filling up almost the whole breadth of the mesogloea, but narrows quickly downwards.

The ectoderm of the tentacles is as usual high and contains numerous spirocysts. Thick-walled capsules if any are very small.

The ectoderm of the œsophagus is high and provided with numerous thick-walled, narrow nematocysts (length 17—19  $\mu$ ). I have also, though seldom, found similar nematocysts as in the body-wall. The ectoderm of the siphonoglyphe is lower, and the mesogloea is in some cases greatly thickened in other cases less so, owing to the greater or less development of the siphonoglyphe.

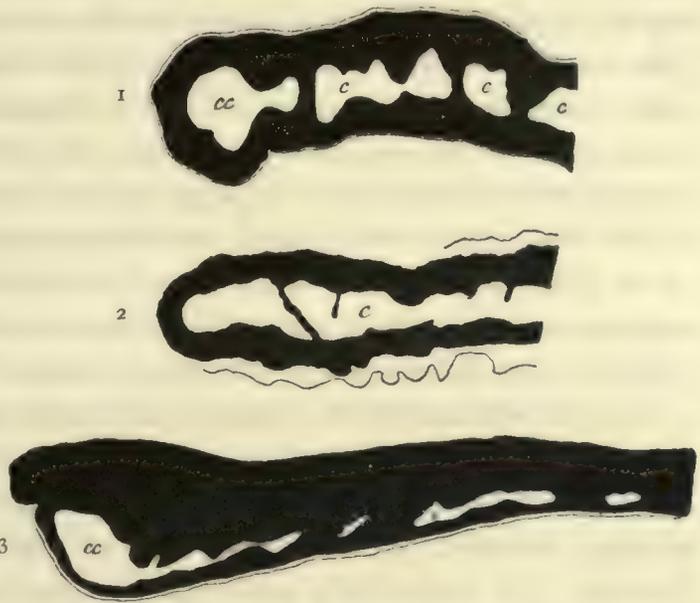
The number of mesenteries is somewhat variable. In smaller specimens I have found 32 mesenteries (18 macro- and 14 micro-mesenteries); a larger specimen had 36 mesenteries, another 38 (10 macro and 9 micro on the one side and 11 macro and 9 micromesenteries on the other). The greatest number of mesenteries I have observed was 42, in which specimen the one side had one macro- and one micro-mesentery more than the other side. The micro-mesenteries are weak and in the lower part of the œsophageal region and under the œsophagus they reach only a little way into the coelenteron. The longitudinal as well as the parieto-basilar muscles are weak and the distribution of these muscles on the body-wall is also inconsiderable.

The filaments have the usual structure. In the cnido-glandular tract we find sometimes sparsely, sometimes more frequently, nematocysts with spiral thread which are broader at the one side than at the other (length about 24  $\mu$ , greatest breadth about 7—8  $\mu$ ), further frequently thick-walled capsules (length 22  $\mu$ , breadth 3  $\mu$ ).

In the mesenteries of a few specimens taken at St. 129 by the Ingolf-Expedition I found numerous egg-shaped nematocysts, sometimes large (length 19–24  $\mu$ , breadth 14–17  $\mu$ ), sometimes smaller (length 17  $\mu$ , breadth 7  $\mu$ ) and also some intermediate sizes. As these only occurred, however, in a few colonies and were wanting in others from the same locality, the doubt arose whether these capsules were of normal occurrence. Sections showed also, that the capsules did not lie in the cnido-glandular tract itself but in the ectoderm immediately within this. It is therefore most probable, that these nematocysts have been taken in with the food and that they are the nematocysts of hydroids, which they greatly resemble.

The species is dioecious.

The walls of the *carcinœcium* have the same structure as the body-wall of the polyps. The ectoderm is provided with a thin cuticle and contains nematocysts of the same kind as in the body-wall, which are especially numerous on the outer side of the carcinœcium. The ectoderm seems to be somewhat thinner on the inner than on the outer side and is by comparison with the mesogloea very thin. The mesogloea resembles the body-wall mesogloea of the polyps and is very much incrustated. The canal-system (c text-fig. 1) of the entoderm is greatly developed and lies almost halfway between the outer and inner margins of the carcinœcium. The canals are large and broad and fuse together to irregular lacunae, which form a network. The mesoglœal pillars between the meshes are rather weak, though not so indistinct as in *E. abyssorum*. Along the upper margin of the carcinœcium runs a canal (cc) as in *E. paguriphilus*. The canal is somewhat broader than the rest of the canal-system.



Text-figure 1–3. Transverse section through the free margin (outer lip) of the carcinœcium of *Epizoanthus incrustatus* (fig. 1), *E. abyssorum* (fig. 2) and *E. paguriphilus* (fig. 3). The mesogloea and partly also the ectoderm are seen but not the epithelium in the canal-system. c canals; cc marginal canal.

Remarks. Danielssen (1890, p. 136) states that a specimen of *Epizoanthus arcticus* was obtained at St. 252 on the Norwegian North Atlantic Expedition. From Bergen Museum I have received a colony under this name and from the above-mentioned station. The colony consisted however of *E. incrustatus*. This is probably due not to an erroneous determination of Danielssen, but more likely to a confusion of localities, for he mentions at the same time that he obtained specimens of (*Zoanthus*) *incrustatus* from St. 200.

### *Epizoanthus abyssorum* Verr.

Pl. 2, fig. 8, Pl. 3, fig. 1, Pl. 5, fig. 7.

*Epizoanthus abyssorum* n. sp. Verrill p. Americ. Journ. Sc. 29 1885, p. 151.

— — Verrill Results Expl. Albatross 1885, p. 535, Pl. o, fig. 27 b.

Occurrence: (37° N., 71° 54' W. 2021 faths. U. S. Fish. Comm. Albatross St. 2226 from U. S. Nat. Mus. R. M.).

Dimensions: On the single specimen I have had for examination the carcinœcium was 2.5 cm. long and 2.3 cm. broad. The largest contracted polyp had a height of 1.4 cm. and a breadth at the base of 1.2 cm.

Colour grayish white purple or orange tinted at summit (Verrill) — in alcohol: whitish.

External appearance: The carcinœcium is snail-shaped with wide opening. On the inner side there seems to be a distinct cuticle as in *E. paguriphilus*. On the dorsal side of the carcinœcium emerge 3 large polyps (fig. 8, Pl. 2) resembling those of *E. paguriphilus*. They are broadest at the base, narrower upwards, somewhat wider in the distal part. The capitular region is uneven in the contracted state and does not form such a distinct, flat disk as in *E. incrustatus*, being more like *E. paguriphilus*. The capitular furrows are very indistinct in all the polyps. On each side of the entrance to the carcinœcium is a polyp, one of which covers the apex of the shell, which in contrast to the other, totally disintegrated part of the gastropod is quite fresh and occupies the greater part of the gastrovascular cavity of the polyp — the third is placed between these two polyps but a good deal further back on the first spiral of the carcinœcium. Ventral polyp not developed. All the polyp-part as well as the carcinœcium is strongly incrustated with foraminifera.

The œsophagus is not long, the siphonoglyphe distinct with well-developed hyposulcus.

Anatomical description: The ectoderm of the body-wall is of moderate height, continuous and contains some equally broad nematocysts with rounded ends and greatly twisted thread (length 24–29  $\mu$ , breadth 10  $\mu$ ). Presumably they are almost always present (the ectoderm was partially removed). The mesoglœa is thick, fairly homogeneous with here and there scattered spool-shaped cells, but no cell-islets (if present they are very scarce Pl. 5, fig. 7). The entoderm is almost as broad as the ectoderm. The incrustation, which consists almost exclusively of foraminifera, though also of sand-grains, fills out the ectoderm as also the mesoglœa in the body-wall.

The sphincter (Pl. 3, fig. 1) is strong, mesoglœal, finely meshed with the muscle-fibres running transversely. In the distal part it occupies the whole of the mesoglœa.

The ectoderm of the tentacles has the usual structure. The spirocysts are extremely numerous in it and the thick-walled capsules are very scarce, if the few met with are at all normal constituents of the ectoderm. The ectodermal longitudinal muscles are strong, the mesoglœa thin.

The ectoderm of the œsophagus is high and contains numerous typical nematocysts (length 24–26  $\mu$ ). Whether other capsules also occur, I am not able to say with certainty owing to the strong contraction of this region. The mesoglœa is thin as usual. The siphonoglyphe and the hyposulcus have a thick mesoglœa and generally a thin ectoderm.

The number of mesenteries is not large, especially when we consider that the polyps generally have a considerable diameter. In the specimen examined by me — the section had a diameter of 0.7 cm. — the number was 46, 13 macro and 11 micro on the one side, 12 macro and 10 micromesenteries on the other. The mesoglœa of the mesenteries is thin; the longitudinal muscles on a part of the mesentery form very few but fairly deep folds especially on the micromesenteries and directive mesenteries. The parieto-basilar muscles are weak and not found on the body-wall. The micromes-

enteries are also weak and only project very little into the coelenteron. The filaments have the usual structure. So far as I can see, the nematocysts of the same kind and size as in the body-wall are scarce. The same is the case with the thick-walled capsules which are very narrow, often curved and not much thickened (length 34–36  $\mu$ ).

Sexual organs. Eggs at different stages of development are found in the single specimen examined by me.

The *carcinœcium*. The inner wall of the carcinœcium is bounded externally by a fairly thick cuticle. Under this lies a continuous ectoderm with numerous nematocyst capsules of the same kind as in the body-wall of the polyps. On the outer side of the carcinœcium the ectoderm was for the most part removed. The mesoglœa on both sides of the entodermal canal-system is fairly thick and almost equally developed on both sides. The entodermal canal-system (text-fig. 2, p. 13) forms large lacunae separated by very narrow bridges of connective tissue, by means of which the two layers of the mesoglœa are easily separated from each other. In the single specimen I had for examination I found no canal in the margin of the carcinœcium that differed in size from the other parts of the canal-system (text-fig. 2). Thus, the entodermal canal-system seems to be more developed than in *E. incrustatus*; I have said, seems to be, for I have only examined the ventral margin of the carcinœcium a little way inwards. The difference in the development of the canal-system is seen most distinctly on comparing *E. abyssorum* with *E. paguriphilus*. The inner as well as the outer parts of the carcinœcium are richly incrustated with foraminifera.

Remarks. The cluster of this species arising from a grain of sand (Pl. 6, fig. 27 a Verrill 1885 b) is probably another species. I have no knowledge of this form.

### *Epizoanthus paguriphilus* Verr.

Pl. 1, fig. 8.

*Epizoanthus paguriphilus* n. sp. Verrill 1882 Americ. Journ. (3) 23 p. 137, 316.

— — — — — Verrill, Verrill 1883 Report Anth. Bull. M. Comp. Zool. Cambridge  
p. 61, Pl. 8, fig. 5.

*Zoanthus (Corticanthus) paguriphilus* Verr. Andres 1883 le Attinie p. 541.

*Epizoanthus paguriphilus* Verr. Haddon & Shackleton 1891, p. 641, Pl. 58, figs. 23–25, Pl. 59,  
fig. 6, Pl. 60, fig. 5 (contains index of literature up to 1891).

*Epizoanthus hirondellei* n. sp. Jourdan Bull. Soc. zool. France. Vol. 16 p. 269. 1891.

— — — — — Jourdan. Jourdan Res. Camp. Albert I. Monaco Fasc. 8. p. 7 Tab. 1. figs. 3–5. 1895.

Occurrence: 61° 44' N., 27° W. 485 Danish fathoms; bottom-temp. 6.1°. Ingolf-Exp. St. 81, 2 sp.

61° 28' N., 26° 25' W. 780 Danish fathoms; bottom-temp. 4.3°. Ingolf-Exp. St. 75, 1 sp.

60° 7' N., 9° 33' W. 750 m. Michael Sars Exp. 14.8. 1902. St. 79 b. Bergen Museum.

59° 28' N., 8° W. 1100–1300 m. temperature at 1000 m. 8.07°. Michael Sars Exp. 12.8. 1902. St. 76.

Geographical distribution. North Atlantic N. E. coast of America to N. W. Europe in deep water (H. & S.), Azores J. Roule.

Dimensions: The largest carcinœcium had a length of 6 cm. and a breadth of 4.5 cm. The largest polyps were in the contracted state about 1.5 cm. broad and 1 cm. high, the smallest colony was 2.5 cm. long and 1.5 cm. broad.

Colour: Brownish or gray in spirit specimens. Verrill gives the colour as "translucent bluish or purplish-gray or grayish brown. The tentacles pale orange or salmon with lighter tips. The polyps more or less of a salmon colour".

The external appearance has been well described by Haddon and Shackleton. The species always forms large carcinoëcia inhabited by *Eupagurus pilosimanus*. The coenenchyme develops on the gastropod shell which it covers completely, thus forming some kind of shelter to the gastropod, especially before its shell is dissolved (Pl. 1, fig. 8). The polyps are arranged in 2 groups, an outer consisting of a row of large polyps — 10 in the largest colony examined by me — and an inner one consisting of a single, smaller polyp lying centrally on the ventral side of the carcinoëcium a little behind the opening of the carcinoëcium.

The marginal polyps in contracted specimens are broader than long and elliptic in transverse section. Some of the polyps on the sides of the carcinoëcium seem to be larger than the others, some smaller polyps occurring in the posterior region, though this is not always very apparent. Whether such a small "posterior" polyp is of normal occurrence, as stated by Haddon and Shackleton, I am unable to say for certain, but it seems hardly to be the case to judge from my specimens. But my material as well as Haddon and Shackleton's is too small to permit of any certain statement on this point, so that it may be left undecided, as also the question regarding the arrangement of the polyps. As this species seems to have been taken in great numbers during the German deep-sea expedition, I shall come back to this question later.

Capitular furrows occur but are indistinct in the preserved specimens partially owing to the irregular contraction of this region.

The species is slightly incrustated with foraminifera, mainly covering the polyps and the neighbouring parts of the coenenchyme. The tentacles are very small.

The œsophagus is short with a deep siphonoglyphe and a well-developed hyposulcus, which has the same length as the œsophagus.

Anatomical description. Haddon and Shackleton have given a good description of the polyps of this species, but on several points their description requires supplementing.

As stated by Haddon and Shackleton the ectoderm of the body-wall is discontinuous. This does not apply however to the capitular region, especially its upper part, where the ectoderm as usual is thicker than at the other places of the body-wall. If the ectoderm is still present, there is in the upper part of the body-wall a fairly common occurrence of equally broad, thick-walled nematocysts (length 24—26  $\mu$ ), but on the other hand no nematocyst capsules with greatly twisted thread, which probably may be found in the lower part. The mesoglœa is very thick in comparison with the ectoderm. It contains numerous but small cell-islets, which may sometimes be fairly elongated and even form canals. In conformity with the often-quoted authors I have not been able to find any connection between the ectoderm and the entoderm and these canals. Spool-shaped cells also occur.

The incrustation is inconsiderable and consists mainly of foraminifera together with some sand-grains. These lie in the ectoderm and in the outermost parts of the mesoglœa. The entoderm is thin and has almost the same size as the ectoderm. Haddon and Shackleton have given a

very instructive figure of a transverse section in Pl. 59, fig. 6. It must be observed however, that in my specimens the strands of the mesogloea, separating the different parts of the ectoderm from each other, do not always lie so closely as in this figure.

As mentioned by Haddon and Shackleton the sphincter is not strongly developed, especially if the size of the polyps is taken into consideration. In the distal part of the sphincter, however, the fibres occupy almost the whole breadth of the mesogloea, the lower third part of the sphincter being inconsiderable. Haddon and Shackleton state that "no cavities are visible, the fibres being completely embedded in the substance of the mesogloea." This is not the case in my specimens. In the proximal part, where the muscle-meshes (in transverse sections through the sphincter) are small, it may be possible that there sometimes are no cavities, in the distal part on the other hand the muscle-meshes are large and as usual extend in a transverse direction. The parts of the mesogloea lying between the muscle-groups are very small. The sphincter is thus fairly strong in this regard.

The ectoderm of the tentacles is high, the mesogloea on the other hand is thin as also the layer of longitudinal muscles. In the ectoderm very numerous spirocysts are found. Whether thick-walled nematocysts occur is uncertain, but if present they are very scarce.

The ectoderm of the œsophagus is fairly high and provided with numerous, thick-walled nematocysts (length 23–29  $\mu$ , generally about 24–26  $\mu$ ). The mesogloea is fairly thin. In the siphonoglyphe the ectoderm is considerably thicker than in the œsophagus, with the condition reversed as regards the mesogloea. The mesogloea in the siphonoglyphe is almost homogeneous, as cells and cell-islets only occur very seldom.

The number of mesenteries is greater than in any other northern Zoantharia. In a small polyp I counted namely 64 mesenteries, 17 macro and 15 micro on each side, in a large one 80 mesenteries. The macro-mesenteries are in the œsophageal region fairly thick, owing to the fact, that the mesogloea is well-developed here, whereas it becomes thinner below the œsophagus. The longitudinal muscles are not strong and the muscular plaits few. The parieto-basilar muscles are very weak and narrow. None of these muscles are expanded in the body-wall. The micro-mesenteries are very weak — the weakest I have ever seen — and do not reach above the entoderm of the body-wall.

The filaments have the usual structure. They contain nematocysts with greatly twisted thread, but not in great number. They are oval and fairly small (length 19–25  $\mu$ , breadth 10–12  $\mu$ ). Further, they contain fairly many thick-walled, rather transparent nematocysts with distinct spiral thread and broader at the one end, with varying length (19–24–26–31  $\mu$ , breadth 6–7  $\mu$ ) and also some thick-walled, narrow, typical nematocysts (length about 26  $\mu$ ).

The species is dicecious.

The *carcinœcium*. The cœnenchyme and the canal-system have not been examined by Haddon and Shackleton. The outer layer of the ectoderm had fallen off. The mesogloea sends out a number of fine outshoots, the presence of which indicates that the ectoderm is also discontinuous here. On the inner side the ectoderm is thin and discontinuous with a well-developed cuticle. On the outer side of the carcinœcium the mesogloea is very thick, on the inner side it is thin. The entodermal canal-system (c, text-fig. 3, p. 13) thus lies quite close to the inner side of the cœnenchyme.

It consists of numerous reticular, anastomosing canals, which are generally fairly narrow but somewhat thicker towards the opening of the carcinœcium. A very large canal cc, which is in connection with the other reticulate branched canals, runs along the upper rim of the opening of the carcinœcium and is afterwards lost in the columellar region, where it divides into some smaller canals. Numerous cells and cell-islets occur in the thick part of the mesoglœa; in the part lying inside the canals, the cells and cell-islets are very scarce. No incrustations are found in the mesoglœa.

**Epizoanthus norvegicus** (Kor. & Dan.) Hadd. & Shackl.

Pl. 1, fig. 12, Pl. 2, fig. 22, Pl. 3, fig. 3, Pl. 5, figs. 2, 3.

*Zoanthus norvegicus* n. sp.      Koren & Danielssen. Fauna littoral. Norveg. 3, 1877 p. 79, Tabl. 9, figs. 5-6.

*Polythoa (Endeithoa) norvegica* (Kor. & Dan.) Andres Le Attinie 1883, p. 531.

*Epizoanthus norvegicus*      (Kor. & Dan.) Haddon & Shackleton Scient. Trans. R. Dublin Soc., p. 614, 132, 651, 652, Pl. 59, fig. 5.

*Palythoa norvegica*      (Kor. & Dan.) Arndt Jahreshb. Schl. Gesells. vaterl. Cultur 1912, p. 123.

Occurrence: Norway Trondhjem Fjord: Skarn Sound on Primnoa 100-200 m. 3-11/9, 1898, Østergren R. M., Storm. Bergen Mus.

Haakon Sound 280 fms. from Bergen Mus. R. M.

(Korsfjord near Bergen 300 fms. Koren & Danielssen, Sars).

Lives on sponges, shells of *Lima excavata*, *Primnoa* and *Paragorgia* (Koren & Danielssen).

Dimensions: The greatest length of the polyps is 2.5 cm., greatest breadth in the distal part 0.8 cm., smallest breadth in the proximal part 0.5 cm. Outer tentacles 0.8 cm., inner ones somewhat longer (Koren & Danielssen).

Colour (from Koren & Danielssen): "The body is grayish yellow, the inside of the epidermis, the proper skin, is pale rose-coloured with a tinge of yellow. The mouth surrounded by a darker rose-coloured ring, from which fine white stripes go radially to the interior tentacles".

External appearance: The polyps are considerably larger than broad, narrow at the base and broader at the distal part. In the contracted state the distal part of the polyp is rounded not truncate. The larger polyps at least have distinct capitular furrows, which are specially prominent in expanded specimens, as they are broad. In the specimens I have examined the number of capitular furrows was 16-20, in most specimens 20, and one specimen (a double individual, see below) had even up to 24. Between the capitular furrows are distinct, fairly sharp ridges, which in the distal part often form irregular, tap-like projections.

The polyps are connected with each other by means of a very well-developed cœnenchyme, which is fairly thick and from which the polyps arise usually at a considerable distance from each other. The canals from the polyps begin to communicate a little way from the polyps, forming a network apparent to the naked eye.

The species forms large colonies. Koren and Danielssen state, that it is found "frequently

in large groups that may occupy as much space as a closed hand, wherein more than 50 polyps are attached by the same coenosark."

The number of tentacles corresponds to the number of mesenteries, being thus in larger specimens considerably greater than stated by Koren and Danielssen.

The oral disc is wide, the mouth lies on a cone, the mouth-opening is like a slit.

The œsophagus is short and the siphonoglyphe well-developed with distinct hyposulcus.

**Fission.** On the colony taken by Storm in Skarn Sound I observed a double polyp in the middle part. (Pl. 2 fig. 22). Almost the whole of the body-wall was continued smoothly without boundary from the one polyp to the other, but the ridges and for the most part also the capitular furrows could be seen in each polyp. The one polyp had 20, the other no less than 24 ridges and furrows. Each polyp had its special circlet of tentacles fully separated. How far a doubling of the tentacle takes place from the directive chamber, I am unable to say, as I did not wish to cut up the polyp completely but there is probably a directive tentacle on each polyp. Each polyp has its distinct œsophagus and siphonoglyphe, but a common directive chamber. The cleavage has thus taken place in the directive chamber. This condition has some resemblance to the double formations in *Cribrina gemmacea* previously described by me (Studien über Regenerations und Regulationserscheinungen. K. Svenska Vet. Akad. Handl. B. 37 1904 p. 82 text-fig. 13, Pl. 2, fig. 21), of course with the difference caused by the different organisation of the two groups.

**Anatomical structure.** Haddon and Shackleton (1891) have given some information regarding the anatomical structure of this species. They state that the ectoderm, the mesogloea and the entoderm of the body-wall reach a considerable size and that numerous nematocysts are found in the ectoderm. Furthermore, they point out that the micromesenteries are strongly developed. In their paper we find a figure showing a section of the body-wall — evidently from the capitular region. Otherwise this species has not been subjected to any anatomical examination.

The ectoderm of the body-wall is very thick and discontinuous (Pl. 5, fig. 3) except at the capitular region (Pl. 5, fig. 2), though the discontinuity is hardly so conspicuous as in *Epizoanthus paguriphilus*. It contains numerous nematocysts with greatly twisted thread, which have a length of 24–29  $\mu$  and a breadth of 12  $\mu$ ; they are oval and almost equally broad at both ends. Haddon and Shackleton state that they contain pigment granules. This is however doubtful; I think it probable that small air-bubbles have penetrated into the nematocysts in sectioning and that these bubbles have been mistaken for granules. This often happens and I have had the same experience with many *Zoantharia*, *Ceriantharia* and *Actiniaria*. The mesogloea is considerably thicker than the ectoderm and now and then runs out into outshoots which cut off parts of the ectoderm from each other and even end in the cuticle, though without forming such small, closed spaces as in *Epizoanthus paguriphilus*. The mesogloea contains fairly many cells with outrunners, now and then cell-islets and very seldom ectodermal lacunae. The entoderm of the body-wall reaches a considerable size. The incrustation in this species is inconsiderable and lies mostly in the ectoderm and in the outer parts of the mesogloea, consisting of sand-grains, foraminifera and sponge-needles.

The sphincter is strong, mesogloecal and finely divided. The meshes in transverse section are drawn out in a transverse direction. The sphincter lies nearer the ectoderm than the entoderm, so

that in the furrows of the capitular region it is only separated from the ectoderm by a very small part of the mesogloea, which in this region is generally higher than in the other parts of the body and contains some nematocysts.

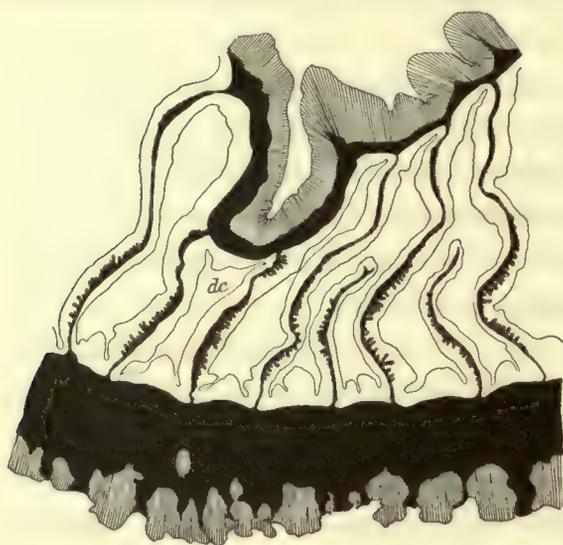
The tentacles have the usual structure. Besides the very numerous spirocysts the ectoderm contains numerous, thick-walled capsules (length  $14-17\ \mu$ ) and a few capsules of the same appearance as in the body-wall (length  $24-26\ \mu$ , breadth  $10\ \mu$ ).

The ectoderm of the oral disc is very broad near the tentacles and contains numerous, closely packed spirocysts, near the mouth it is thinner and contains some nematocysts. The ectodermal longitudinal muscle layer is fairly strong in the outer part of the oral disc, weaker in the inner part.

A layer of fibrillae and ganglion cells is distinctly visible in the oral disc.

The ectoderm of the œsophagus is high and arranged in longitudinal folds supported by mesogloœal ridges, which emerge between the furrows. The nematocysts are scarce and thick-walled (length about  $20\ \mu$ ). Large-grained gland-cells are found especially in the inner parts of the ectoderm. Ectodermal longitudinal musculature is absent in this species. At the base of the ectoderm of the oral rim there seem to be numerous cells and a thread-like layer. As far as I can see — the material was not so well preserved as could be desired — it consisted of a well-developed layer of

ganglion-cells and nerve-fibrillae. The mesogloea is fairly thick; its upper part is provided with numerous cells which are scarce in the aboral part. The ectoderm of the siphonoglyphe is of the usual structure and lower than in the other part of the œsophagus. The mesogloea is broad and much thicker than in the œsophagus. The hyposulcus has the same structure as the siphonoglyphe but the entodermal muscles here run in longitudinal direction and form some folds in the outer parts. The free border is thick and even provided with more numerous gland-cells than the inner parts.



Text-fig. 4. Transverse section through a piece of the body-wall with mesenteries and œsophagus of *Epizoanthus norvegicus*. Ectoderm shaded, mesogloea and muscles black, entoderm not specially marked, dc: directive chamber.

and 11 micromesenteries on the one side of the sagittal plane, and 12 macro and 10 micromesenteries on the other. The other polyp had 11 macro and 9 micro mesenteries respectively and 14 macro and 12 micro. The micromesenteries are strong. The longitudinal musculature of the mesenteries is vigorous and forms fairly numerous folds. The parieto-basilar muscles are weak. The distribution of the longitudinal and the parieto-basilar muscles on the body-wall is slight. The muscles of the micromesenteries are generally well-developed (text-fig. 4).

The filaments have the usual characteristic structure. The glandular tract contains only the

frequently occurring nematocysts of the same kind and size as in the œsophagus. The species is dioecious.

The ectoderm of the cœnenchyme contains numerous nematocysts of the same shape as in the body-wall, but seems here to be continuous. The mesogloea contains numerous ectodermal lacunae, in which the large nematocysts, that occur in the body-wall of the polyps, are also found. The entoderm is very large in the canals.

**Epizoanthus lindahli** n. sp.

Pl. 2, figs. 11—13, Pl. 4, fig. 5

*Zoanthus arcticus* Marenzeller 1878, p. 379.

Occurrence: Baffins Bay 72° 4' N., 59° 50' W. 227 fms. Hard, gray clay. Ingegerd and Gladan Exp. 19/7, 1871. Josua Lindahl 3 sp. R. M. (sp. a.)

79° 13' 1" N., 63° 21' 7" W. 230 fms. 1 sp. Museum at Vienna (sp. b.)

66° 42' N., 26° 40' W. 590 m. Temp. at 550 m. 0° 11'. 3/8. 1900 Michael Sars Exp. St. 13 1 colony. Bergens Museum (sp. c.)

65° 00' N., 11° 16' W. 310 Danish fms. bottom-temp. 0° 01' Ingolf Exp. St. 59 1 sp. (sp. d.)

66° 35' N., 56° 38' W. 318 Danish fms. bottom-temp. 3° 9' Ingolf Exp. St. 32 1 colony (sp. e.)

var. *Nordgaardi* Lyngen, Nordgaard 1 sp. R. M. (sp. f.)

Dimensions: (a) Length of the colony about 2.1 cm., breadth of the largest polyp 0.6 cm., of the smallest polyp 0.3 cm. (b) length of the colony about 1.5 cm., breadth 0.4 cm. (c) breadth of the colony 2.3 cm., length of the largest polyp 1.3 cm., breadth 0.45 cm.

Colour in alcohol: dirty-gray (c) sand colour with white points of foraminifera and black points of sand-grains, specimen d dark with black sand-grains, f clear, uncoloured.

External appearance: The cœnenchyme is inconsiderable and tube-shaped as in *E. erdmanni*. The polyps are elongated just in *E. erdmanni*, narrowest at the base, increasing in size towards the point. They are broadest in the capitular region. The body-wall is rough owing to the incrustations, which mainly consist of sand-grains and also of foraminifera (especially in b). The upper contracted border is somewhat rounded — truncate. The capitular furrows are not so distinct owing to the incrustation and contraction, on the largest specimen of the colony I counted 20, on b at least 16, on d 18 probably.

The œsophagus is short, the siphonoglyphe distinct with a hyosulcus which is as long as the œsophagus.

Anatomical description: (1 specimen from Baffins Bay and another from c have been closely examined). The ectoderm of the body-wall is continuous and of moderate size, provided with a cuticle, on which detritus particles are fixed. In the lower part of the polyp the ectoderm contains many equally broad nematocysts with greatly twisted thread, having a length of 38—43  $\mu$  and a breadth of 10—12  $\mu$ . In the capitular region similar but narrower capsules of the same kind and dimension as in the filaments. The mesogloea is fairly thick, several times thicker than the ectoderm; it is generally rather homogeneous with a frequent occurrence of very small cells and sometimes even cell-islets (Pl. 4 fig. 5). The entoderm is extremely thin in the body-wall as well as in the mesenteries and

the œsophagus and its differentiations. The ectoderm and the mesoglœa are incrustated with sand-grains, foraminifera and a fairly large number of sponge-needles. In e and f sand-grains were almost exclusively present. The incrustation is often considerable and fills almost the whole of the mesoglœa.

The sphincter is very strong and has some resemblance to the sphincter in *E. erdmanni*.

The tentacles have the usual structure. The spirocysts of the ectoderm are very numerous. Besides there generally occur some thick-walled, equally broad nematocysts (length 17—19  $\mu$ ) and more seldom nematocysts of the same type as in the capitular region of the body-wall (length 38—48  $\mu$ , breadth 7  $\mu$ ). The ectoderm of the œsophagus is high and contains large numbers of equally broad nematocysts with greatly twisted thread (length (38) 43—48  $\mu$  breadth 7  $\mu$ ). Further, very numerous typical thick-walled nematocysts occur (length 24 (26)  $\mu$ ). The mesoglœa is thick. The ectoderm of the siphonoglyphe is of the typical appearance, the mesoglœa thick, though very little thicker than that of the œsophagus.

The number of mesenteries was 38 in the specimen sectioned, on one side 11 macro and 9 micro-mesenteries, on the other 10 macro and 8 micro-mesenteries. In the larger specimen of the colony the number was presumably 36 (it was opened partially lengthwise). Another from colony c had 36, specimen d about 40. The micro-mesenteries are well-developed in the œsophageal region. The mesoglœa of the macro-mesenteries is fairly thick, the entoderm thin. The longitudinal musculature is moderately developed and forms few folds; in one specimen from colony c which had a very wide œsophagus and the mesenteries consequently very contracted in breadth, the musculature lay in thick folds, the mesoglœa being also here thicker than in a, where the mesenteries were much expanded in breadth. The parieto-basilar muscles are very weak. The distribution of the mesenteric muscles on the body-wall is fairly considerable.

The filaments have the usual structure. The glandular tract contains numerous, equally broad nematocysts with greatly twisted thread (length (34) 38—49 (53)  $\mu$ , breadth 6—7  $\mu$ ). I have not observed any thick nematocysts resembling those found in the lower part of the body-wall, if on the whole they occur they must be very scarce; in one specimen I have found a single one (length 36  $\mu$ , breadth 11  $\mu$ ). Further, many thick-walled capsules occur here with distinct basal part to the spiral thread, broadest in the one end (length about 22 (19—24)  $\mu$ , sometimes 26  $\mu$ , breadth about 5—6  $\mu$ ). The polyps are dioecious, one of the specimens examined was a male with developed testes.

**Systematic remarks.** This species is closely related to *E. danielsseni*, from which it differs however in external appearance, especially in the form of the coenenchyme and with regard to the structure and distribution of the nematocysts and the mesenteries. As in *E. danielsseni* the capsules in the lower part of the body-wall and in the capitular region are different in this species.

*var. nordgaardii* Pl. 2, fig. 7.

As already pointed out above, the external appearance of *E. lindahli* is very much like that of *E. erdmanni*. At Lyngen Dr. Nordgaard has collected material of a Zoantharia which I determined as *E. erdmanni* (Carlgren in Nordgaard. Hydro. and Biol. Invest. 1895, p. 159). Two of the specimens in the collection I retained for the Riksmuseum in Stockholm. On closer examination, however, it appeared that the one specimen was not *E. erdmanni* but a species which must be closely related to

*E. lindahli* or identical therewith. But as it differs somewhat from *E. lindahli* with regard to the nematocysts, I have for the present set up this species as a variety of *E. lindahli*, leaving to later investigations, when more material has been obtained, to prove if it may possibly form a separate species. I may also mention that among the specimens sent back to Dr. Nordgaard there may possibly still be found a few specimens of this variety which I have called *Nordgaardi*. All these specimens certainly need revision.

Occurrence: 63° 37' N., 20° 24' E. Lyngen off Kaafjord. 1 sp.

Dimensions: Length 2.1 cm., smallest breadth 0.2 cm., greatest breadth 0.7 cm.

Colour in alcohol: In the lower part gray, in the upper light sand-coloured.

External appearance (fig. 7 Pl. 2). The polyp was truncate and somewhat contracted in the lower part, the upper part being expanded. The distal margin was rounded. The capitular furrows were very distinct and their number was 20. Tentacles and œsophagus as in the main form. The mesoglœa of the body-wall was considerably incrustated in the outer part, less in the inner. The incrustation consisted of sand-grains and some sponge needles. But I have not observed any foraminifera, which however are possibly dissolved, as the animal, so far as I remember, had been preserved in formaline or formaline spirit.

The *anatomical structure* seems to agree with that of *E. lindahli* with the exception regarding the nematocysts mentioned already. The number of mesenteries was 36, 10 macro- and 8 micro-mesenteries on either side of the polyp.

The nematocysts are generally larger than in the typical *E. lindahli*. In the lower part of the ectoderm of the body-wall there is a fairly frequent occurrence of equally broad nematocysts with greatly twisted thread (length 43–48  $\mu$ , breadth 10–12  $\mu$ ). In the capitular region large capsules of the same kind as in the filament occur somewhat frequently (length 38–48  $\mu$ , breadth 7  $\mu$ ).

The ectoderm of the tentacles contains numerous spirocysts, the thick-walled nematocysts being very scarce (length 17–19 (22)  $\mu$ ). Large nematocyst capsules with greatly twisted thread also occur here sparsely (length 43–48  $\mu$ , breadth 7  $\mu$ ), and even sometimes smaller nematocysts of the same kind as in the filament. The oral disc has, as regards the nematocysts, almost the same structure as the tentacles.

The œsophagus is provided with numerous, thick-walled capsules about 24  $\mu$  long and less than 5  $\mu$  broad. Further very few nematocysts with greatly twisted thread occur of the same size and structure as in the filament.

The glandular tract of the filament contains partly nematocysts with greatly twisted thread, partly larger ones 43–60  $\mu$  long and 7  $\mu$  broad, sometimes curved, partly smaller ones generally curved 26–34  $\mu$  long and 5  $\mu$  broad; further thick-walled capsules with distinct basal part of the spiral thread and broader at the one end (length 22  $\mu$ , breadth 5  $\mu$ , length 24–26  $\mu$ , breadth 6  $\mu$  in the broadest end).

#### ***Epizoanthus erdmanni* (Dan) Hadd. & Shackl.**

Pl. 1, fig. 14, 16, 17, Pl. 2, fig. 24, Pl. 4, fig. 3, Pl. 5, fig. 4.

*Mardoel erdmanni* n. sp. Danielssen Norwegian North Atlantic Exped. Actinida 1890 p. 116, Pl. 6, fig. 1, Pl. 21, 22, figs. 1–7.

*Epizoanthus erdmanni* (Dan) Haddon & Shackleton Revision British Actiniae 1861 p. 623, 633, 635, 639;

— (Dan). Carlgren in Nordgaard Hydrograph. and Biol. Invest. Norweg. Fjord 1905 p. 159.

? *Mamillifera* sp. M. Sars Nyt mag. Nat. 6:2 No. 10 1851 p. 142.

? *Zoanthus arcticus* n. sp. M. Sars Förh. Skand. Nat. Möde 8. 1860 p. 692 Forh. Vid. Selsk. Christiania 1860 p. 144.

? *Zoanthus* (str. s.) *arcticus*, Andres Le Attinie 1883 p. 546.

Occurrence: Spitzbergen 81° 14' N., 22° 50' E., N. E. of Seven Isls. 150 m. gray clay. Bottom temp. 2° Spitzb. Ex. 20/8 1898 No. 37 R. M. several specimens.

80° 3' N., 8° 28' E. 475 m. clay Bott. temp. 1.1° 14/8. 1878 N. N. A. E. St. 363 R. M.

Beeren Island 75° 38' N., 13° 18' E. 350 m. Bottom temp. 2.73° Spitzb. Exped. 1898 1/9 No. 41 R. M. several spec.

73° 3' N., 18° 30' E. 410 m. Bott. temp. 2°. Spitzb. Exp. 4/9 1898 No. 42 R. M. some spec.

73° 27' N., 23° 11' E. 460 m. black grayish clay Bott. temp. 2.67°. Spitzb. Exped. 12/6 1898 No. 2 R. M. 2 spec.

72° 53' N., 21° 51' E. 408 m. clay. Bott. temp. 1.5°. N. N. A. Exp. 30/7 1878 St. 363.

72° 27' N., 20° 51' E. 349 m. Sabulous clay, Bott. temp. 3.5°. N. N. A. Ex. 7/7 1878 St. 290.

Norway 70° 2'.5 N., 21° 41' E. Kvænangen 300—343 m. Bott. temp. 2.3°. 19/4 1899 Nordgaard R. M. Altenfjord 80 fms. clay bott. July 1890 Jägerskiöld U. U. Z. M.

69° 54' N., 20° 27' E. Lyngen between outer Garvik and Ulö 300 m. Nordgaard 3/5 1899. R. M.

Lyngen off the Kaafjord 250 m. bott. temp. about 2.85° 3/5 1899. Nordgaard R. M.

69° 41' N., 15° 51' E. 1591 m. Sabulous clay Bott. temp. 1.2°. N. N. A. E. 7/7 1877 St. 190.

Foldenfjord 530 m. 6/4 1900 Nordgaard.

Komagfjord Danielssen (*E. arcticus*) Bergens M. (R. M.).

Skatören Tromsö. 40 fms. Tromsö M.

Malangen 69° 33' N., 18° 0' E. 380 m. Bott. temp. 4.1°. Nordgaard 14/4 1899 (R. M.).

66° 45' N., 15° 36' W. 200 m. Bott. temp. 2.39°. 5/8 1900. Michael Sars Ex.

Budderbay 30/6 1884 C. Aurivillius.

Greenland 74° 52' N., 17° 16' W. 350 m. clay mud with sand and small stones. 4/7 1899 Greenland Ex. No. 18.

Iceland Øfjord Möller, 1 colony Copenh. M.

Dimensions: According to Danielssen the polyps in expanded state may reach a length of 3.5 cm. and a breadth of 2 cm. While considering the first to be very probable, I feel however some doubt as to whether the breadth can be so great. The specimens examined by me were very variable in size. The largest polyp (fig. 24 pl. 2) had a length of about 2.7 cm. and a breadth of 0.6 cm. at the broadest place.

Colour: (Danielssen). "The body is light brownish red almost brick-colour, somewhat grayish green with a violet play (var. *aurivillii*?). The tentacles lighter coloured, brownish red and transparent. The oral disc is still lighter in colour than the tentacles and round the outer margin of the oral disc, exactly at the base of the inner tentacular series, there is a narrow light coloured rose-

red annulus." In the preserved state most of the specimens were dirty-coloured light brown. Some of the specimens were grayish e. g. those from Altenfjord. The colony taken during the Michael Sars Expedition was black with incrustated, small, black sand-grains and the colony originating from Iceland Øfjord was even darker than is generally the case with this species.

The external appearance has been well described by Danielssen, who has also given some rather good drawings of the external appearance of the colonies. The species forms free, unfixed colonies of 1—6 seldom more polyps connected with each other by a small tube-shaped cœnenchyme, which is generally so inconsiderable that the polyps seem to grade smoothly over from one to the other (see fig. 14, 17 Pl. I). The more developed polyps are narrow at the base, but expand gradually towards the distal part, so that the animal has its greatest breadth in the capitular region. The small, not fullgrown polyps approach the cylindrical shape. Sometimes the polyps are provided with cross-furrows, which undoubtedly have only been caused by contraction. The capitular region has generally quite distinct ridges and furrows. The number of furrows varies considerably according to the size of the polyps. Danielssen states that the species has 18 capitular furrows, here they vary between 14 and 15 in small specimens and in the large between 16 and 20, and in one polyp I have even counted up to 22. But generally the majority seem to have 18 furrows. Of 116 specimens 42 had 18 capitular furrows, 26 had 16, 17 had 17, 9 had 19, 11 had 20 and 1 specimen 22. Of the smaller specimens 14 polyps had 15 capitular furrows and 5 had 14. On the majority of the small specimens the capitular furrows were however so indistinct, that the number could not be determined with any certainty. The body-wall is more or less rough owing to the greater or less incrustation.

The tentacles are arranged as usual and seem to correspond in number with the mesenteries. The œsophagus is short with a well-marked siphonoglyphe and a fairly long and broad hyposulcus.

The anatomical structure has also been described by Danielssen, but on several points incorrectly, as e. g. with regard to the arrangement of the mesenteries, which does not differ from that of the other Zoanthidae. The ciliated streaks on the macromesenteries however have been observed by Danielssen who gives a comparatively good picture of them (fig. 5, Tab. 22 Danielssen, 1890). But on the other hand the arrangement of mesenteries and the length of the filaments on fig. 4, Tab. 22 of the same work are not in agreement with the reality. Some anatomical details are also given by Haddon & Shackleton (1891).

The ectoderm of the body-wall is fairly high, continuous and contains nematocysts with twisted thread (length 24—30  $\mu$ , breadth 10—12  $\mu$ ). They are equally broad and common except in the capitular region where they are scarce. The ectoderm is provided with a distinct cuticle, on which particles of detritus are attached. According to the state of contraction of the animal, the mesogloea may be thin or very thick, but is several times thicker than the ectoderm. It is provided with fairly numerous cells with long outshoots, whereas cell-islets only very seldom occur (pl. 5, fig. 4). Sometimes the latter may be found at the base of insertion of the mesenteries but as a rule they are not present at these places, a fact I have ascertained by means of a large number of sectioned specimens from different localities.

Haddon and Shackleton state (1891 p. 635), that on the specimens sent them by Danielssen there was "a well-marked lacuna in the mesogloea at the base of the insertion of each mesentery."

This I have not observed and therefore think it probable, that another species has been concealed in Danielssen's specimens — such things have happened before — and been examined by Haddon and Shackleton. Thus among the specimens of *E. erdmanni* from St. 42 collected during the Spitzbergen Expedition 1898 there were many individuals which at first glance resembled *E. erdmanni* (fig. 15, Pl. 1) but actually did belong to another Epizoanthus species, i. e. *E. danielsseni*. Also a third Epizoanthus, *E. beerenislandicus*, was dredged at the same time. This latter species has lacunae at the above-mentioned places. The entoderm is thinner than the ectoderm.

The incrustation consists almost exclusively of sand-grains sometimes interspersed with a few sponge-needles and foraminifera. Sometimes the incrustation in the mesogloea is quite inconsiderable, sometimes it fills up the whole, so that it is very difficult to study the structure of the latter.

The sphincter is not long but strong and in the greater part of its course it covers almost the whole breadth of the mesogloea. In transverse sections through the sphincter the meshes are large whereas the ridges of connective tissue between the muscle meshes are small (Pl. 4, fig. 3).

The tentacles have the usual structure. The ectoderm is provided with numerous spirocysts and scarce thick-walled capsules (length about 17 (14—19)  $\mu$ ). The longitudinal muscles are fairly well-developed.

The ectoderm of the œsophagus is fairly high and elongated. The large nematocysts of the kind and size seen in the body-wall are scarce or absent, while the thick-walled capsules are numerous and 19—24  $\mu$  long. The ectoderm of the siphonoglyphe is as usual somewhat lower than that of the œsophagus, as the mesogloea is thicker than in the œsophagus.

The number of mesenteries varies between 28 and 40. Of the following 19 specimens

2 specimens had 28 mesenteries (1 spec. was labelled <i>E. arcticus</i> ,	
3 — — 30 —	Komagfjord; see below).
5 — — 32 —	
4 — — 34 —	
2 — — 36 —	
2 — — 38 —	
1 — — 40 —	

Thus, the most frequent numbers seem to be 32—34, which corresponds with the most frequent number of capitular furrows. The specimens with 30, 34 and 38 mesenteries had a few mesenteries more on the one side than on the other. The micromesenteries are fairly well-developed and project into the gastric cavity, as long as the main part of the entoderm of the body-wall is high. The longitudinal muscles of the macro-mesenteries are fairly well-developed, the mesogloea is thin. The parieto-basilar muscles are rather weak. The distribution of the longitudinal and the parieto-basilar muscles on the body-wall is inconsiderable.

Of the proto-mesenteric filaments the shortest are those corresponding to the 6th pair of proto-mesenteries in Actiniaria, while the others are long. The filaments of the metamesenteries decrease in length towards the siphonoglyphe. The filaments have the usual structure. Nematocysts with greatly twisted thread resembling those in the body-wall occur sometimes very scarcely, sometimes more frequently. They are equally broad and 24—31  $\mu$  long, the breadth being generally 10  $\mu$  (9—12). The

thick-walled capsules have a distinct basal part to the spiral thread and are somewhat broader at the one end. They are about 19–24  $\mu$  long and of fairly common occurrence.

Both polyps from the colony taken in the Øfjord at Iceland differ from the main form with regard to the nematocysts of the mesenteries. On maceration, namely, besides the above-mentioned nematocysts, some egg-shaped capsules occurred, partly larger about 22  $\mu$  long and 19  $\mu$  broad, partly smaller, about 14  $\mu$  long and 11  $\mu$  broad, both kinds being fairly numerous. On a closer examination of the rather bad sections of this form, I found however, that these egg-shaped capsules do not lie in the filaments but inside these, though it is possible that such a foreign capsule may lie in the filaments. It is at any rate probable, that these nematocysts, just as was the case with some similar capsules in *E. incrustatus*, do not belong to the animal but are foreign capsules absorbed by it (see p. 13). It is worth observing, that the abnormal specimens of *E. incrustatus* and *E. erdmanni* originate from almost the same region.

The species is dioecious.

Remarks: I have here taken *Zoanthus arcticus* as synonym to *E. erdmanni*, though I have not been able to prove the correctness of this assumption, no type-specimens of *Z. arcticus* being present seemingly in the Bergen Museum. On the other hand, there are some specimens taken by Danielsens in Komagfjord and determined (by whom?) as *Z. arcticus*. As far as I am able to see from the anatomical examination these are no other than *E. erdmanni*, though they form no colony but are single specimens. According to the rules of priority, the species should be called *E. arcticus* and not *E. erdmanni*, if the supposition is correct that they may belong to one species. As type-specimens seem to be wanting, however, and the description of *Z. arcticus* is fairly poor, it seems advisable to retain the name *E. erdmanni*.

Danielssen states, that *E. erdmanni* occurs in two forms different as to colour, the one being darker and the other lighter grayish. Several specimens may even be quite grayish, as e. g. those from Altenfjord, but otherwise their external appearance does not differ much from that of the others. On the other hand, from the localities mentioned below there is a more slender form, which in other respects also differs a little from the main form. This variety has been named var. *aurivillii*, though it hardly differs essentially from the main form, grading into this through some transitional forms.

#### ***E. erdmanni* var. *aurivillii*.**

Pl. 2 figs. 18, 28, 29 Pl. 5, fig. 5.

*Zoanthus Couchi* Johnst. C. *Aurivillius* 1886 p. 52.

Occurrence: Norway Outer part of the Kwæangfjord 50–100 fms. Stone and clay. June 1884 Carl Aurivillius, several specimens Ups. M.

Finmarken Goës & Malmgren R. M. some specimens.

Jagfjord 200 m. 18.2. 1899. Nordgaard 1 colony.

Dimensions: Length of the largest polyp: 1.7 cm., greatest breadth 0.4 cm.

Colour light grayish, in the distal end reddish (*Aurivillius*) in alcohol: light grayish.

External appearance: the polyps are either separate, or form colonies connected by a small tube-shaped cœnenchyme as in the main form. The number of polyps in the colonies is variable, the

greatest number observed being 7. The polyps are arranged in the same way as in the main form, but they are considerably more slender and narrower in comparison with the length than in the main form. As in the latter they are narrow at the base but expand gradually towards the distal part. The capitular region, which was contracted in most of the specimens, had distinct capitular furrows varying in number between 14 and 19 — 2 polyps had 14, 4 had 15, 13 had 16, 1 polyp 17 and another 19 furrows — the maximum frequently being thus 16. The preserved specimens had often more or less distinct cross-furrows. The tentacles were much narrower than in the main form. The œsophagus is short, the siphonoglyphe distinct, hyposulcus well-developed, though shorter than the œsophagus.

**Anatomical description.** The ectoderm is fairly high, continuous and contains few nematocysts or none. The mesogloea is several times thicker than the ectoderm and like this is richly incrustated with sand-grains, which make the anatomical examination difficult. As the incrustation is not very strong, however, I have been able to make out, that the mesogloea contains a few, large cell-islets but numerous cells (and small cell-islets). (Pl. 5 fig. 5).

The sphincter is strong. Seen in transverse sections through the sphincter the mesogloéal meshes are however fairly large.

The ectoderm of the tentacles is of the typical structure with very numerous spirocysts and fairly common thick-walled nematocysts (length  $17\mu$ ).

The ectoderm of the œsophagus is high. There is a frequent occurrence of equally broad nematocysts with twisted thread (length  $24-36\mu$ , breadth  $10-11\mu$ ) and of thick-walled nematocysts (length  $22-25\mu$ ). The mesogloea is thin, in the lower part it forms longitudinal ridges corresponding to the insertions of the mesenteries. The ectoderm of the siphonoglyphe is as usual thinner than in the œsophagus, the mesogloea on the other hand is several times thicker than there. In two specimens the number of mesenteries was 32, in a third 30. At least one of the first-mentioned polyps had the normal number of developed mesenteries. The third had 9 macro and 7 micro on the one side and 8 macro and 6 micro-mesenteries on the other. The micro-mesenteries are fairly well-developed and from the œsophageal region they reach somewhat into the chambers. The longitudinal muscles are strong, especially on the directive mesenteries. The folds are however large. The parieto-basilar muscles are very weak. Moderate distribution of the longitudinal and parieto-basilar muscles on the body-wall.

The filaments have the usual structure. The glandular tract contains numerous capsules, some equally broad with greatly twisted thread (length  $26-34\mu$ , breadth  $10\mu$ ), others thick-walled capsules broader at the one end and with distinct base to the spiral thread (length  $19-22\mu$ ).

The sexual organs were not developed in the specimens examined by me.

### ***Epizoanthus danielsseni* n. sp.**

Pl. 1 fig. 13, 15 Pl. 2 fig. 6 Pl. 5 fig. 1.

*Epizoanthus glacialis* n. sp. pro parte Danielssen Norwegian N. Atlantic Ex. p. 129 fig. 9. Pl. 6.

Occurrence:  $64^{\circ}21'N.$ ,  $10^{\circ}40'E.$  Sabulous clay. Bottom temp. —  $07^{\circ}$  Norwegian North Atl. Ex. Stat 164 June 29th 1879. 5 sp. Bergens Museum. (sp. a).

73° 3' N., 18° 30' E. Beeren Island—Norway 410 m. Bott. temp. 2°. Gray clay. Spitzbergen Ex. 1898 4/9 No. 42 several colonies R. M. (sp. b).

Davis Straits 80 fms. 20/10. 1884. Holm. several colonies. Copenh. Museum. (sp. c).

75° 26' N., 67° 27' W. 260 fms. Sophia Ex. No. 582. 1 sp. R. M. (sp. d) var. *loveni* Finmarken. Øxfjord Loven. 1 colony. R. M.

Dimensions: (a) Length of the largest polyp 0.8 cm., breadth 0.7 cm., (b) length of the largest polyp 1 cm., breadth 0.7 cm. (c) length and breadth about 0.5 cm. (d) height 0.8 cm., breadth 0.6 cm.

Colour. According to Danielssen's figure 9 Pl. 6, which I consider to represent this species, the body-wall must be light-red with a yellowish tint, the latter being due to the large amount of sand in the incrustation. The capitular furrows are reddish, with a tinge of brown. The tentacles and the oral disc (the central part in the middle?) are reddish brown. In alcohol a, c and d are light sand-coloured, b dirty grayish.

External appearance. The polyps from the localities a and d formed no colonies and were fixed on stones, whereas most of the specimens from b and c generally formed colonies; c was fixed on Balani, b on stones and Rhizopoda (Rhizammina?). The polyps are seldom placed quite close together; the cœnenchyme between the different polyps is generally fairly well-developed, but very thin. On a colony from c and on those from b, when viewed externally, it looks as if the cœnenchyme is thick. This is generally not the case, however, though the irregular under-layer of tubuli pressed together makes it look thickened at some places. All the polyps were contracted and the tentacles not to be seen; in this state the breadth and the length are almost equal or the length a little greater. The distal part is somewhat broader than the proximal. On most of the polyps the upper aspect is truncate<sup>1</sup>, sometimes they are a little rounded, especially the smaller polyps. The capitular furrows are more or less distinct, most distinct in d (fig. 13), in the smaller specimens their number could not be determined. They seem to vary between 16 and 22, a) 22, b) 18, 18—16, 16, 17, 21—18—17—18, c) 20—20—22—22, d) 18. The polyps as well as the cœnenchyme were strongly incrustated with sand-grains, which made the sectioning very difficult.

In a closely examined specimen the number of tentacles was 36. If the tentacles are double the number of capitular furrows, they must vary between 32 and 44.

The œsophagus is short with distinct siphonoglyphe and a hyposulcus which is as long as the œsophagus.

Anatomical description. The ectoderm of the body-wall is fairly high and continuous with a weak cuticle. In the lower part of the polyp are equally broad nematocysts with greatly twisted thread (length 34—41  $\mu$ , breadth 11—12  $\mu$ ). In the capitular region we find similar capsules, which are however considerably narrower (length 34—41  $\mu$ , breadth 7  $\mu$ ). The mesogloea is very large, at least twice as thick as the ectoderm and is generally strongly incrustated with sand and some fora-

<sup>1</sup> Among the specimens of *Epizoanthus glacialis* collected by the Norwegian North Atlantic Expedition were also some polyps of *E. danielsseni*. Danielssen 1891 p. 130 says that "when the polyp (of *E. glacialis*) is retracted the uppermost extremity appears truncated but with a little depression in the middle and a rounded margin carrying it Pl. 6, fig. 9." This description agrees well with a polyp found in the collection which I consider to be the original of Danielssen's fig. 9, Pl. 6 — represented in my paper in fig. 6 Pl. 2. This polyp belonged to the species *E. danielsseni*. The description of the upper part of the body on the other hand does not agree with *E. glacialis*.

minifera. It contains fairly many small cells with outshoots (Pl. 5, fig. 1). In the specimen from the locality c, which was somewhat less incrustated than the rest, there seemed to be a sparse occurrence of cell-islets of moderate size near the entoderm. Whether these may also be found in the other colonies I am unable to say owing to the strong incrustation. The ectoderm is almost as high as the entoderm.

The sphincter is very strong and resembles that of *E. glacialis*. It almost fills up the whole breadth of the mesogloea. In transverse sections we find large muscle fibres separated by fairly thin mesogloea-ridges, which divide up forming smaller meshes.

The tentacles have the usual structure. The ectoderm is provided with very numerous spirocysts. It contains besides many small nematocysts of the same kind and size as in the capitular region and typical thick-walled capsules (length 17—19  $\mu$ ).

The ectoderm of the oesophagus is high and contains numerous thick-walled capsules with fairly distinct basal part to the spiral thread (length 24—27  $\mu$ ). There is besides a sparse occurrence of large nematocysts as in the capitular region (length 38—48  $\mu$ , breadth 7  $\mu$ ). The mesogloea is thin, but thickened in the siphonoglyphe.

The number of mesenteries is variable. In two of the polyps of b it was 38 and 32 respectively, typically developed in the latter and in the first with two mesenteries more on the one side of the sagittal plane than on the other. One specimen from a had 36 mesenteries and 2 specimens from c had 36 and 30 respectively. The latter was however a small polyp.

The macro-mesenteries are large with thick mesogloea (all the specimens were however strongly contracted). In the lower part of the oesophagus the micro-mesenteries were fairly weak and only projected very little above the entoderm of the body-wall. The longitudinal musculature is comparatively strong and when seen in transverse section lies in close folds. The parieto-basilar muscles are weak. The longitudinal and the parieto-basilar muscles extend a long way onto the body-wall.

The filaments have the usual structure. In the glandular tract there is a numerous occurrence of nematocysts with greatly twisted thread (length 34—48  $\mu$ , breadth 7  $\mu$ , sometimes 8  $\mu$ ) and thick-walled capsules with distinct basal part to the spiral thread, broader at the one end than at the other (length 22  $\mu$ ). Further, I have sometimes observed some very scarce nematocysts of the same kind as in the lower part of the body-wall (length (24) 26—29  $\mu$ ).

The polyps are dioecious.

var. *loveni* Pl. 2, fig. 9.

Together with the species *E. glacialis* and *Isozoanthus ingolfi* collected by Sven Lovén in Oxfjord in Finmarken, occurred a small colony with 2 polyps (fig. 9 Pl. 2), which had a great outward resemblance to these species and a similar incrustation of sand-grains, among which a number of black. Examination of the nematocysts and the subsequent anatomical investigation showed, however, that they did not belong to these species but stood in better agreement with *E. danielsseni*, to which I provisionally refer them, though they are not in absolute agreement with this species, measurements especially of the large nematocysts, with regard to length, lie somewhat below the values found in *E. danielsseni* (even among the specimens from locality c which showed the lowest values). The incrustation is also considerably weaker, so that we may possibly have a new species before us, but

as the material is so small and not very well-preserved, I have preferred to consider this colony as a variety of *E. danielsseni*, the more so as the anatomical investigation is incomplete.

Dimensions of the largest polyp: length 0.4 cm., breadth in the capitular region 0.45 cm.

Colour in alcohol: grayish with black sand-grains.

External appearance: the polyps were cylindrical, broader in the capitular region. The distal margin is truncate, the upper part sunken. The capitular furrows are indistinct. The incrustation was not so strong as in the main form and mainly restricted to the outer part of the mesogloea.

Anatomical description. Regarding the inner structure the lower part of the body-wall contains in the ectoderm numerous nematocysts with greatly twisted thread (length 24–36  $\mu$ , breadth 11–12  $\mu$ ), in the capitular region similar capsules often occur (length 29–31  $\mu$ , breadth only 7  $\mu$ ).

The sphincter was very strong, resembling that in the main form, but not drawn out so much as in the latter.

The ectoderm of the tentacles contains numerous spirocysts, fairly many nematocysts of the same kind as in the capitulum (length 31–36  $\mu$ , breadth 7  $\mu$ ) and a few thick-walled capsules (length 14–17  $\mu$ ). Similar capsules are also found in the oral disc.

The oesophagus contains numerous narrow, thick-walled nematocysts (length 19–22  $\mu$ ). I cannot determine the number of mesenteries with any certainty, but it must be about 32 or a little more.

The glandular tract of the filament is provided with very few, uniformly broad capsules of the same kind as in the lower part of the body-wall (length 29–36  $\mu$ , breadth 12  $\mu$ ) and with many capsules like those in the capitular region (length 29–38  $\mu$ , breadth 7  $\mu$ ). Further, many thick-walled, narrow nematocyst capsules occur (length 19–22  $\mu$ ) and thick-walled capsules with distinct basal part to the spiral thread, which are broader at the one end (length about 19  $\mu$ ).

### **Epizoanthus roseus Dan.**

Pl. 3, fig. 4, Pl. 5, fig. 6.

*Epizoanthus roseus* n. sp. Danielssen Norwegian North Atl. Ex. 1890. Actinida Tab. 6 fig. 10 Tab. 25  
figs. 4–6.

Occurrence: 71° 25' N., 15° 41' E. clay 1134 m. Bott. temp. 1.0. Norw.-North Atl. Ex. 1877  
19.7 B. M. R. M.

Dimensions. The polyps reach a length of up to 15 mm. (Danielssen). In the preserved state the length of the largest polyp was about 1.1 cm., largest diameter a little under the tentacles 0.5 cm., smallest diameter 0.3 cm.

Colour. "The sarcosoma is semi-transparent, grayish. The polyp is grayish-yellow owing to the incrustated sand, but the rose-red integument shines through. The oral disc is rose-red with lighter-coloured radii. The tentacles are, upon their lowest broad part rose-red like the oral disc, but upon their superior half are paler in colour and almost white at the point" (Danielssen). In the preserved state they are dirty sand-coloured.

External appearance. The polyps are connected with each other by a flat cœnenchyma of moderate size. The single polyps are placed quite close to each other. With regard to shape the

polyps according to Danielssen are "almost piriform." The small contracted polyps with quite retracted tentacles are somewhat narrower in the proximal than in the distal part, which is somewhat rounded. The expanded polyp was narrowest a little above the base, then gradually becoming wider and reaching its greatest breadth some way below the tentacles, afterwards tapering a little towards the base of the tentacles. The distal part is provided with capitular furrows, which Danielssen states to be 12 in number. This is too few, as far as I can see. The ridges and furrows are certainly not so distinct in the preserved polyp, but I have found 16—18. The polyps are incrustated with sand-grains, especially in the proximal part and in the coenenchyme.

The number of tentacles probably agrees with the number of mesenteries.

The oesophagus has a very distinct siphonoglyphe.

**Anatomical description.** The ectoderm of the body-wall is fairly thin, considerably thinner than in *E. glacialis*, continuous and provided with a thin cuticle. In the ectoderm are fairly many spirocysts (normal shape?) and large nematocysts with greatly twisted thread. The latter have a length of 29—31  $\mu$  and a breadth of 12  $\mu$  (the lower part being broader than the upper). Small cells occur in great numbers, but no lacunae or groups of cells seem to be present in the mesogloea, at least not in the distal part (Pl. 5, fig. 6). The incrustation is fairly strong and consists of comparatively large sand-grains, here and there a sponge-needle and exceptionally foraminifera. The entoderm is well-developed and thicker than the ectoderm.

The sphincter is mesogloal but not so strong as in the other Epizoanthus-species examined by me (Pl. 3, fig. 4). In the distal part the meshes are considerably larger than in the proximal and extend horizontally, i. e. in the direction from the ectoderm to the entoderm. The bridges of connective tissue between the muscle-meshes were broad.

The tentacles have the usual structure. The ectoderm is very high with numerous large spirocysts; further, it contains the same kind of large nematocysts as occur in the body-wall and typical thick-walled capsules (length 17  $\mu$ ). The mesogloea is thin, the longitudinal musculature moderately developed.

The ectoderm of the oesophagus is fairly thick and contains large capsules, almost of the same kind and size as those in the body-wall, besides not a few typical thick-walled capsules (length 24—26  $\mu$ ). The mesogloea is thin, being however considerably thickened in the siphonoglyphe.

The single specimen examined by me had 32 regularly arranged mesenteries. Danielssen's statements on this matter cannot be correct, as it is quite evident from his figure, that he has not seen the macro-type arrangement but has supposed the macro and micro-mesenteries to be alternating everywhere. The mesogloea of the macro-mesenteries is fairly thick, the micro-mesenteries rather long but narrow and not much developed. The musculature is comparatively weak.

The filaments seem to have the usual structure. The glandular tract contains the same kind of nematocysts as occur in the oesophagus. The thick-walled capsules may sometimes be a little smaller (22—24  $\mu$ ).

The sexual organs were not developed in the polyp closely examined by me.

**Epizoanthus beeren-islandicus** n. sp.

Pl. 2, fig. 10, Pl. 3, fig. 2, Pl. 4, fig. 1.

Occurrence: 73° 3' N., 18° 30' E. Beeren Island-Norway 410 m. Bott. temp. 2°. Gray clay. Spitzbergen Exp. 1898 4/9. No. 42 3 sp. R. M.

Dimensions of the largest polyp: height and breadth about 1 cm.

Colour in alcohol: yellowish.

External appearance. The three specimens of this species formed no colonies. One was attached to a stone, one other to a Retepora. The cœnenchyme was very thin, disc-shaped. The polyps are cylindrical, almost as high as broad — the animals however were very contracted — and the distal part was a little broader than the proximal. The upper margin was truncate on the contracted polyps. The capitular region has some fairly distinct furrows. In the large specimens I counted 21 capitular furrows with distinct, incrustated ridges between them. The incrustation, which is comparatively inconsiderable, consists of small light sand-grains, now and then interspersed with a few small black sand-grains.

The œsophagus is short with distinct siphonoglyphe and hyposulcus of almost the same length as the œsophagus.

Anatomical description based on two specimens. The ectoderm of the body-wall is continuous and provided with a distinct cuticle. It is fairly high and contains nematocysts with greatly twisted thread, which are uniformly broad, 31—37  $\mu$  long and 11—12  $\mu$  broad, and fairly common except in the capitular region. The mesogloea is always thicker than the ectoderm, double as thick at the most. It contains fairly many small cells with long thread-shaped outshoots, here and there cell-islets and lacunae. The latter often, though not always, lie at the base of the mesenteries, so that in certain sections (Pl. 4, fig. 1) the lacunae are very characteristic in appearance. The entoderm is almost of the same size as the ectoderm. The incrustation is rather inconsiderable in the ectoderm; the greater part of the mesogloea has no incrustation, this is mostly found near the mesenteries from which it often penetrates into the above-mentioned lacunae.

The sphincter is strong and long (Pl. 3, fig. 2) and lies nearer the ecto- than the entoderm, so that in the capitular furrows it is only separated from the ectoderm, by a thin mesogloæal lamella. The muscle-meshes are drawn out crosswise and the mesogloæal meshes are thin.

The ectoderm of the tentacles contains as usual numerous spirocysts, whereas the thick-walled nematocysts (length 17  $\mu$ ) are very scarce. Further, there is a very sparse occurrence of the same large nematocysts as found in the filaments. The ectodermal musculature is fairly strong.

The ectoderm of the œsophagus contains fairly many large nematocysts (length 34—41  $\mu$ ) and numerous typical, thick-walled capsules (length 22—25  $\mu$ ). The structure of the siphonoglyphe agrees with that in other species of Zoanthidae described here.

The number of mesenteries in the three specimens was 44, 40 and 39 respectively. In the first specimen, which was regularly developed, the 6th proto-mesentery on the one side of the sagittal plane was a micro instead of a macro-mesentery. In the second specimen the one side was more developed and had one pair of mesenteries more than the other. The micro-mesenteries in the lower part of

the œsophageal region were fairly well developed. The longitudinal muscles on the macro-mesenteries are fairly strong but form few folds. The parieto-basilar muscles are very weak and narrow. The distribution of the longitudinal and parieto-basilar muscles on the body-wall is quite distinct.

The filaments have the usual structure. The nematocysts of the glandular tract are 34—41  $\mu$  long and 10—12  $\mu$  broad (very seldom only 9  $\mu$  broad). They are uniformly broad and very common and there is also a frequent occurrence of thick-walled capsules with distinct basal part to the spiral thread (length 22—26  $\mu$ ).

The sexual organs were undeveloped in the two specimens sectioned in the sexual region.

### **Epizoanthus glacialis** Dan.

Pl. 2 fig. 1—5, Pl. 4 fig. 2, 6, 7.

*Epizoanthus glacialis* n. sp. Danielssen Norw. Atl. Exp. Actinida p. 129, Tab. 6 figs. 7—9, Tab. 24 figs. 5—8, Tab. 25 figs. 1—3 pro parte.

*Palythoa norvegica* Kor. & Dan. Marenzeller K. Acad. Wiss. Wien 3 1886. IV p. 16 var *jan. mayeni*.

Occurrence: 68° 21' N., 10° 40' E. 836 m. Sabulous clay. Bott. temp. — 0.7°. Norw. North Atl. Ex. 1876, 29. 6. St. 164. many specimens Bergen M.

71° 25' N., 15° 41' E. 1134 m. Clay. Bott. temp. — 1.0°. North Atl. Ex. 1877. 17. 7 St. 200. a few specimens B. M.

Altenfjord 80 fms. clay. June 1890. Jägerskiöld. some colonies Upsala M., R. M.

Öxfjord Finmarken. Loven 1 sp. R. M.

Greenland Umanak 250 fms. clay Amundsen 15. 8. 1860. several specimens R. M.

Greenland Umanak 397 fms. light clay. Ingegerd and Gladans Ex. J. Lindahl 13. 7. 1871. 2 specimens R. M.

Greenland off Umanakfjord 122 fms. hard light grayish clay. Ingegerd and Gladans Ex. J. Lindahl 14. 7. 1871. several large colonies R. M.

Greenland 70° 53' N., 52° 18' W. 397 fms. light clay. Bott. temp. — 2.8° (27° F.) C. Nyström Upsala M.

Jan Mayen 200 m. Austrian polar stations 1882—1883. 1 colony: var *jan mayeni*.

Dimensions. The column measures about 2.0 cm. in height, 0.6 cm. in breadth at the base, 0.6—0.7 cm. broad at the uppermost extremity and 0.4 cm. broad at the middle (Danielssen). Specimens from Umanak fjord, which were considerably larger than the specimens of *E. glacialis* I have seen from the Norwegian North Atlantic Expedition, had in the preserved state a length of about 1.8 cm. and a breadth of 0.6 cm., the smallest breadth being 0.4 cm.

Colour. The incrustated portion of the body is greenish-yellow but when the animal is extended almost yellow, having a somewhat greenish play of colour at the base only. The oral disc is faint brick-red with darker folds round the oral aperture. The tentacles are more intensely red than the oral disc, but are somewhat paler in colour at the extremities (Danielssen). In alcohol dirty yellowish.

**External appearance.** This species forms larger or smaller colonies, sometimes almost of the size of a hand (the colonies dredged off Umenak Fjord). The polyps are connected with each other by a flat, rather thick cœnenchyme with a fairly well developed net-work of entodermal canals. The polyps are either placed close to each other as in the Umenak material or emerge from the cœnenchyme at greater intervals. They are cylindrical in shape especially in the longitudinally expanded specimens, in the more contracted the middle part becomes somewhat narrower than the capitular region especially. The length is generally at least double the breadth. On contracted polyps the distal margin is rounded not truncate. Danielssen states however that "when the polyp is retracted the uppermost extremity appears truncated but with a little depression in the middle." As far as I can see, this is not the case but a specimen of *E. danielsseni* found in the same sample as *E. glacialis* had this shape, so that Danielssen's description was probably in this regard taken from that species (cf. *E. danielsseni*). The capitular furrows are distinct and vary in number. The greatest number observed by me was 28 the smallest 16, the latter in a small specimen. The polyps taken near the coast of Greenland, which generally were considerably larger than the Norwegian ones, had also as a rule a larger number of capitular furrows. In 15 of the first named specimens I counted the following number of capitular furrows 20, 20, 20, 20, 20, 21, 21, 22, 23, 23, 23, 25, 27, 28. Five type specimens had 16, 18, 18, 20, 20. Specimens from Altenfjord have 17, 17, 18, 18, 20, 20, 20, capitular furrows. That the number of furrows may also be high in the Norwegian forms may be seen from the fact, that I found among them a specimen with no less than 52 mesenteries. The incrustation, which consists almost exclusively of sand interspersed with a few sponge-needles, is not very strong and restricted to the ectoderm and the outer part of the mesogloea. The œsophagus has the usual appearance lengthwise. The siphonoglyphe is distinct with a well-marked, though not very long hyposulcus.

**Anatomical description.** The ectoderm of the body-wall is high and sometimes as thick as the mesogloea; it is continuous, but may at times show a slight tendency to become discontinuous, and is provided with a thin cuticle. The nematocysts of the ectoderm consist partly of large nematocysts with greatly twisted thread (length 26—34  $\mu$ , breadth 10—12  $\mu$ ) partly of thick-walled capsules (length 19  $\mu$ ), which however occur in small quantities.

The mesogloea is thick, sometimes thicker on one side than on the other. In the distal part it contains fairly many cells, often provided with long outshoots (Pl. 4, fig. 6). Further, there is a sparse occurrence of cell-islets of moderate size, which however are more numerous in the Umanak specimens. In the proximal part both cells and cell-islets occur more frequently (Pl. 4, fig. 7). No muscles are present in the mesogloea except the sphincter and the mesogloéal muscles of the body-wall which may break through the mesenteries; the structures (muscle-meshes) observed by Danielssen are nothing but breaches in the mesogloea. Lacunae are absent, except in the sexual region, where some signs of these are seen. The entoderm is remarkably well-developed in comparison with the other layers of the body.

The sphincter (pl. 4 fig. 2) is very strong. Seen in transverse section the muscle-meshes in the proximal part are separated by large portions of mesogloea, in the distal part they are divided into large meshes, extending in the direction from within outwards and almost filling the whole breadth of the mesogloea, or even more split up here, though smaller and lying nearer the ectoderm than the entoderm

The tentacles have the usual structure. The spirocysts in the ectoderm are as usual very numerous, the thick-walled ones (17—22, 19—24  $\mu$  long) scarce. Further, some large nematocysts of the same kind as in the body-wall occur in very small quantities. The longitudinal musculature is moderately developed.

The ectoderm of the oesophagus is high. It contains fairly great numbers of nematocysts partly large with much coiled thread and uniformly broad, length (26) 29—36  $\mu$ , breadth about 12  $\mu$ , partly thick-walled 19—24  $\mu$  long. The mesoglœa is thin but that of the siphonoglyphe on the other hand is considerably thickened. The ectoderm of the siphonoglyphe is as usual thinner than in the oesophageal region.

The number of mesenteries varies according to the size of the polyps, 3 of the examined Umenak specimens had 40, 46 and 50 mesenteries. The arrangement of the mesenteries in the first polyp was typical, both the others had a pair of mesenteries more on the one side of the directive chamber than the other. One of the type specimens (the smallest) had 36, another 40 and a third no less than 52 mesenteries. While the first and last polyp were symmetrical the third one was very asymmetrical, the one side having 22, the other no more than 18 mesenteries. Specimens from Öxfjord Finmarken had 36 mesenteries. Danielssen's statement that the number of micro-mesenteries is the same as the number of macro-mesenteries is of course incorrect, as Zoanthidae-species with the mesenteries arranged according to the macro-type do not have as many micro as macro-mesenteries.

In the oesophageal region the macro-mesenteries are fairly thick with well-developed mesoglœa. The longitudinal musculature is strong with fairly many folds (text-fig. 5). The parieto-basilar muscles are weak. Extension of the longitudinal and parieto-basilar muscles onto the body-wall inconsiderable. In the sexual region the macro-mesenteries are thin and the musculature weak. The micro-mesenteries are moderately developed.

The structure of the filaments is as usual. The glandular tract sometimes contains greater sometimes smaller numbers of large, uniformly broad nematocysts with much coiled thread — length (26) 29—36  $\mu$  breadth 10—13  $\mu$  — and thick-walled capsules 19—26  $\mu$  long with distinct basal part to the spiral thread.

The species is diœcious.

**Systematic remarks.** In the sample from St. 164 Norw. North Atl. Ex., — the only type-specimens of *E. glacialis* which I have had for examination, — there were two species which have undoubtedly been mixed in Danielssen's description. The one is the species described here, which I have considered the type-specimen of Danielssen's species *glacialis*, as his description, at any rate with regard to the external appearance, may in the main be referred to this species. Figures 7 and 8 on Pl. 6 in Danielssen's work evidently represent the above-described species and the same is certainly the case with fig. 5 and probably also with fig. 6 on Pl. 24. On the other hand, fig. 9 Pl. 6 probably represents *E. danielsseni*. With regard to the anatomical figures of *E. glacialis* in Danielssen's work they are so poor that they may represent the one as well as the other of the species, though the weak incrustation seems to indicate the species I have described as *glacialis*. Both species are namely so unlike each other, not only with regard to the nematocysts but also in external

appearance and inner structure, that there can be no doubt that they represent 2 species quite different from each other.

var. *jan mayeni* Pl. 2 fig. 2.

Through the kindness of Prof. Marenzeller, I have had the opportunity of examining the specimens from Jan Mayen which he considered *Palythoa norvegica*. They could not be referred to this species with absolute certainty, but may well be considered as a variety of *E. glacialis*, from which they differ but little, mostly with regard to the nematocysts which are generally somewhat larger than in the main form.

Occurrence. See above under the main form.

Dimensions. Length of the largest polyp 1.2 cm., breadth in the capitular region 0.7 cm.

Colour in alcohol. Ectoderm uncoloured. Mesogloea interspersed with black sand-grains.

External appearance. 1 colony consisting of 2 polyps, which lie close to each other projecting from a thin coenenchyme (fig. 2 Pl. 2). In the contracted state the polyps are elongated, cylindrical somewhat broader at the upper end and with rounded capitular region. The capitular furrows are very distinct, in the smaller specimen I counted 21, in the larger 24. The siphonoglyphe is well developed.

Anatomical description. The ectoderm of the body-wall is continuous, very high and thicker than the mesogloea, in which we frequently find broad nematocysts with greatly twisted thread (length 34–36  $\mu$ , breadth 12–13  $\mu$ ). Incrustation of small sand-grains. Otherwise like the main form.

While the spirocysts in the ectoderm of the tentacles were very numerous, the thick-walled capsules only occurred in small numbers (length 24  $\mu$ ).

The ectoderm of the oesophagus has the typical appearance. The large nematocysts resembling those in the body-wall are scarce but somewhat larger than usual (length 38–43  $\mu$ , breadth 12–13  $\mu$ ), the thick-walled nematocyst capsules are numerous and longer than in the main form — 26–29 (31)  $\mu$  long.

The mesenteries. The specimen examined has 42 mesenteries, 12 macro and 10 micro on the one side, 11 macro and 9 micro on the other. Of the latter the 1st proto-mesentery (according to the developmental scheme adopted) was not much developed and very little larger than a micro-mesentery. Otherwise the mesenteries are as in the main form.

In the glandular tract occur some large nematocysts with much coiled thread (length 34–36  $\mu$ , breadth 13  $\mu$ ). Further, it contains fairly many thick-walled capsules, with distinct basal part to the spiral thread (length 27–30  $\mu$ , breadth 6  $\mu$ ).



Text-fig. 5. Transverse section through the body-wall with adjacent mesenteries and oesophagus of *Episoanthus glacialis* (specimens dredged by C. Nyström). Mesogloea and muscles black. Ectoderm not drawn and entoderm only in part. dc directive chamber. In the mesogloea of the body-wall the incrustations are marked by dots.

**Epizoanthus koreni** n. sp.

Pl. 2 fig. 23, Pl. 4 fig. 4.

Occurrence: 62°49' N., 7°12' W. 276 fms. Bott. temp. 1·6°. Ingolf Ex. St. 144 1 colony of two polyps.

Dimensions: Length of the largest polyp 1·1 cm; smallest breadth 0·35 cm.; largest breadth 0·55 cm.

Colour in alcohol: dirty sand-coloured.

External appearance. The cœnenchyme was large and covered among other things an arm of an Ophiurid. It is fairly thin but has a very robust appearance, probably owing to the imbedded small foreign particles on which it grows. The 2 polyps are not close to each other but separated by a fairly great interval. The largest polyp is elongated, almost double as long as broad, narrow at the base but gradually increasing in breadth upwards. The smaller polyp on the other hand is higher than broad and more cylindrical. The capitular furrows are distinct, in the largest specimen their number was 18, in the smaller probably 15. The upper margin of the polyps is truncate, the tentacles being retracted. The incrustation is inconsiderable and restricted to the outer part of the body-wall.

The œsophagus is short, siphonoglyphe and hyposulcus distinct.

Anatomical description. The ectoderm of the body-wall is fairly high, continuous and incrustated with sand-grains, sponge-needles and foraminifera, though not very strongly. It is also incrustated with detritus particles attached to the cuticle. The ectoderm frequently contains nematocysts with coiled thread, in the capitular region these are scarce. They are uniformly broad 26—29  $\mu$  long, about 10  $\mu$  broad and rounded at both ends. The mesoglœa is thick and considerably thicker than the ectoderm; only the outer part of the mesoglœa has a slight incrustation consisting of the above-mentioned particles. The mesoglœa contains numerous oval or round cells and fairly many, middle-sized cell-islets, and rarely large cavities filled with round or oval cells, the nature of which I have not been able to determine with certainty (Pl. 4, fig. 4 ml?). The entoderm is fairly large and seems to contain zooxanthellæ, which however are more numerous in the entoderm of the œsophagus and the mesenteries. In the mesoglœa of the mesenteries similar cavities filled with cells may also occur as in the mesoglœa of the body-wall.

The sphincter is very strong and resembles the sphincter in *E. erdmanni*. It lies considerably nearer to the ectoderm than the entoderm.

The ectoderm of the tentacles contains great numbers of spirocysts but only few thick-walled capsules (length about 19  $\mu$ ) and nematocysts with much coiled thread (length 26—31  $\mu$ , breadth 10  $\mu$ ).

The œsophagus has the usual structure. I have not been able to make any macerated preparations of the high ectoderm. The siphonoglyphe is deep with thinner ectoderm and considerable thicker mesoglœa than in the œsophagus.

In the specimens examined anatomically the number of mesenteries (in the large polyp) was 36, 10 macro and 8 micro on either side of the directive line. The micro-mesenteries are moderately developed, the macro-mesenteries strong. The longitudinal musculature on the macro-mesenteries is fairly strong, but not much folded, the parieto-basilar musculature is weak. The distribution of the longitudinal and parieto-basilar musculature on the body-wall is inconsiderable.

The filaments have the usual structure. The glandular tract contains numerous nematocysts with much coiled thread 26—36  $\mu$  long and 10—12  $\mu$  broad, sometimes even narrower. Further, some thick-walled capsules are found (length 19—22  $\mu$ ).

The colony was not sexually ripe.

### Genus *Isozoanthus* Carlgren.

*Isozoanthus* n. gen. Carlgren in Nordgaard Hydrogr. and Biol. Investig. 1905 p. 159.

Macrocnemic Zoantheae with a diffuse entodermal sphincter muscle. The body-wall incrustated. The ectoderm is always continuous. Cell-islets and lacunae in the mesogloea but no encircling sinus. Dioecious polyps. Polyps solitary or in small clusters, as a rule connected with a comparatively thin coenenchyme.

The genus, which has been briefly characterised by me on an earlier occasion (1905 p. 159), forms a link between the genera *Epizoanthus* and *Parazoanthus*. With regard to the appearance of the sphincter, *Isozoanthus* agrees with the latter, but in the structure of the body-wall it agrees with the former. In the genus *Isozoanthus* the encircling sinus so characteristic of *Parazoanthus* is wanting.

If attention is only paid to the appearance of the sphincter in arranging the genera within the macrocnemic Zoanthidae, the *Isozoanthus*-species would have to be referred to the older genus *Parazoanthus*, but if the structure of the mesogloea of the body-wall is considered to be of some importance in the characterisation of the genera, it is most reasonable to let the species, which have no incircling sinus but are otherwise in the main in agreement with *Parazoanthus*, form a separate genus, i. e. *Isozoanthus*. In the latter case the diagnosis given by Haddon and Shackleton for the genus *Parazoanthus* would need no revision, in the first case on the other hand their diagnosis would have to be altered with regard to the encircling sinus, as for example "encircling sinus absent or present." If the species comprised by me under the genus *Isozoanthus* are referred to the genus *Parazoanthus*, it would at any rate be advisable to let them form a separate sub-genus named *Isozoanthus*. Future investigations must decide, whether *Isozoanthus* should be considered a separate genus or a sub-genus.

The type for the genus *Isozoanthus* is *Isozoanthus (Epizoanthus) arborescens* (Dan.). Another species, by the way the longest Zoantharia known, has been figured by me in Chun's work: "Aus den Tiefen des Weltmeeres" 2 Aufl. 1905 p. 520. It has been dredged on the Agulhas Bank during the German deep-sea expedition and provisionally named by me *I. giganteus*. The genus thus occurs in northern as well as in southern seas. A revision of the Zoanthidae already described would possibly show, that certain forms described as *Parazoanthus* should in reality be referred to *Isozoanthus*.

Of the 9 *Isozoanthus*-species mentioned here only one, namely the type of the genus, *I. arborescens*, has been described before by Danielssen, who referred it to the genus *Epizoanthus*. Danielssen's anatomical description leaves much to be desired in many respects. All the species with exception of *I. danicus* have been dredged during the Ingolf Expedition. *I. danicus* has been taken in the Limfjord and determined by Mortensen (1897) as *Z. couchii* (Johnst.).

**Synopsis of the *Isozoanthus*-species described here.**

- A. Single polyps or small colonies of two specimens with tube or groove-shaped cœnenchyme, which is well-developed, but probably unattached. The mesogloea of the body-wall contains few cells exceptionally cell-islets. Number of mesenteries 28—32 ..... *bulbosus*.
- B. Single polyps or small colonies of densely placed polyps connected by an inconsiderable cœnenchyme. The polyps are elongated, slightly attached.
- a. Mesogloea of body-wall contains few small cells. Number of mesenteries 32—36. Specific nematocysts in the filaments  $31-38\mu \times 11-12\mu$  ..... *arborescens*.
- aa. Mesogloea of body-wall contains numerous, granular, fairly large cells. Number of mesenteries 34—38. Specific nematocysts in the filaments  $36-53\mu \times 12\mu$  ..... *davisi*.
- C. Colonies with large, fairly well-developed cœnenchyme.
- b. Elongated, small polyps.
- c. Number of mesenteries about 34. Specific nematocysts in the filaments partly large  $26-34\mu \times 10-12\mu$  partly smaller  $14\mu \times 5\mu$ . Well developed cœnenchyme tube-shaped covering needles of Hexactinellidae (always?) ..... *islandicus*.
- cc. Number of mesenteries about 30. Specific nematocysts in the filaments partly large  $19-26\mu \times 10-12\mu$ , partly smaller  $12-14\mu \times 5-6\mu$ . Cœnenchyme band-like (on *Cidaris* spines, always?) ..... *dubius*.
- bb. Polyp of moderate length or short.
- d. Number of mesenteries 18—22. Specific nematocysts in the filaments  $22-26\mu \times 7\mu$ . Mesogloea of the body-wall almost homogeneous with very scarce cells. Cœnenchyme band-like, branched ..... *danicus*.
- dd. Number of mesenteries about 32. Specific nematocysts in the filaments partly large  $31-43\mu \times 12\mu$ , partly smaller  $15\mu \times 7\mu$ . Mesogloea of the body-wall contains numerous small cell-islets and less numerous large cell-islets often fused together to form lacunae. Cœnenchyme band-like, branched ..... *magninsulosus*.
- ddd. Number of mesenteries 38—40. Specific nematocysts in the filaments partly large  $41-48\mu \times 14-17\mu$ , partly smaller  $17-19\mu \times 7\mu$ . Mesogloea of body-wall contains numerous small cell-islets and scattered large ones. Lacunae-system slightly developed, cœnenchyme of small dimensions ..... *multinsulosus*.
- dddd. Number of mesenteries 38—40. Specific nematocysts in the filaments partly large  $31-40\mu \times 12-14(19)\mu$ , partly smaller  $17-19\mu \times 7\mu$ . Mesogloea of body-wall contains numerous, often elongated cells and larger or smaller cell-islets sometimes fused together at the base of the mesenteries. Large, thin cœnenchyme ..... *ingolfi*.

***Isozoanthus bulbosus* n. sp.**

Pl. 1, figs. 5, 6. Pl. 2, figs. 14—16. Pl. 6, fig. 1.

Occurrence: 65° 34' N., 7° 31' W. 762 Danish fathoms. Bott. temp. — 0.8°. St. 105 Ingolf Ex. Several specimens.

66° 23' N., 7° 25' W.	957 Dan. fms.	Bott. temp. — 1.1°.	St. 104	Ingolf Exp.	several spec.
68° 08' N., 16° 02' W.	729 — — — —	— 0.8°.	- 125	— —	2 spec.
69° 13' N., 8° 23' W.	1003 — — — —	— 1.0°.	- 117	— —	12 spec.
69° 31' N., 7° 06' W.	1309 — — — —	— 1°.	- 113	— —	several spec.
70° 05' N., 8° 26' W.	371 — — — —	— 0.4°.	- 116	— —	several spec.
73° 3' N., 18° 30' W.	410 m.	— — 2°.	- 32	Spitzbergen Ex. 1898 4/9	2 spec. R.M.
81° 20' N., 20° 30' E.	1000 m.	— — — —	- 41	Römer & Schaudinn.	Berlin M.
66° 35' N., 56° 38' W.	318 Dan. fms.	— — 3.9°.	- 32	Ingolf Exp.	several spec.

Dimensions in the preserved state. The largest breadth of the polyps was about 0.55 cm. The height was about 0.7 cm. excluding the groove-shaped coenenchyme which may be of variable length (greatest length observed 1.4 cm.).

The colour of living specimens has not been observed. In the preserved state the polyps are dirty coloured, lighter or darker. The polyps which are strongly incrustated with foraminifera look as if they were covered with white grit.

External appearance. The polyps are pear-shaped, in the proximal part often drawn out into a long narrow stalk, which often again increases a little in diameter towards the point and is sometimes somewhat swollen (see fig. 6 Pl. 1 showing the most typical appearance of the polyps). This stalk which often had a groove-shaped appearance (fig. 15—16 Pl. 2) does not however belong to the polyp itself but to the coenenchyme. The cavity of the polyp namely is continued in the stalk part only as large canals, in contrast to what is found in *I. arborescens*. As the polyp, also in contrast to *I. arborescens*, is always unattached, this part which is strongly incrustated probably serves as a sort of anchor for the polyp. The groove-shaped part may possibly have surrounded some object, though the large material collected affords no evidence of this. The polyps are nearly always single, and only very seldom (observed in a few cases only, fig. 5, 6, Pl. 1) does the stalk-shaped part send out another polyp. The body-wall is richly incrustated, probably mostly with foraminifera densely placed, further, with a smaller number of sand-grains and sponge-needles, the latter found mostly in the upper part. In the specimens from St. 116 the sand-grains predominate and these polyps are darker; in specimens from St. 32 the incrustation consisted exclusively of lighter or darker sand-grains interspersed with a few sponge-needles. In the specimens collected at St. 105 as also in those dredged by Römer & Schaudinn, the capitular region was well-marked, owing to the main incrustation being made up of sponge-needles, while the lower part was richly beset with foraminifera. In another specimen I was able to remove large pieces of a sponge, and it is possible that this is symbiotic with the polyp. In two specimens collected during the Spitzbergen Expedition of 1898 the incrustation consisted mainly of sand-grains and sponge-needles, while the foraminifera were scarce. The capitular furrows were indistinct and generally not to be seen in the contracted, preserved polyps. In a half expanded specimen (fig. 5 Pl. 1) on the other hand faint capitular furrows could be observed. In a specimen from St. 32 I counted 13 capitular furrows with well-marked sand-grain ridges in the distal part. The whole polyp is of a more vigorous appearance than *I. arborescens*.

The oesophagus is very short, the siphonoglyphe broad, the hyposulcus almost of the same length as the oesophagus.

**Anatomical description.** The ectoderm of the body-wall is large, continuous and richly incrustated. It contains sparse, uniformly broad nematocysts with greatly twisted thread (length  $31-36\ \mu$ , breadth  $12\ \mu$ ). The mesogloea is fairly thick, mostly incrustated and contains a few large cell-islets and now and then cell-groups, surrounded by inconsiderable protoplasm (Pl. 6, fig. 1). The entoderm is thin. In the capitular region the ecto- and entoderm become thicker, especially the former, while the mesogloea gets thinner.

The sphincter is straight with few folds, the musculature strong.

The longitudinal musculature of the tentacles is strong. The spirocysts of the ectoderm very numerous, whereas the thick-walled nematocysts are scarce, about  $22\ \mu$  long sometimes smaller.

The oesophagus is almost without longitudinal folds, probably because it is very much expanded. The ectoderm contains numerous thick-walled capsules (length  $17-24\ \mu \times 6\ \mu$ ) and is several times thicker than the mesogloea. In the distinct siphonoglyphe the mesogloea is considerably thickened, especially where the directive mesenteries are attached. The ectoderm of the siphonoglyphe is thinner than in the oesophagus.

The number of mesenteries is  $28-32$ , i. e. less than in *I. arborescens* though the latter has a much smaller diameter than *I. bulbosus*. 9 specimens examined had 28 mesenteries, 1 had 32 and 3 had 30, 9 macro and 7 micro on the one side and 8 macro and 6 micro on the other. In one case at least the right side was the most developed. The mesenteries are thin, somewhat thickened inwards and extending below the oesophagus a long way into the gastrovascular cavity, the micro-mesenteries are thin but become broader below the oesophagus. The lamella of the longitudinal muscle is fairly well-developed especially just below the oesophagus, where it is provided with some closely-lying folds. The parieto-basilar muscles are weak. The longitudinal and parieto-basilar muscles extend some distance out onto the body-wall.

The structure of the filaments is typical. The glandular tract contains sparse thick-walled nematocysts broader at the one end and with distinct basal part to the spiral thread (length  $19-22$  ( $24$ )  $\mu$ , breadth  $6\ \mu$ ), further there are also granular thick-walled capsules (length  $26-31\ \mu$ , breadth  $5\ \mu$ , sometimes smaller). In a specimen from St. 32 I found some very few small egg-shaped capsules (length  $10-11\ \mu$ , breadth  $4\ \mu$ ). These may possibly also be present in other specimens but owing to their small size and scarce occurrence may easily have escaped notice. The large nematocysts with greatly twisted thread are very seldom observed (length about  $36\ \mu$ , breadth  $12\ \mu$ ) and are generally absent altogether. I have examined these nematocysts of the filaments in various specimens from different localities and found them in the main to be in agreement with each other. It seems characteristic, that the nematocysts with greatly twisted thread are extremely scarce if present at all. Nor do smaller nematocysts of the same kind as the preceding seem to occur, in contrast to what we find in many other Isozoanthus-species, or if occurring are extremely scarce. In their place thick-walled nematocysts of a somewhat granular appearance may be observed.

The polyps are dicecious.

**Isozoanthus arborescens** (Dan) Carlgr.

Pl. 1 figs. 1—2, Pl. 2 fig. 27, Pl. 3. fig. 5, Pl. 6, fig. 2.

*Epizoanthus arborescens* n. sp. Danielssen Norw. North Atl. Ex. Actinida. 1890. Tab. 6 fig. 6 Tab. 24  
figs. 1—4.

*Isozoanthus arborescens* (Dan) Carlgren in Nordgaard 1905 Investig. in Norwegian fjords p. 159.

Occurrence: 60° 37' N., 27° 52' W., 799 Dan. fms. Bott. temp. 4.5°. Ingolf Ex. 1 spec.

65° 28' N., 27° 39' W. 450 Dan. fms. Bott. temp. 5.5°. Ingolf Ex. St. 97 5 spec.

67° 52' N., 13° 58' E. 247 m. clay Bott. temp. 4.9°. Norw. North Atl. Ex. 23/6 1877. St. 149.

Bergen M. R. M.

S. E. of Mortsund 200 m. Bott. temp. 6.6°. 22/2 1899 Nordgaard. 1 colony.

12 miles E. by S. of Reine 150 m. 3/3 1899 Nordgaard. 2 spec.

68° 15' 5" N., 15° 49' E. Tranödybet 607—640 m. Bott. temp. 6.3°. 16/3 1899 Nordgaard.

Dimensions in the expanded state, probably measured on living specimens: "up to 3.5 cm. in length with a basal part only 0.5—0.6 cm., the uppermost extremity 1.2 cm. in breadth." Danielssen. The largest specimen from the Ingolf Expedition had in preserved state a length of 2.8 cm., a breadth at the base of 0.2 cm. and at the apex of 0.35 cm.

Colour according to Danielssen. "The incrustated portion of the body is grey with a play of a slightly greenish colour. The oral disc is almost white with a reddish tinge. The tentacles pale rosy-red."

External appearance. Danielssen has given a good description thereof. The polyps are solitary and connected with each other by a very small cœnenchyme attached to stones (or Serpula-tubes or similar objects, see Danielssen fig. 6, Tab. 6, fig. 1, Tab. 24). The colonies are often attached by means of a thin membranous part, from which an inconsiderable tube-shaped cœnenchyme extends sending out numbers of polyps which make the colony look like a plant branching off at the base. Though not a little incrustated the polyps are rather slender and very elongated with a narrow, long basal part, which gradually becomes broader towards the distal part. In the contracted polyps the broadest part lies a little way from the distal end. The polyps from Mortsund (fig. 1 Pl. 1) were strongly contracted and consequently very firm, and the basal part of the polyps did not project so much as in the other, more developed polyps from other localities. Danielssen states that they have 16 capitular furrows. On the preserved specimens these are however very indistinct and only in the Mortsund specimens have I been able to trace them. The body-wall is incrustated with sand-grains, though not in very great quantities, so that "when the animal is extended and in full vigour, they permit the white-red integument to shine through it." (Danielssen).

The number of tentacles agrees in all probability with the number of mesenteries, in which case it is 32—36. The innermost row of tentacles are according to Danielssen very long. The same author also states that the oral disc is "rather flat and finely folded, the oral aperture is almost circular."

The œsophagus is short with well-marked siphonoglyphe and distinct hyposulcus.

Anatomical description. Danielssen has described the anatomy of this species but as usual very unsatisfactorily, especially with regard to the musculature, which according to his work

does not differ from that of the other Zoanthidae. He has even made a mistake with regard to the arrangement of the mesenteries, as can be seen from his figure showing the grouping of the mesenteries where he has not observed the couple of mesenteries forming the macro-type. This is for example seen from the fact, that fig. 4 Tab. 24 shows 18 macro-mesenteries, whereas fig. 3 only has 16, which according to the later number of macro-mesenteries is in agreement with the description. As I think it superfluous to point out Danielssen's mistakes in detail, I shall in the following pay no attention to his anatomical description of this species, but only describe the structure as I found it in a type-specimen from Bergens Museum, supplemented by examination of the material collected by Nordgaard and during the Ingolf Expedition.

The body-wall is more or less incrustated with sand-particles, here and there sponge-needles occur and sometimes also foraminifera. The incrustation reaches a longer or shorter distance into the mesogloea, which however is not so much filled with the incrustation that its structure cannot be seen. The ectoderm is continuous with a generally thin but sometimes thicker cuticle on which are fixed particles of detritus. Though comparatively broad the ectoderm is considerably thinner than the mesogloea and is, as usual, most developed in the capitular region. In the greater part of the body-wall there is a fairly frequent occurrence of nematocysts with greatly twisted thread (length 31—41  $\mu$ , breadth 12  $\mu$ ). The mesogloea is thick and contains small cells of more or less frequent occurrence Pl. 6 fig. 2). Ectodermal canals are also found though very seldom. On certain sections of one of the type-specimens I observed some elongated cells, the long outshoots of which were parallel to the margin of the mesogloea. They lay either very far into the mesogloea or near its inner margin. If the position of these cells were not variable, they might possibly be considered as the remnants of a ring-sinus, which however can hardly be the case, as these elongated cells are not of constant occurrence. An encircling sinus is absent. The entoderm is not large and several times thinner than the ectoderm.

The sphincter is entodermal and in transverse sections deep semicircular folds may be seen (fig. 5, Pl. 3). Where the sphincter breaks through the mesenteries one may, as in all Parazoanthus-species, obtain sections which if viewed externally give the impression that the sphincter is mesogloea, but this is not the case.

The structure of the tentacles and the oral disc is in agreement with other Zoanthidae. The ectoderm of the tentacles contains numerous spirocysts and many 14—17  $\mu$  long, typical thick-walled capsules. The longitudinal musculature of the tentacles is fairly strong. The mesogloea of the tentacles is also incrustated.

According to the more or less contracted state, the oesophagus is rounded, oval-shaped or more flattened. The siphonoglyphe is fairly distinct, but the mesogloea is only somewhat thicker than in the other parts of the oesophagus. The ectoderm of the oesophagus is considerably larger than the thin mesogloea. The difference in height between the ectoderm of the oesophagus and the siphonoglyphe is on the other hand quite inconsiderable. Owing to the small development of the oesophagus I have not been able to make glycerine-preparations.

Mesenteries. Of 4 specimens examined 2 had 32, 1 had 36 typically arranged mesenteries. The 4th specimen with 34 mesenteries had 9 macro and 7 micro-mesenteries on the one side, while on the other side there were 18 mesenteries irregularly arranged. This side namely was partly arranged

according to the micro-type, and the 12th mesentery from the endocoele of the micro-directive mesenteries was a macro-mesentery instead of a micro-mesentery.

In the sexual region the macro-mesenteries are short and reach only a little way into the gastrovascular cavity. Their mesogloea is fairly well-developed. The longitudinal musculature forms few but fairly deep folds. The parieto-basilar muscles are weak and unfolded. The micro-mesenteries are moderately developed with muscles as on the macro-mesenteries.

The filaments have the typical structure. The glandular tract contains many uniformly broad nematocysts with greatly twisted thread (length 32—38  $\mu$ , breadth 11—12  $\mu$ ). In the type-specimen I found also some very small oval nematocysts (length 17  $\mu$ , breadth 7  $\mu$ ). Further, the glandular tract contains fairly many thick-walled nematocysts with distinct basal part to the spiral thread, which are broader at the one end (length 17—22  $\mu$ ).

The animals are dioecious. The macro-mesenteries bear as usual the sexual organs. On the 1st couple of macro-mesenteries reckoned from the directive micro-mesenteries these are weaker than on the other proto-mesenteries, and the same applies to the youngest meta-macro-mesenteries.

#### **Isozoanthus davisii** n. sp.

Pl. 2, fig. 17. Pl. 7, fig. 1.

Occurrence: Davis Straits 66° 35' N., 56° 38' W. 318 Dan. fms. Bott. temp. 3.9°. Ingolf Expedition St. 32 several specimens (together with *I. bulbosus* and *Epizoanthus lindahli*).

Dimensions: The length of the polyps reached up to 1.4 cm., largest breadth about 0.4 cm. in the contracted state.

Colour in alcohol: light or dark sand-coloured.

External appearance. The majority of the specimens formed small colonies consisting of a few polyps connected with each other by a small, generally thin coenenchyme and attached to small yellowish, sometimes branching sand-tubes (of *Rhizammima*?). All the polyps were probably attached to such objects, though in one case it looks as if the colony was free, probably arising from the fact that a piece of the coenenchyme is worn off. The polyp is narrowest at the base, from which part it becomes more or less wide upwards, according to the more or less state of contraction. The capitular furrows are very indistinct. The whole body-wall and coenenchyme of the polyps is richly incrustated with sand-grains, here and there also sponge-needles occur, especially in the uppermost part.

The tentacles are short.

The oesophagus is short, the siphonoglyphe distinct with well-marked hyposulcus of almost the same length as the oesophagus.

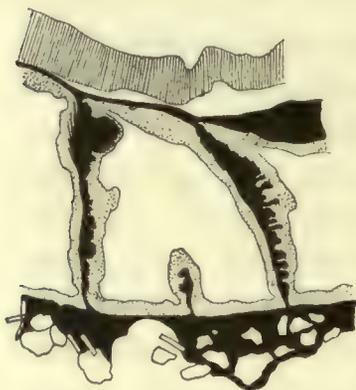
Anatomical description. The ectoderm of the body-wall does not seem to be very high except in the capitular region. It is mostly absent and if present filled with detritus and incrustated. Nematocysts with greatly twisted thread 38—48  $\mu$  long and 11—12  $\mu$  broad are fairly common in the proximal part, but very scarce distally. Further, the ectoderm of the body-wall contains egg-shaped nematocysts resembling those in the filaments (length 22—26  $\mu$ , breadth 5—7  $\mu$ ). The mesogloea is thick, several times thicker than the ectoderm and contains numerous, scattered large cells, generally

oval-shaped and with granular contents of close-lying grains (Pl. 7. fig. 1). The whole mesogloea with exception of the very innermost part is incrustated. The entoderm is moderately developed, sometimes darkly pigmented.

The sphincter is long and strong, in the distal part it forms a few deep folds, in the proximal numerous but small folds.

The ectoderm of the tentacles contains numerous spirocysts, whereas the thick-walled capsules (length about  $22\mu$ ), are very scarce. The mesogloea is richly incrustated.

The ectoderm of the œsophagus is very high and contains numerous nematocysts  $24-26\mu$  long and thick-walled; further, there is a sparse occurrence of larger or smaller nematocysts with coiled thread as in the filaments. The mesogloea is thin though however thickened in the siphonoglyphe.



Text-fig. 6. Transverse section through a portion of the body-wall with mesenteries and œsophagus of *Isozoanthus davisi*. Mesogloea and muscles black, ectoderm of the œsophagus shaded, entoderm dotted. The light parts in and outside the mesogloea of the body-wall represent incrustations. Ectoderm of the body-wall absent.

The number of mesenteries varied in the two specimens examined between 34 and 38. In both specimens the one side had one mesentery more than the other.

The macro-mesenteries are rather thick even in specimens with expanded mesenteries, whereas the micro-mesenteries are weak and in the lower part of the œsophageal region extend a little over the main part of the entoderm of the body-wall. In specimens having the mesenteries contracted broadwise the longitudinal musculature lies in deep folds even extending below the œsophagus (Text-fig. 6). The parieto-basilar muscles are very weak. The distribution of the longitudinal musculature on the body-wall is fairly considerable, whereas hardly any parieto-basilar muscles occur. Below the œsophagus extend the mesenteries, which contain the undeveloped sexual organs reaching some way into the gastrovascular cavity.

The filaments have the usual structure. Two kinds of nematocysts with greatly twisted thread and often of a somewhat curved shape occur, the one kind larger  $37-53\mu$  long and  $10-12\mu$  broad, the other smaller elongated, egg-shaped, somewhat broader at the one end (length  $15-22\mu$ , largest breadth  $6-7\mu$ ). Further, the filaments contain thick-walled nematocysts broader at the one end than at the other (length  $22-24\mu$ , breadth  $5-6\mu$ ).

One of the specimens investigated had undeveloped testes.

### *Isozoanthus islandicus*.

Pl. 2. fig. 20. Pl. 7 fig. 2.

Occurrence:  $64^{\circ}45'N$ ,  $29^{\circ}06'W$ . 568 Dan. fms. Bott. temp.  $4.4^{\circ}$ . Ingolf Exp. St. 90. 1 colony.

Dimensions: Length of the largest polyp 0.9 cm., greatest breadth about 0.2 cm.

Colour in alcohol: dark.

External appearance. The only colony of this species was attached to a couple of spicules of a Hexactinellida. The thin cœnenchyme was very large encircling the spicules almost entirely, so that it formed a tube round these. In fig. 20 Pl. 2 we see very little of the spicules. The polyps,

which in the full-grown specimens especially are very elongated in shape, lie very far from each other. They are narrowest at the base but expand somewhat towards the distal part. The capitular furrows are very indistinct. The upper margin of the polyps is somewhat rounded. The polyps as well as the cœnenchyme are richly though not very conspicuously incrustated.

The œsophagus is short, the siphonoglyphe distinct. Hyposulcus?

Anatomical description. The ectoderm of the body-wall is high and reaches almost the same size as the mesogloea. Except in the capitular region it contains fairly many nematocysts with greatly twisted thread, length 29–34  $\mu$ , breadth 10–12  $\mu$ . Particles of detritus are found in and on the ectoderm. The mesogloea is moderately developed, and very much incrustated with foraminifera (dissolved in the section on Pl. 7, fig. 2), sand and sponge-needles, the latter heaped up especially in the capitular region. Scattered granular cells of moderate size, sometimes also larger, occur fairly commonly here (Pl. 7, fig. 2). The entoderm is considerably thinner than the ectoderm.

The sphincter is long and strong, of the same appearance as in other *Isozoanthus*-species.

Regarding the tentacles I am unable to give any other information than that their ectoderm as usual contains numerous spirocysts.

In the œsophagus the ectoderm is high, the mesogloea thin, whereas in the siphonoglyphe the conditions are reversed.

In the single specimen sectioned, the number of mesenteries, as far as I was able to see on the somewhat torn sections, was 34, 10 macro and 8 micro on the one side and 9 macro and 7 micro on the other. The micro-mesenteries are moderately developed. The longitudinal musculature is but moderately developed, forms few or no folds at all, the parieto-basilar muscles weak. So far as I was able to see on the not well-fixed material the longitudinal and parieto-basilar muscles extended only a moderate distance on the body-wall.

The filaments have the usual structure. The glandular tract region contains large nematocysts with coiled thread (length 26–34  $\mu$ , breadth 10–12  $\mu$ ), but they only occur sparsely as is also the case with some smaller, similar capsules (length 14  $\mu$ , breadth 5  $\mu$ ) and some thick-walled capsules broader at the one end (length 22  $\mu$ ). Inside the filaments in the entoderm of the mesenteries we also find many nematocysts (length 14–17  $\mu$ , breadth 10–11  $\mu$ ) and numerous elongated, generally curved nematocysts (length 22–26  $\mu$ , breadth 5  $\mu$ ). These capsules probably do not belong to the animal, but are foreign nematocysts taken up by the ectoderm (2 specimens examined).

The animals were not sexually ripe.

Remarks. The above-mentioned species is undoubtedly closely related to *Isozoanthus dubius* from St. 45, but differs from the latter mainly in the larger nematocysts, and the stronger sphincter. Later examination of a larger material may possibly show that they can be thrown together to form one species, but till then I think it best to separate them.

#### ***Isozoanthus dubius* n. sp.**

Pl. 2, fig. 19. Pl. 7, fig. 3.

Occurrence: 61° 32' N., 9° 43' W. 643 Dan. fms. Bott. temp. 4.17°. Ingolf Exp. St. 45 1 colony.

Dimensions: Length of the largest polyp 0.8 cm., greatest breadth 0.3 cm.

Colour in alcohol: tawny sand-coloured.

**External appearance.** The only colony of this species was attached to a fragment of a *Cidaris* spine. The colony had a thin, disc-like coenenchyme from which two polyps emerged at a long distance from each other. The polyps are elongated, narrow at the base and broader upwards. The distal margin, which completely covered the tentacles, was truncate. The capitular furrows were very indistinct. The incrustation of the polyps and the coenenchyme consisted of sand-grains, foraminifera and sponge-needles. The oesophagus is short, the siphonoglyphe distinct. Hyposulcus?

**Anatomical structure.** The ectoderm of the body-wall is high, slightly incrustated with the above mentioned foreign bodies and detritus particles. In the distal part the nematocysts are very scarce, in the proximal part on the other hand nematocysts with coiled thread are common (length 22—29  $\mu$ , breadth 12  $\mu$ ). The mesogloea is thicker than the ectoderm, richly incrustated and contains scattered, fairly numerous, often oval-shaped, granular cells of moderate size (Pl. 7, fig. 3). In the section figured, the foraminifera have been dissolved by means of nitric acid, so that only the cavities in which they were lying can be seen. The ectoderm is thin.

The sphincter is considerably shorter than in *I. islandicus* and has in the distal part some large folds, which soon pass over into the ring-muscle layer of the body-wall.

The tentacles, of which I made no macerated preparation, contained in the ectoderm numerous spirocysts. Whether also thick-walled nematocyst capsules occur, I am unable to tell from the material sectioned.

The oesophagus is as in *I. islandicus*.

In the examined specimen the number of mesenteries was 30, 9 macro- and 7 micro-mesenteries on the one side, 8 macro- and 6 micro-mesenteries on the other. In the lowest part of the oesophageal region the micro-mesenteries are weak and only reach a little beyond the main lamella of the entoderm. The macro-mesenteries are thin, the longitudinal and parieto-basilar muscles weak, but reach a long way on the body-wall. The macro-mesenteries below the oesophagus seem to be longer than in *I. islandicus*.

The glandular tract of the filaments contains a few, large nematocysts with coiled thread (length 19—26 (29)  $\mu$  generally 24, breadth 10—12 generally 10—11  $\mu$ ) with rounded ends and fairly many, smaller, similar capsules (length 12—14  $\mu$ , breadth 5—6  $\mu$ ). Further, there is a common occurrence of thick-walled capsules, broader at the one end (length 14—17  $\mu$ ).

The sexual organs were not developed in the specimen sectioned.

Remarks. See under *I. islandicus*.

### ***Isozoanthus danicus* n. sp.**

Pl. 1, fig. 3—4. Pl. 7, fig. 4.

*Zoanthus couchii* Gosse, Mortensen. Smaa biol. o. Faun. Iagttagelser, Videnskab. Medd. 1897. p. 316.

Occurrence: Denmark, Limfjord. Mortensen; R. Hörring Sept. 1902. Copenh. Museum R. M.

Dimensions. Height of the retracted polyps 0.25—0.4 cm., breadth about 0.2 cm.

Colour in alcohol. The coenenchyme and the majority of the polyps dark or dirty-coloured,

capitular region light. In the living condition: cœnenchyme and the proximal part of the polyps brown, disc brown frequently with white radial stripes (Mortensen).

**External appearance.** The cœnenchyme consists of an irregularly branched network with a thin attachment to dead oyster-shells. The polyps emerge from the cœnenchyme sometimes at smaller, sometimes greater intervals. They are small, cylindrical and when much contracted almost as high as broad or the breadth is a little larger (Pl. 1, fig. 4), in less contracted state (Pl. 1, fig. 3) they are twice as high as broad. In the contracted state the distal part is rounded. The capitular furrows are indistinct on the not very well preserved material, so that their number cannot be given.

The œsophagus is short, the siphonoglyphe distinct, but the hyposulcus seems to be short.

**Anatomical description.** The ectoderm of the body-wall is moderately developed and as far as I am able to see continuous (owing to the strong contraction and the folding resulting therefrom it is difficult to determine this with certainty). It is incrustated with coarse sand-grains, some sponge-needles and detritus, in which numerous diatoms occur. The ectoderm contains uniformly broad nematocysts with greatly twisted thread (length 22–26  $\mu$ , breadth generally 7 sometimes 10  $\mu$ ). Whether they are numerous or not I am unable to say for certain. The mesoglœa is moderately developed, the outer part incrustated, it has no lacunae and very few cells (cell-islets) which sometimes lie in groups close to each other. The cells are however so scarce that the mesoglœa looks almost as if it was homogeneous and cell-free, this being fairly characteristic of the species (Pl. 7, fig. 4). The entoderm is of moderate thickness and contains fairly many zooxanthellae, which besides occur everywhere in the entodermal layer of the polyp.

The sphincter is entodermal, somewhat folded at the upper part and fairly long in consideration of the small size of the animal. The musculature is strong so that the capitular region is very much retracted in the contracted state.

The structure of the œsophagus seems to be the same as in the other Zoanthidae. The ectoderm is high, the mesoglœa thin. I have not been able to make any macerated preparations of the œsophagus, because this is so short and folded and badly preserved. The siphonoglyphe has a somewhat lower ectoderm than the œsophagus, and the mesoglœa is a little thicker than in the œsophagus.

In 7 specimens examined the number of mesenteries were 18, 20, 20, 20, 22, 24, 24; the specimens with 18 and 22 mesenteries had 1 couple of mesenteries more on the one side of the body than on the other. It is difficult to see the arrangement, as the specimens especially in the œsophageal region were badly preserved. It is worth noticing especially, that the sixth couple of proto-mesenteries, i. e. the proto-mesenteries lying nearest to the meta-mesenteries, as also the macro-meta-mesenteries, have not yet grown out to the œsophagus and had no filament (at least not in the specimen with 18 mesenteries). The sixth couple of proto-mesenteries, the micro-proto-mesenteries and all meta-mesenteries seem to be almost equally developed. Though it might be supposed, that the polyps were brachycnemic, it is however probable, that they are macrocnemic, though the 6th couple of proto-mesenteries have not yet reached the œsophagus. This is also indicated by the small development of the macro-meta-mesenteries. The micro-mesenteries at any rate are well-developed. The longitudinal musculature is strong on the complete mesenteries, especially on the directive mesenteries, where it forms deep folds.

The parieto-basilar muscles are weak, and as far as I have been able to see the longitudinal and parieto-basilar musculature does not extend onto the body-wall or only very little.

The filaments have the usual structure. The glandular tract contains fairly many, often curved, uniformly broad nematocysts with greatly twisted thread (length 22—26  $\mu$ , breadth about 7  $\mu$ ). Further, it contains numerous thick-walled capsules about 17  $\mu$  long.

The species is dioecious. In most of the polyps ovaries or testes were found though at a fairly early stage.

**Isozoanthus magninsulosus n. sp.**

Pl. 1, fig. 7. Pl. 6, figs. 4—5.

Occurrence: 64° 24' N., 28° 50' W. 788 m. Bott. temp. 3.5°. Ingolf Ex. St. 10. 1 colony.

Dimensions in the contracted state. Length of the largest polyp 0.6 cm., breadth 0.3 cm.

Colour in alcohol: dirty yellowish-brown. It may possibly have absorbed this colour from a brown piece of paper covering the stone on which the colony was fixed, and which coloured the alcohol.

External appearance. The only colony of this species in the collection consisted of 8 larger and smaller polyps placed fairly close to each other and separated by a large flat and very thin, band-like coenenchyme (Pl. 1 fig. 7), attached to a stone. The polyps are cylindrical not elongated, with distinct capitular forrows. All the polyps were retracted so that no tentacles were visible, the upper margin was rounded. The polyps as well as the coenenchyme were incrustated with numerous foraminifera, giving the colony a granulated appearance. The oesophagus is very short, the siphonoglyphe distinct with well-marked hyposulcus.

Anatomical description. The ectoderm of the body-wall is fairly high, continuous and in the lower part of the polyp provided with fairly numerous and uniformly broad nematocysts about 34  $\mu$  long and 13  $\mu$  broad with greatly twisted thread. In the capitular region they seem to be wanting but are replaced by small egg-shaped capsules like those in the filaments (length 12—14  $\mu$ , breadth 6  $\mu$ ). The mesogloea is more than twice as thick as the ectoderm and like this incrustated with numerous foraminifera and some few sponge-needles. The incrustation is mostly present in the outer half of the mesogloea but may often reach further into this. The part of the mesogloea which is not incrustated contains numerous cell-islets of larger or smaller size (Pl. 6, fig. 5). The smaller as well as the larger of these are often in connection with each other, thus forming a lacunae-system which is mostly observed in the lower part of the body (Pl. 6, fig. 4). A section through the mesogloea of the body-wall has therefore quite a different appearance from *I. multinsulosus*, where such lacunae-systems are only seldom found. In sections of *I. multinsulosus* the cell-islets are consequently as a rule round or oval whereas in *I. magninsulosus* they have a more irregular appearance owing to their connection with each other. The large islets (the lacunae) are also considerably larger in *I. magninsulosus* than in *I. multinsulosus*. In spite of the presence of a fairly well-developed lacunae-system one cannot speak here of any defined encircling sinus. The entoderm is thin and slightly pigmented.

The sphincter has the same structure as the other *Isozoanthus* species described.

The ectoderm of the tentacles contains numerous spirocysts and fairly many thick-walled nematocysts (length 17—19  $\mu$ ). The mesogloea of the tentacles is often incrustated.

The ectoderm of the œsophagus has the usual structure. Nematocysts probably also occur there, but as parts of the filaments are connected with the ectoderm of the œsophagus the macerated preparation has given no certain information regarding the occurrence and appearance of the nematocysts. The mesoglœa is thin and considerably weaker than in the siphonoglyphe.

Mesenteries. Of 3 specimens sectioned only one was so well fixed that I could determine the number of mesenteries. This polyp has 32 typically arranged mesenteries. The mesenteries are thin, the longitudinal as well as the parieto-basilar musculature weak. These muscles extend a long way onto the body-wall. The micro-mesenteries are fairly well-developed even below the œsophagus.

The filaments have the usual structure. The nematocysts are partly large, uniformly broad capsules with greatly twisted thread (length 31–43  $\mu$ , breadth 12  $\mu$ ), partly smaller often somewhat curved (length about 15  $\mu$ , breadth 7  $\mu$ ). The latter are common. Further, the filaments contain fairly many, thick-walled capsules with distinct basal part to the spiral thread and somewhat broader at the one end (length 22–24  $\mu$ , breadth 7  $\mu$ ). The species is diœcious. The best preserved specimen had well-developed testes on the macro-mesenteries.

Systematic remarks. In some respects this species resembles *I. multinsulosus*, from which it differs however in a number of features. In *I. magninsulosus* the large cell-islets (the lacunae) in the mesoglœa of the body-wall are, for example, more numerous and larger than in *I. multinsulosus* (cf. above), in this species the incrustation consists of foraminifera, in *I. magninsulosus* of sand-grains, and in this the ectoderm is less pigmented than there. In *I. magninsulosus* the number of mesenteries is 32, in *I. multinsulosus* 38–40. Also the large nematocysts are somewhat shorter and especially narrower here than in *I. multinsulosus*, though otherwise they resemble each other with regard to the nematocysts.

#### ***Isozoanthus multinsulosus* n. sp.**

Pl. 1, fig. 18. Pl. 6, fig. 3.

Occurrence: 64° 15' N., 14° 22' W. 68 m. Bott. temp. 7° 07'. Ingolf Ex. St. 51. 1 colony.

65° 43' N., 14° 34' W. 90 m. Bott. temp. 7°. Ingolf Ex. St. 6. 1 colony.

Dimensions. The polyps were strongly contracted. Largest polyp about 0.45 cm. broad and 1 cm. high.

Colour. The polyps are black owing to the incrustation of black sand-grains. It is probable, however, that the polyps are dark in themselves as the ectoderm and especially the entoderm are darkly pigmented.

External appearance. One of the colonies consisting of 4 polyps was attached to a stone, the other colony with 3 polyps to a Dentalium-tube. The greatly contracted polyps were connected with each other by a very thin, spread cœnenchyme from which the polyps emerge, sometimes at smaller, sometimes larger intervals. The polyps are short, the upper margin of the polyps retracted in the distal end, not truncate but rounded. Capitular furrows present but so indistinct that I am unable to state their number. The tentacles have the usual structure. The œsophagus is short, siphonoglyphe deep, hyposulcus distinct.

**Anatomical description.** The ectoderm of the body-wall is continuous, fairly high and contains fairly many, uniformly broad nematocysts with greatly twisted thread — length (38) 41—48  $\mu$ , breadth 14—17  $\mu$ . The ectoderm and outer part of the mesogloea are strongly incrustated, almost exclusively with black sand-grains interspersed with a few sponge-needles. The mesogloea is thick, the inner half and probably also the outer one (owing to the strong incrustation it has been rather difficult to study the structure of the mesogloea) contains cells and numerous cell-islets (Pl. 6, fig. 3), the majority of which are small but others reach quite a considerable size though not so large as in *I. magninsulosus*. More seldom the cell-islets fuse together to form elongated lacunae but not so great as in *I. magninsulosus*. An encircling sinus however is not found. The entoderm is thin, with black pigmentation.

The sphincter is entodermal, long and in the upper end has some fairly deep, often large folds.

The ectoderm of the tentacles is high and contains numerous spirocysts, besides many thick-walled nematocysts (length 19—24  $\mu$ ) and a few large capsules with greatly twisted thread of the same kind as in the body-wall, but somewhat small (34  $\mu$  long).

The ectoderm of the oesophagus is fairly high and contains numerous thick-walled capsules (length 22—24  $\mu$ ), and the same kind of large nematocysts as found in the body-wall though somewhat smaller (38—41  $\mu$  long). The mesogloea is thin and considerably weaker than in the siphonoglyphe, whose ectoderm as usual is lower than that of the oesophagus.

In the two specimens examined the number of mesenteries was 38 and 40. The second polyp was typical, the first had 1 couple of mesenteries more on the one side than on the other. The micro-mesenteries are moderately developed even below the oesophagus and several times broader than the entoderm of the body-wall. The mesogloea of the mesenteries is thin, the longitudinal musculature weak and partly folded, the parieto-basilar muscles weak. The extension of the longitudinal and parieto-basilar muscles on the body-wall is distinct though not considerable. Below the oesophagus the mesenteries are narrow, so that the gastrovascular cavity is large.

The filaments have the usual structure. In the glandular tract there is a rich occurrence of large capsules of the same kind as in the body-wall (length 41—48  $\mu$ , breadth 14—17  $\mu$ ) and a sparse occurrence of similar smaller capsules (length 17—19  $\mu$ , breadth 7  $\mu$ ); further, it contains fairly many thick-walled capsules with distinct basal part to the spiral thread and somewhat broader at the one end (length 22—24  $\mu$ , largest breadth 6  $\mu$ ).

The sexual organs were not developed in the specimens examined.

#### ***Isozoanthus ingolfi* n. sp.**

Pl. 2, fig. 25. Pl. 6, fig. 6.

**Occurrence.** 64° 54' N., 55° 10' W. 393 fms. Bott. temp. 3·8°. Ingolf Ex. St. 27 several specimens (type).

Finmarken Ögsfjord Loven, 1 colony with 2 polyps.

**Dimensions.** Largest polyp (from Davis Straits) 1 cm. long and 0·55 cm. broad.

**Colour** in alcohol: light sand-coloured, the specimen from Finmarken containing small, scattered black sand-grains.

**External appearance.** Small colonies consisting of some polyps connected by a thin, fairly extensive cœnenchyme attached to small stones, mollusc-shells or worm-tubes. The polyps are cylindrical and sometimes, owing to contraction, a little thicker in the distal part, and longer than broad. In the retracted state the distal part is almost truncate with a depression in the middle. Capitular furrows present but very indistinct, in the best preserved specimen 20 were observed. The polyps as well as the cœnenchyme were incrustated with sand, now and then with sponge-needles; near the ectoderm mud-particles are fixed. The incrustation is not very strong and restricted to the ectoderm and especially the outer part of the mesoglœa.

The œsophagus is short with a very distinct deep siphonoglyphe and well-developed hyposulcus, which is somewhat longer than the œsophagus.

**Anatomical description.** The ectoderm of the body-wall is moderately developed, yet several times thinner than the mesoglœa. In the proximal part of the body-wall large nematocysts with coiled thread are found, sometimes sparsely (specimens from the Ingolf Expedition), sometimes more commonly (length 31—36  $\mu$ , breadth 12—14  $\mu$ ). In the Finmarken specimen some smaller capsules of the same appearance as the smaller egg-shaped capsules of the filaments are also found. The mesoglœa is thick and contains numerous cells with long outshoots, sometimes running in the direction from ecto- to entoderm (Pl. 6, fig. 6) and sometimes even more irregularly arranged. Further, there is a sparse occurrence of small cell-islets and large cells. The latter sometimes fuse together to form (ectodermal?) lacunae. The large cell-islets lie often near the insertions of the mesenteries. As the cell-islets fuse together forming lacunae, it may sometimes on certain parts of the proximal part of the polyps look as if traces of an encircling sinus might be present. As the cell-islets lie fairly irregularly and are generally separated from each other by large portions of mesoglœa, especially in the distal end of the polyp, the lacunae cannot however be considered as an encircling sinus. The entoderm is thinner than the ectoderm.

The sphincter resembles that of *I. arborescens* and forms large folds.

The ectoderm of the tentacles has the usual structure and contains numerous spirocysts and fairly thick-walled nematocysts (length 19—20  $\mu$ ). Besides there are very sparsely large capsules of the same kind as in the ectoderm of the body-wall. In the specimen from Finmarken I observed small capsules with coiled thread (length 19  $\mu$ , breadth 7  $\mu$ ). The mesoglœa of the tentacles is incrustated though only inconsiderably.

The ectoderm of the œsophagus is high and contains fairly many thick-walled nematocysts (length 17—22  $\mu$ ). Further, there also occur, though only very sparsely, some larger or smaller capsules with coiled thread of the same appearance as in the filaments. The ectoderm of the siphonoglyphe is as usual considerably lower than in the œsophagus, whereas with regard to the mesoglœa the condition here is reversed.

In the two specimens taken during the Ingolf Expedition the number of mesenteries was 40 and 38; the first of them had the mesenteries arranged typically, whereas the second had a pair of mesenteries less on the one side than on the other. Of the specimens from Finmarken one had 46 mesenteries, 13 macro and 11 micro on one side and 12 macro and 10 micro on the other. Another specimen probably had 44 mesenteries — 11 being observed in one fourth part of the polyp.

The longitudinal musculature is fairly well-developed but forms large folds. The parieto-basilar muscles are moderately developed but in transverse section no folds are seen. The parieto-basilar and longitudinal musculature extend a long way onto the body-wall. The micro-mesenteries are not very well-developed.

The filaments have the usual structure. The glandular tract contains larger and smaller nematocysts with greatly twisted thread, the larger are uniformly broad  $31-43\ \mu$  long and  $12-14\ \mu$ , sometimes even  $17$  broad, and scarce to not seldom, the smaller are egg-shaped  $17-19\ \mu$  long and  $7\ \mu$  broad and not seldom. Further, it contains thick-walled capsules with distinct basal part to the spiral thread and broader at the one end than at the other (length  $17-19\ \mu$  long, largest breadth  $5\ \mu$ ). Sometimes also typical thick-walled capsules are present (length  $24\ \mu$ ).

The sexual organs were not developed in the specimens examined by me.

Besides the above-mentioned Isozoanthus-species a specimen of an Isozoanthus type which I could not refer with certainty to any of the above-described was dredged at St. 27 during the Ingolf Expedition. The polyp has a length of 2 cm. and a breadth in the capitular region of 0.4 cm., at the base it measured 0.3 cm. and was of a dark colour. The polyp was attached to a stone by an inconsiderable, irregularly triangle-shaped coenenchyme on which a faint indication of another polyp was visible. The large polyp gradually increased in breadth towards the capitular region which is somewhat rounded. The capitular furrows are indistinct. The oesophagus is short, the hyposulcus well-developed. The body-wall at least in the upper part is greatly expanded and consequently thin. The ectoderm is almost half as thick as the mesogloea, continuous and incrustated with mud and detritus particles, which partly at least give the animal its dark colour. The mesogloea is quite filled with sand-grains and a few sponge-needles. It also contains numerous cell-islets and cells, but owing to the strong incrustations it is very difficult to get a true idea of the nature of the mesogloea.

The sphincter resembles that of the other Isozoanthus-species. The oesophagus has the usual structure. The ectoderm contains thick-walled capsules  $19-22\ \mu$  long. There are 36 mesenteries which are very much expanded so that the mesogloea becomes very thin. The musculature seems to be weak; the micro-mesenteries are well-developed. The filaments contain a few specific, uniformly broad nematocysts (length  $29-38$ , breadth  $10-11\ \mu$ ) besides some more frequently occurring egg-shaped capsules  $13-15\ \mu$  and thick-walled capsules with distinct basal part to the spiral thread and somewhat broader at the one end (length  $19\ \mu$ ). The sexual organs were undeveloped.

Owing to the small amount of material I have not named this form.

### Genus Parazoanthus Haddon and Shackleton.

Macrocyclic Zoanthidae with a diffuse entodermal sphincter muscle. The body wall is incrustated, the ectoderm is continuous. Encircling sinus as well as ectodermal canals, lacunae and cell-islets in the mesogloea. Dioecious. Polyps connected by thin coenenchyme, (coenenchyme without cylindrical horny skeleton).

I have given the diagnosis of Haddon and Shackleton, which seems to me good, and have added the information, for the Genus *Gerardia*, that a true cylindric horny skeleton is wanting. I have placed this however in brackets, as I consider further examination of the *Gerardia* skeleton desirable, in order to ascertain how much of the skeleton actually belongs to the polyp, a determination that can hardly be made without fresh or at least well-preserved material. Though I consider the cylindric, connecting tissue of horn between the branches of the skeleton as being secreted by the polyps themselves, it is not quite excluded, that the other part of the skeleton belongs to another Anthozoon, — a condition undoubtedly existing as regards the basal part of the branched skeleton (cf. Lacaze-Duthiers 1864). If it should be the case, that only the peripheral branches of the so-called *Gerardia* skeleton have been secreted by the Zoanthid, the genus *Gerardia* approaches still more to the genus *Parazoanthus* and comes so near to this, that the question is, whether the two genera could not be thrown together, especially as the inner structure of the *Gerardia* polyp agrees completely with that of the *Parazoanthus* polyp even in such details as the presence of a well-developed encircling sinus. In this case the only difference would lie in the skeleton, certain parts of which are tube-shaped in *Gerardia*, while in *Parazoanthus* it is only present as a thin flat layer under the coenenchyme, a difference which is not essential but gradual and certainly is only dependent on the somewhat unequal growth of the colonies. According to the rule of priority the genus name *Gerardia* would in such a case have to be changed to *Parazoanthus* — an alteration which cannot be made, however, until the question of the *Gerardia* skeleton has been definitely settled. Haddon has for the rest already in 1898 p. 408 expressed some doubt as to whether the skeleton in *Gerardia* was actually secreted by the polyps themselves, though without making any further investigation into the matter himself.

The *Parazoanthus* species described here are two in number, one of which has already (1889) been described in detail by Haddon and Shackleton, the other is new, named *P. haddoni*. Further, I give here some supplementary details regarding the anatomy of *P. dixonii* Hadd. & Shackl.

No species of *Parazoanthus* were dredged by the Ingolf Expedition.

#### Synopsis of the *Parazoanthus* species described here.

- A. Capitular region in the contracted state not or very little swollen. Number of mesenteries 36—46..... *P. haddoni*.  
 B. Capitular region in the contracted state swollen. Number of mesenteries 36—38.. *P. anguicomus*.

#### *Parazoanthus haddoni* n. sp.

Pl. 1, figs. 9—11. Pl. 7, fig. 5.

Jutland Reef 100—200 fm. G. Pettersson 1881 R. M.

Jæderen 100—170 fm. Tob. Andersson & Westergren 1877 R. M.

N. W. of Egersund 100 fm. N. Olsson & M. Uddström R. M.

Haugesund and Bergen in S. E. 15—21 miles from land 100—170 fm. Ol. Johansson R. M.

Stora Fiskebanken, Bergen in S. E. 100—180 fm. T. Andersson R. M.

N. W. of Bergen 30—200 fm. M. Olsson 1873, 1878; 90—200 fm. O. Mattson 1880; 100—150 fm. M. Uddström 1880 R. M.

N. N. W. of Bergen 90—200 fm. M. Uddström, G. Nilsson, M. Olsson 1880 R. M.

North Sea M. Uddström 1880 R. M.

North Sea north edge of the Fisher Bank 100—160 fm. B. Olsson R. M.

**Size:** The colonies form large aggregates sometimes of the size of a clenched fist and almost always fixed on sponges (1 spec. on an Ascidian). In the contracted state the polyps of the largest colonies (Pl. I, fig. 16) reach a length of 19 cm. and a breadth at the base of 1 cm. In most of the colonies the polyps are however considerably smaller.

**Colour.** In alcohol the colour varies from dirty yellowish (Pl. I fig. 10) to dirty grayish or pure white (Pl. I fig. 9—11). The dirty gray colour is generally predominant.

**External appearance.** The polyps form colonies often of large dimensions, which are attached to large sponges. The cœnenchyme is fairly thin and extensive and sometimes forms narrow outshoots, on the end of which new polyps are formed (Pl. I, fig. 9). A single colony, which by the way was not quite typical, was found on an Ascidian. The polyps generally sit quite close to each other, but sometimes the intervals between may be larger, especially when the cœnenchyme forms string-like outshoots. Even when the tentacles are completely covered by the body-wall, the polyps are generally considerably higher than broad. The breadth is however very considerable, greatest at the base and tapering upwards; sometimes the distal part may be somewhat swollen, especially in greatly contracted polyps, though never so much as in *P. dixonii* and *anguicomus*. Otherwise, the polyps vary much in size, as can be seen from figs. 9—11 on Pl. I, but there is no doubt that we are only dealing with one and the same species. The body-wall is more or less wrinkled especially in the larger specimens. The capitular furrows are generally distinct and reach up to 18—21 in number. The œsophagus is of moderate length. The siphonoglyphe is distinctly marked, the hyposulcus developed but rather short and does not attain to half the length of the œsophagus.

The cœnenchyme as well as the polyps is incrustated with sand-grains and sponge needles, to which are sometimes added a few foraminifera. The sand-grains are generally predominant, but in some cases the sponge-needles occur in quantities. The incrustation is not so strong as in *P. anguicomus* but is very variable. Sometimes polyps are also found which are very little incrustated.

**Anatomical structure.** The ectoderm of the body-wall is very high and continuous and contains nematocysts with greatly twisted thread of two different kinds, either large 41—46  $\mu$  long and 17—18  $\mu$  broad or small 24  $\mu$  long and 12—13  $\mu$  broad. The number of capsules is variable but the smaller ones are always more numerous than the larger and the proportional occurrence of both kinds of capsules seems to be always the same. When the polyps are not strongly expanded, the mesogloea is somewhat thicker than the ectoderm. It is provided with numerous cells, cell-islets and lacunae and a well-developed encircling sinus. The cell-islets and lacunae are generally numerous (Pl. 7, fig. 5), sometimes however scarce. The lacunae are here and there in distinct connection with the ectoderm and encircling sinus. As a rule the latter is interrupted at a few places by mesogloal parts and narrow. Sometimes, however, I have found fairly strong mesogloal bridges together with a broader encircling sinus at the bases of the mesenteries, while the connecting canals between

these broader canal parts are narrow. This variation in structure of the encircling sinus is however probably due to different states of contraction in the polyps, which may be concluded from the fact, that the more abnormal encircling sinuses had a thicker mesogloea and were more contracted, while the polyps with a more typical encircling sinus were expanded. But the fact also, that both kinds of encircling sinus may be found in the same colony, goes to show, that we are not dealing with a variety. The encircling sinus contains the same kind of nematocysts as the ectoderm of the body-wall.

The sphincter is more developed than in *P. anguicomus* and *dixoni*. While the muscular furrows in the distal part are large and semicircular, they lie on the other hand closer to each other in the proximal part (Pl. 3, fig. 6), though this cannot always be quite distinctly seen. The bases of the mesenteries are broken through by the sphincter, a condition that seems always to be present in the Zoanthidae with entodermal sphincter. In this region the sphincter has thus the appearance of being mesogloéal.

The ectoderm of the tentacles has the usual structure. The spirocysts are very numerous; further, there are numerous thick-walled capsules (length  $22\mu$ ) and very few capsules of the same kind as in the body-wall.

The ectoderm of the œsophagus is fairly high and deeply furrowed or smooth according to the varying state of contraction and provided with numerous, ca.  $24\mu$  long, nematocysts. The ectoderm of the sulcus is somewhat thicker than in the œsophagus, while the mesogloea is thicker.

The number of mesenteries varies between 36 (34?) and 46, but the latter is only seldom found and even specimens with 42 mesenteries seem to be scarce. Of the 14 specimens closely examined one (a small yellowish specimen from the same locality as the colony figured on Pl. I, fig. 10), has 34, possibly 36 mesenteries, 3 had 36, 4 had 38, 3 had 40, 2 had 42 and 1 had 46 mesenteries. Below the œsophagus the macro-mesenteries reach only a short way into the cœlenteron (in specimens not sexually mature). The longitudinal muscles are distinctly marked but form no or very faint furrows; the parieto-basilar muscles are weak. The distribution on the body-wall of both kind of muscles is fairly considerable. The micro-mesenteries are fairly well-developed, in the aboral part of the œsophagus several times longer than the ectoderm of the body-wall is high.

The glandular tract contains numerous thick-walled capsules with distinct basal part to the spiral thread. They are somewhat broader at the one end and  $17-22\mu$  long and  $5\mu$  broad. Further, it contains capsules with spiral thread of the same appearance as in the body-wall; they seem always to be scarce and have a length of  $36-43\mu$  and a breadth of  $17-18\mu$ ; smaller capsules are also found. Sometimes I have not found any of the large capsules in the filaments.

The polyps are dioecious.

In the cœnenchyme, which is more or less incrustated, the canals lie nearer to the under than the upper side.

For systematic remarks see under *P. anguicomus*.

**Parazoanthus anguicomus** (Norm.) Haddon & Shackl.

Pl. I, fig. 19; Pl. II, fig. 21.

*Zoanthus sulcatus* Bowerbank 1867. Proc. Zool. Soc. p. 351.

— *anguicomus* Norman 1868. Shetland Report. Rep. Brit. Assoc. p. 310.

*Polythoa (Taeniothoa) anguicoma* Andres, Le Attinie 1883 532, 1884. p. 317.

*Epizoanthus americanus* var. Verrill, Report Blake. Bull. Harvard. Coll. 1883—85. Pl. 8, fig. 6.

*Polythoa* sp. Ridley, 1886. Proc. Roy. Irish Acad. (2) 4. Ser. p. 617.

*Parazoanthus anguicomus* (Norm.) Haddon. Trans. Dubl. Soc. 4 (2) 1891. Pl. 58, figs. 34—36, Pl. 59 figs. 11—12.

Localities: 35° 45' 30" N., 74° 48' W. Verrill 1883—85.

40° 01' N., 70° 22' W. 98 fm. U. S. F. C. St. 2245. 1 colony of 4 specimens together with the typical *Epizoanthus incrustatus (americanus)*. Fig. 19, Pl. I. R. M.

50° 57' N., 10° 46' W. 184 m. Michael Sars Exp. 1910. St. 96. 3 single spec. and 2 small colonies on Ascidians and Serpula tubes.

Shetland 1899. 1 colony.

Ireland; various specimens from Dublin Museum.

Formerly known localities: Shetlands. W. and S. W. of Ireland. See Haddon 1891.

Dimensions: Column 3—5 times as high as broad (Norman). Height of column, when fairly expanded (in spirit) 13 mm. The specimens from U. S. F. C. Height of column 0.7 cm., diameter of capitulum 0.4 cm.

Colour: Pinkish-white (Norman); preserved specimens sand-coloured.

External appearance. This species has been well described by Haddon and Shackleton (1891). Characteristic are the very deep furrows and the coarse ridges between these in the capitular region. The number of furrows and ridges seems to be about 18, as stated by Haddon. 6 of the polyps examined by me had 18 furrows, 1 had 17 and another 19. On small polyps the capitular furrows are less distinctly seen, but the future appearance of the furrows and ridges may be discerned. Haddon mentions, that the capitular region is swollen, when contracted. This is easily seen on some specimens, on others it is less distinct, as was the case with the specimens from the American coast (fig. 19, Pl. I). The œsophagus as well as the hyposulcus is of moderate length. The incrustations mainly consist of sand-grains but also of foraminifera and sponge-needles. The specimens dredged on the Michael Sars Expedition were very strongly incrustated and foraminifera also occurred in quantities.

Anatomical description. In 1891 Haddon described the anatomy of this species, but I am able to supplement his description on some points. The fairly numerous nematocysts with greatly twisted thread are almost double as long as broad (length ca. 24  $\mu$ , breadth ca. 12  $\mu$ ). Very seldom large capsules also occur with slightly twisted thread, length 41—48 by 17—22, which are equally broad, rounded in the ends, but somewhat broader at the one end. In the sphincter region the encircling sinus is weak but otherwise it is very well-developed and has the appearance described by Haddon.

The sphincter has the appearance described by Haddon.

The ectoderm of the tentacles contains numerous spirocysts and some few, ca. 19  $\mu$  long, thick-walled capsules. The ectodermal musculature is moderately developed. Incrustations are also found in the tentacles.

The ectoderm of the œsophagus contains numerous thick-walled, narrow capsules with distinct basal part to the spiral thread; these are generally 19  $\mu$ , sometimes even 24  $\mu$  long. If present at all,

the nematocysts with twisted thread are very scarce. The mesogloea is generally thick, so that the difference in thickness between this and the mesogloea of the siphonoglyphe, which is somewhat thickened, is not so great as is usual among the Zoanthidae. The entoderm is thin and several times thinner than the ectoderm.

I have examined the arrangement of the mesenteries in 3 specimens, namely, 2 of those represented in fig. 19, Pl. I, and 1 from the Michael Sars Expedition. The first had 36 mesenteries, 19 on the one side, 17 on the other, otherwise the arrangement was typical according to the macro-type, the two mesenteries lying nearest the sulcus, one on each side, being micro-mesenteries. The second specimen had 38 mesenteries, 18 on the one side, 20 on the other, the third 36 mesenteries, 18 on each side; in the last two cases the mesenteries lying nearest the sulcus were macromesenteries. As the oesophagus in the aboral part is very wide, the mesenteries there become short, so that in the glandular tract and genital region they only occupy a small part of the gastrovascular cavity; the micromesenteries are moderately developed. The longitudinal muscles were strong but no folds were seen on my specimens; the parieto-basilar muscles were neither broad nor furrowed, they reach a long way on to the body-wall.

The filaments are very large and strong. The mesogloea in the glandular region is very thick both in the intermediate tract and the glandular tract. This is undoubtedly in connection with the fact, that the mesogloea of the oesophagus is so thick. The filaments thereby assume a very robust appearance. The ectoderm of the intermediate and the glandular tracts contains numerous thick-walled nematocysts, the spiral thread of which is plainly visible. They are much longer than in the oesophagus (length ca. 26–29  $\mu$ , in the North American form they are in greater agreement with the capsules in the oesophagus, breadth ca. 5  $\mu$ ). Further, I have even observed some few large capsules of the same appearance as those in the body-wall but larger (length about 31  $\mu$ , breadth half the length).

Both the North American specimens sectioned by me were sexually mature and in both cases also ovaries were present.

Systematic remarks. As indicated by me in the synonymy list, the variety of *C. americanus* figured by Verrill in the Report on the Blake Expedition was no other than Norman's *Parazoanthus anguicomus*.

The three species *P. haddoni*, *dixonii* and *anguicomus* are evidently so closely related to each other, that in many cases it seems difficult to separate them, and especially *P. haddoni* and *dixonii* are very much alike in outer appearance. As Prof. Haddon, who had at his disposal a larger material of *P. haddoni* and *P. dixonii* than I have had for investigation and who also several years ago was so kind as to examine a colony (a coloured one with large polyps) of *P. haddoni* sent him by me, is of opinion, however, that they differ, I think I ought to consider them as two different species, though it is difficult to find really good distinguishing characteristics, especially in material which is not well preserved. The nematocysts agree quite well in *haddoni* and *anguicomus*, whereas they are somewhat but not very much larger in *P. dixonii*. In a colony of *P. dixonii* sent me by Prof. Haddon I found the following series of capsules. The large nematocysts of the body-wall with greatly twisted thread were 46–53  $\mu$  long and 19–20  $\mu$  broad, the smaller ones found in the capitular region were 26–29  $\mu$  long and 13–15  $\mu$  broad and occurred in quantities. The thick-walled capsules in the

oesophagus were 24—26  $\mu$  long. The filaments contained very few capsules 41  $\mu$  long and 18  $\mu$  broad like those in the body-wall and fairly many 19—22  $\mu$  long and thick-walled. In a polyp closely examined by me the number of mesenteries was 42 (20 on the one side and 22 on the other).

In the collections of the Riksmuseum there is a small colony of a Parazoanthus species from the Faeroes, but badly preserved. The nematocysts mostly resemble those of *P. haddoni*, but might quite well belong to *P. anguicomus* though not to *P. dixonii*, as they agree with the shortest ones in *P. haddoni* and *anguicomus*, while those of *dixonii* agree better with the longest ones. A transverse section of the body-wall of this form is given in fig. 6, Pl. VII, of this paper.

## Appendix.

During the printing of this work a paper has appeared dealing with the genus Epizoanthus (Lwowsky: Revision der Gattung Sidisia Gray (Epizoanthus Auct.), Zool. Jahrb. Abt. Systematik Bd. 34, pp. 557—614, 1913). As this paper among other things sets up a new diagnosis for the genus I wish to discuss here the extent of this genus.

With regard first of all to the name, the author has replaced Epizoanthus with Sidisia, a change that would be justifiable according to modern rules of priority, if the type of Sidisia, *S. barlesi*, were in reality identical with *E. incrustatus*. Haddon and Shackleton (1891) certainly state, that this is the case, but they nowhere indicate, that they have had type specimens of *S. barlesi* for investigation. For this reason, as also that the Zoanthidae are difficult to determine from outer characteristics, I have above used the name Epizoanthus instead of Sidisia. Moreover I am in agreement with Haddon (1891, p. 634): "We do not propose to keep the name Sidisia for the genus, although it has priority and for this reason; it was solely erected for a species which is only a variety of an older form; and the name has only been occasionally retained for this variety of that particular species, whilst Epizoanthus has been universally adopted for the more typical forms of this genus. Both names were originated by Gray and we have therefore less hesitation in keeping to the latter".

In his diagnosis of the genus Sidisia Lwowsky states, that the sphincter in its proximal part may be entodermal as also that an encircling sinus may occasionally be present; he relies here on his investigation of *S. gracilis*. But in my opinion *S. gracilis* is in all probability not a Sidisia but a Parazoanthus species. So far as I can find, namely, the sphincter figured of *E. gracilis* is not a mesoglœal but an entodermal structure. That it seems mesoglœal in the distal part is due to this, that the section has cut through not only the body-wall but also a mesentery. And since the entodermal sphincter in the genus Parazoanthus becomes mesoglœal from cutting through the mesoglœa of the mesenteries, a great part of the sphincter in sections which just meet the mesenteries may have the appearance of being a weak mesoglœal sphincter. Such figures, like that drawn by Lwowsky for

*S. gracilis*, I have often obtained both in Isozoanthus and Parazoanthus species. It is difficult especially to obtain good figures of the entodermal sphincter in those polyps where the mesenteries lie very close together, for in such cases the section cuts not only the body-wall but also at the same time a mesentery. As *E. gracilis* is a form with small polyps and with numerous mesenteries, the section has certainly at one and the same time cut through the body-wall and mesenteries. I thus believe, that *S. gracilis* is a Parazoanthus species (a fact that Lwowsky in a letter to me seems willing to accept). Under such circumstances the additions in the diagnosis which Lwowsky makes with regard to the sphincter and encircling sinus must be dropped, for the indication of an encircling sinus, which the ectodermal canals are said to form in *S. balanorum*, has little resemblance to a true encircling sinus especially in the upper part of the polyp.

Thus the assumption, that an encircling sinus occurs in Epizoanthus, must also be rejected, though it is not inconceivable theoretically, that such may occur there. When we see, namely, that the macrocnemic Zoanthidae with entodermal sphincter may have (Parazoanthus) or lack (Isozoanthus) an encircling sinus, it is quite possible, that the same condition may be present in the macrocnemic Zoanthidae with mesogloæal sphincter. In this case it might be advisable to set up a new genus for forms with encircling sinus, distinct from Epizoanthus. Nevertheless *S. gracilis* cannot be taken as a type for this conceivable genus and just as little, it seems to me, *S. balanorum*.

Lwowsky states, that a specimen of *Epizoanthus norvegicus* examined by him had a brachycnemic arrangement of the mesenteries (l. c. p. 608) and thinks it probable, that Haddon and Shackleton (1891), just on account of the external habitus and the appearance of the sphincter, had concluded that this species was an Epizoanthus. Since Haddon and Shackleton in their short notice on this species remark upon the appearance of the incomplete mesenteries, they have certainly also examined the arrangement of the mesenteries. The specimens I have examined here above show a macrocnemic arrangement; 2 other specimens, of which I made sections, had the same arrangement. Lwowsky's specimen has thus — unless some mistake of locality has taken place — been a malformation, which sometimes occurs both in brachycnemic and macrocnemic Zoanthidae, the brachycnemic showing a macrocnemic type and the macrocnemic a brachycnemic, but only exceptionally, so far as I know (*Polythoa caribæa*), on more than on side of the body (Carlgren: Beobachtungen über die Mesenterienstellung der Zoantharien etc. Festschrift for Lilljeborg 1896, fig. 6a Pl. 8; Duerden: Jamaican Actiniaria Pl. 1, Zoantheae Sc. Trans. R. Dublin Soc. 6 (2) 1898 p. 331; this work p. 34). Further, disarrangement of the mesenteries sometimes occurs (Carlgren 1896 l. c. Pl. 8, fig. 5 a, 7). That a brachycnemic species should occur in Trondhjem Fjord is indeed little conceivable, since we know of no brachycnemic forms from European seas; these belong to tropical and subtropical seas. In any case Lwowsky's colony of *E. norvegicus* certainly merits closer examination.

Finally, I wish to point out an oversight of Lwowsky, which may possibly be misleading for his readers. On p. 568 he identifies "the reflected entoderm" with the cnido-glandular region instead of with the ciliated tract of the filaments (cf. Haddon & Shackleton's figs. 1, 6, Pl. 60. 1891).

I cannot conclude this appendix without emphasizing, that our investigations on the various Zoanthidae species require to be extended, if we are to reach more accurate knowledge as to whether

a form has to be regarded as a special species or as a growth form or variety. It is very probable indeed, that the Zoanthidae display great variation during growth, though the extent of this variation cannot be judged without exact investigation (it can hardly be more than supposed), but it also seems to me, that the number of species of Zoanthidae is large. I emphasize this especially with regard to Lwowsky's combining Zoanthidae described as separate species into one species *Sidisia fatna*. It is certain, that this requires revision. Even if the nematocysts in the body-wall are difficult to find or are lacking, yet the nematocysts in the filament especially would give valuable information.

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## BIBLIOGRAPHY.

- Andres, A., *Le Attinie*. Atti. R. Accad. dei Lincei. Roma, 1883.
- Arndt, W., Zool. Ergebn. erst. Lebr.-expedition etc. Jahresb. Schl. Gesellsch. vaterl. Cultur 1912 p. 110.
- Aurivillius C. W. S., Haisevertebrater från nordligaste Tromsö Amt och Vestfinmarken. Bihang K. Svenska Vet. Akad. Handl. 11 No. 4. Stockholm 1886.
- Carlgren O., in Nordgaard. Hydrographical and biological investigations in Norwegian Fjords. Bergens Museum. Bergen 1905 p. 158—159.
- Danielssen, D. C., Beretning om en zoologisk Reise foretagen i Sommeren 1857 *Nyt Mag. Naturv.* XI 1859 p. 45.  
— Actinida. The Norwegian North Atlantic Expedition 1876—1878. Bergen 1890 *Zoology*.
- Düben, M. W. and Koren, L., Om nogle norske Actinier. *Forh. Skand. Naturf. Møde* 1847 p. 266.  
— Über einige norwegische Actinien. *Isis* 1848 p. 236.
- Gosse, P. H., *Actinologia Britannica*. A history of the british Sea-Anemones and Corals. 1860.
- Haddon, H. & Shackleton, A. W., A revision of the British Actiniae P. 2. Zoantheae. *Sc. Trans. R. Dublin Soc.* 4 (2) 1891.
- Koren, I. and Danielssen, D. C., *Fauna littoralis Norvegiae* III 1877.
- Marenzeller, Emil E., Die Coelenteraten etc. der K. K. oesterreichisch-ungarischen Nordpol-Expedition. *Denkschr. Akad. Wiss. Mat.-Nat. Classe.* 35 p. 357. Wien 1878.  
— Anthozoen in Die Internationale Polarforschung 1882—83. Die oest. Polar Station Jan Mayen. Beobachtungsergebnisse herausg. v. d. Akad. Wiss. Wien Bd. 3. 1886.
- Mortensen, T., Smaa faunistiske og biologiske Meddelelser. *Vidensk. Medd. Naturh. Forening.* Kjøbenhavn 1897 p. 311.
- Norman, A. M., Last Report on Dredging among the Shetland Isles. *Rep. Brit. Assoc.* p. 232. 1868.
- Parker, G. H., Synopsis of North-American invertebrates. *The Americ. Naturalist.* 34. 1900 p. 787.
- Sars, M., Beretning om en i Sommeren 1849 foretagen Reise i Lofoten og Finmarken. *Nyt Mag. Naturv.* 6 (2) 1851 p. 122.  
— Oplysninger om nogle Coelenterater fra Norges Kyster. *Forh. Skand. Naturf. Møde* Kjøbenhavn. 1860 p. 690.  
— Om nogle nye eller lidet bekjendte norske Coelenterater. *Forh. Vid. Selsk. Christiania* 1860.
- Verrill, A. E., Revision of the polypi of the Eastern Coast of the United States. *Mem. Boston Soc. Nat. Hist.* 1864 p. 1.  
— On the Polyps and Echinoderms of New England. *Proc. Boston Soc. Nat. Hist.* 10 1866, p. 333.  
— Report upon the Invertebrate Animals of Vineyard Sound. *Rep. U. S. Comm. of Fish and Fisheries* 1873 p. 275.  
— Notice of the remarkable Marine Fauna occupying the outer banks off the southern coast of New England. *Americ. Journ. Sc.* (3) 23 p. 135; *ibidem.* No. 5. p. 309.  
— Report on Anthozoa and on some additional species dredged by the Blake in 1877—1879 etc. *Bull. Mus. Comp. Zool.* Cambridge Mass. 11 1883 (85).  
— Notice of the remarkable marine Fauna occupying the outer banks off the southern coast of New England etc. *U. S. Fish. Comm. Rep. for* 1882 p. 641.  
— Notice of the remarkable marine Fauna occupying the outer banks off the southern coast of New England No. 11. *Americ. Journ. Sc.* (3) 29. 1885.  
— Results of the Explorations made by the steamer Albatross off the northern coast of the United States in 1883, 8. *U. S. Fish. Comm. Report for* 1883. 1885 p. 535.

## EXPLANATION OF LETTERS.

c. cuticula.	iss. incrustations of spicula.
d. detritus.	m. mesoglœa.
di. diatoms.	mc. mesoglœal-cells.
eb. ectodermal bay.	me. mesenteries.
ek. ectoderm.	mi. cell-islets in the mesoglœa.
en. entoderm.	ml. lacunae in the mesoglœa.
enc. encircling sinus.	mu. muscles.
i. incrustations.	n. nematocysts.
if. incrustations of foraminifera.	rm. transverse muscles.
is. incrustations of sand.	z. zooxanthellae.

## ABBREVIATIONS IN THE TEXT.

N. N. A. E.: Norwegian North-Atlantic Expedition.

R. M.: Riksmuseum of Stockholm.

U. S. F. C.: United States Fish Commission.

Ups. M., U. U. Z. M.: Zoological Museum of the university Upsala.

Plate I.

## Plate I.

- Fig. 1. *Isozoanthus arborescens*  $\frac{2}{1}$  (from Mortsund).  
— 2. — —  $\frac{1}{1}$  (from Tranödybet).  
— 3, 4. — *danicus*  $\frac{2}{1}$  on oyster shells. In fig. 3 also on the right side an Ascidian.  
— 5. — *bulbosus*  $\frac{2}{1}$  (Römer & Schaudinn).  
— 6. — —  $\frac{2}{1}$  (from Ingolf Exp. St. 104).  
— 7. — *magninsulosus*  $\frac{1}{1}$  (from Ingolf Exp. St. 10).  
— 8. *Epizoanthus paguriphilus*  $\frac{1}{1}$  (from Michael Sars Exp. 1900).  
— 9. *Parazoanthus haddoni* on sponges  $\frac{1}{1}$  (from N. N. W. of Bergen. Uddström R. M. No. 270).  
— 10. — —  $\frac{1}{1}$  (from N. W. of Bergen. Mattsson 1880 R. M. No. 740).  
— 11. — — on sponges  $\frac{1}{1}$  (from N. N. W. of Bergen. Uddström R. M. No. 270).  
— 12. *Epizoanthus norvegicus* (from Trondhjem Fjord).  
— 13. — *danielsseni*  $\frac{2}{1}$  (from Sophia Exp.).  
— 14. — *erdmanni*  $\frac{1}{1}$  (from Spitzbergen Exp. St. 42).  
— 15. — *danielsseni* a little magnified (from Spitzb. Exp. St. 42).  
— 16. — *erdmanni*  $\frac{4}{1}$  capitulum from the oral side.  
— 17. — *erdmanni*  $\frac{1}{1}$  (from Greenland Exp. 1899).  
— 18. *Isozoanthus multinsulosus*  $\frac{2}{1}$  (from Ingolf Exp. St. 51).  
— 19. *Parazoanthus anguicomus*  $\frac{2}{1}$  (= *E. americanus* var. Verrill U. S. F. C. St. 2245).
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Plate II.

## Plate II.

- Fig. 1—5. *Epizoanthus glacialis* (fig. 1 from Umenak  $1^{5/1}$ ; fig. 2 from Jan Mayen  $2/1$ ; fig. 3 from Norw. Nord. Atl. Exp. St. 164 (type)  $2/1$ ; fig. 4 from Øgsfjord, Lovén  $2/1$ ; fig. 5 from Umenak 25 fms.  $2^{5/1}$ .)
- 6. *Epizoanthus danielsseni* (from Norw. N. Atl. Exp. St. 164) about  $2/1$ .
- 7. — *lindahli* var. *nordgaardi* about  $2/1$ .
- 8. — *abyssorum* about  $2/1$ .
- 9. — *danielsseni* var. *loveni*  $2/1$ .
- 10. — *beerenislandicus*  $2/1$ .
- 11. — *lindahli* (from Baffins Bay, Lindahl) enlarged somewhat more than 2 times.
- 12. — — (from Michael Sars Exp.)  $2/1$ .
- 13. — — (from Ingolf Exp. St. 32) about  $2/1$ .
- 14. — *bulbosus* dissected specimen showing the mesenteries (from Ingolf Exp. St. 104 about  $2/1$ ).
- 15. *Epizoanthus bulbosus* (from Ingolf Exp. St. 104 about  $2/1$ ).
- 16. — — (from Ingolf Exp. St. 32 about  $2/1$ ).
- Fig. 17. *Epizoanthus davisii* (from Ingolf Exp. St. 32 about  $2^{5/1}$ ).
- 18. — *erdmanni* var. *aurivillii* (from Kvenangen) about  $2^{5/1}$ .
- 19. *Isozoanthus dubius* (from Ingolf Exp. St. 45) about  $2/1$ .
- 20. — *islandicus* (from Ingolf Exp. St. 90) about  $2/1$ .
- 21. *Parazoanthus anguicomus* (from Dublin Museum) about  $1^{75/1}$ .
- 22. *Epizoanthus norvegicus* (from Trondhjem Fjord, Bergen Museum)  $1^{5/1}$ , on the left a large double polyp.
- 23. *Epizoanthus koreni* (from Ingolf Exp. St. 144)  $2/1$ .
- 24. — *erdmanni* (from Iceland Øfjord) about  $2/1$ .
- 25. *Isozoanthus ingolfi* (from Ingolf Exp. St. 27) about  $2/1$ .
- 26. *Epizoanthus incrustatus* (R. M. 23. 5. 1888) about  $1^{75/1}$ .
- 27. *Isozoanthus arborescens* (from Ingolf Exp. St. 97) about  $1^{75/1}$ .
- 28—29. *Epizoanthus erdmanni* var. *aurivillii* (from Kvenangen)  $2^{25/1}$ .





Plate III.

## Plate III.

Vertical sections through the sphincter muscles. In the figs. 1—3, 5 the distal part of the sphincter is turned upwards, in the figs 4 and 6 downwards.

Fig. 1 of *Epizoanthus abyssorum*  $\frac{2}{3}$ <sup>1</sup>.

— 2 - — *beerenislandicus*  $\frac{4}{3}$ .

— 3 - — *norvegicus* (from Skarnsund)  $\frac{2}{3}$ .

— 4 - — *roseus*  $\frac{2}{3}$ .

— 5 - *Isozoanthus arborescens* (from Ingolf Exp. St. 97)  $\frac{4}{3}$ .

— 6 - *Parazoanthus haddoni* (from N. W. of Bergen, Mattson 1880  $\frac{2}{3}$ ).

<sup>1</sup> Magnifications refer to Reichert's system "Austria". Figures drawn on the level of the microscope's foot.

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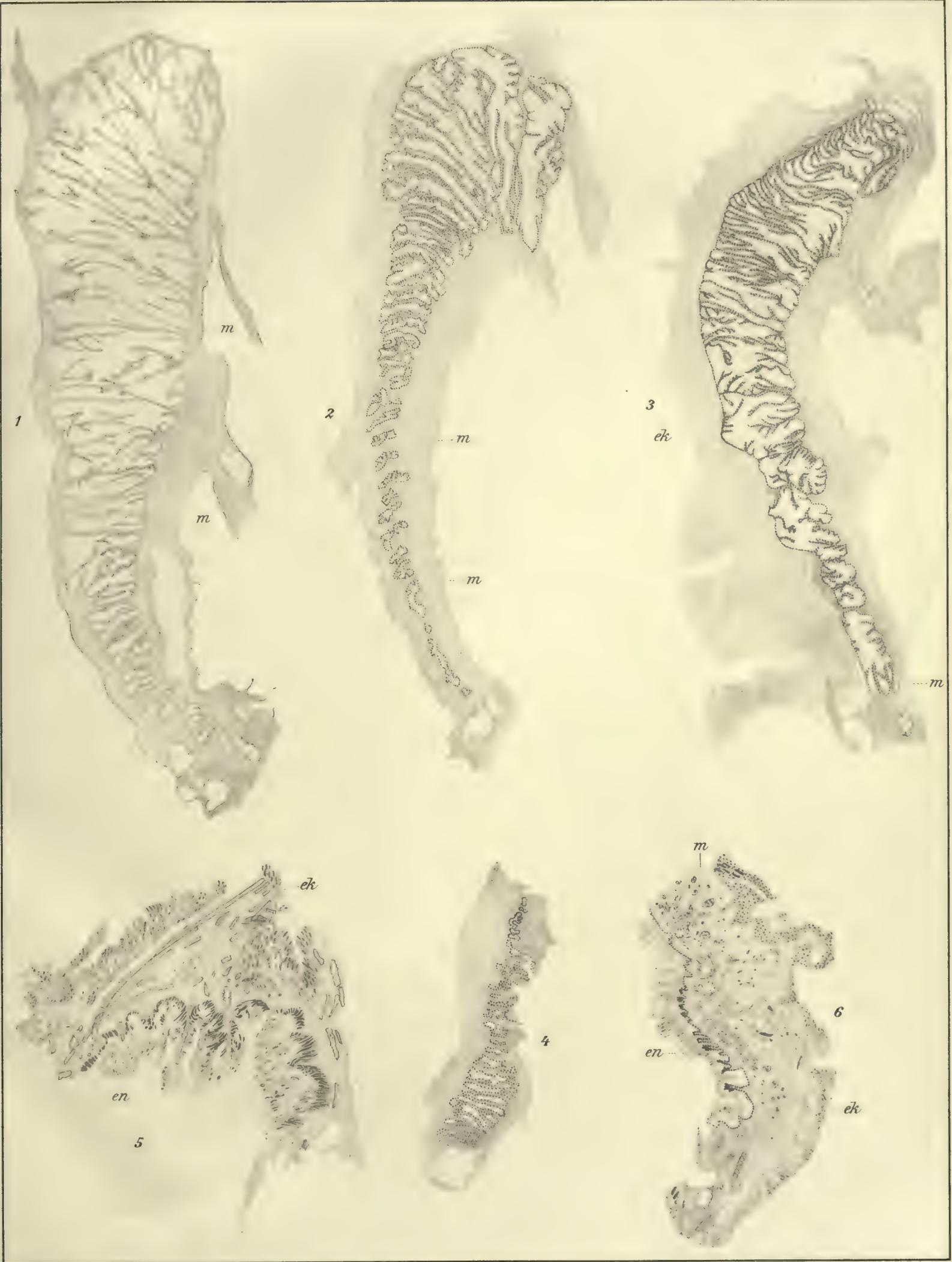




Plate IV.

## Plate IV.

- Fig. 1. *Epizoanthus beerenislandicus*. Transverse section through the body-wall  $\frac{4}{3}$ .<sup>1</sup>
- 2. — *glacialis*. Vertical section through the sphincter (from Norw. N. Atl. Exp.)  $\frac{2}{3}$ .
- 3. — *crdmanni* — — — — — (from Lyngen, Nordgaard)  $\frac{4}{5}$ .
- 4. — *koreni*. Transverse sections through the body-wall  $\frac{4}{3}$ .
- 5. — *lindahli*. — — — — — (from Baffins Bay)  $\frac{4}{3}$ .
- 6. — *glacialis*. — — — — — upper part.  $\frac{4}{3}$ .
- 7. — *glacialis*. — — — — — lower part.  $\frac{4}{3}$ .

<sup>1</sup> Cf. Pl. III.

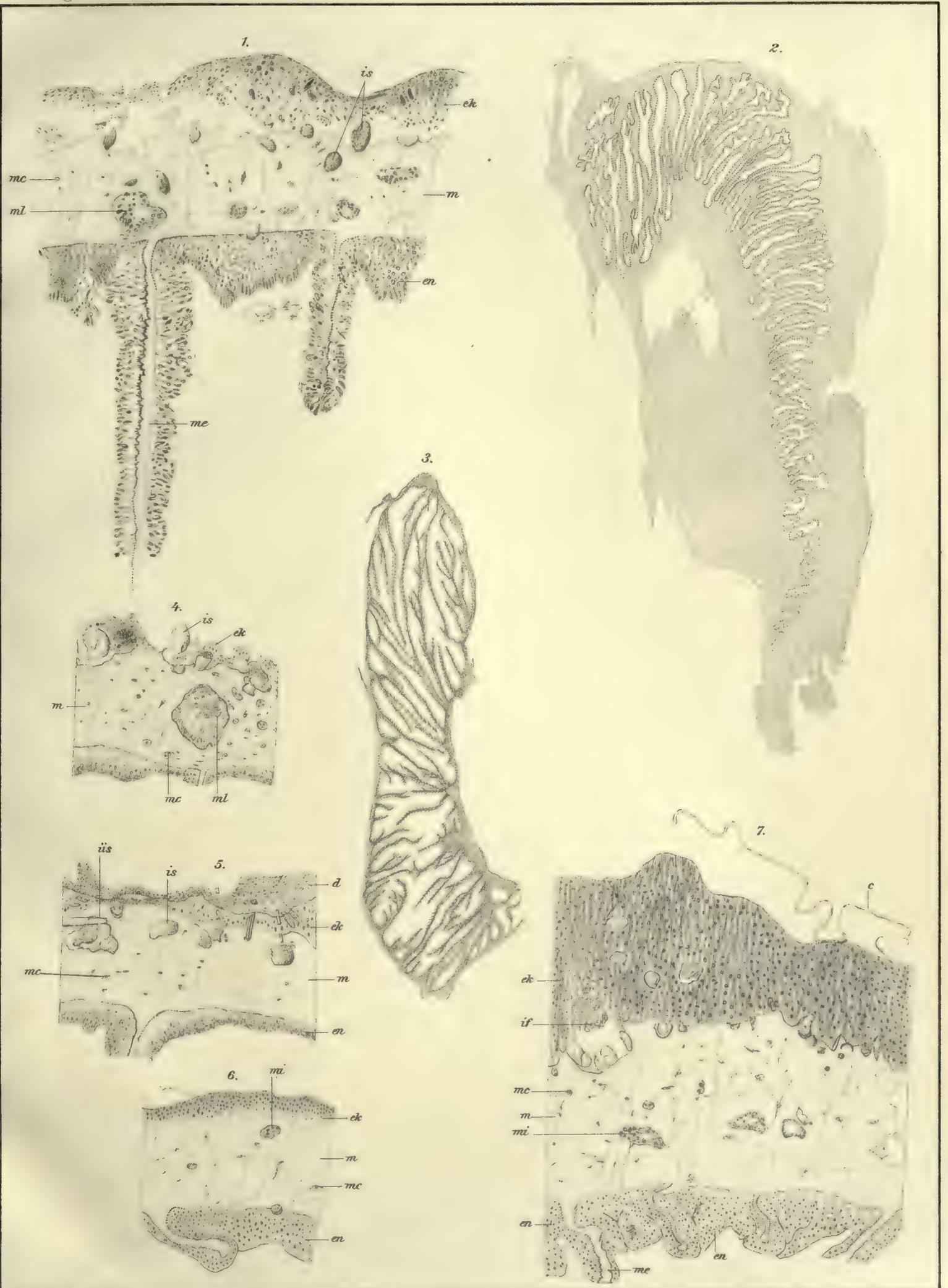




Plate V.

## Plate V.

Transverse sections through the body-wall, figs. 1, 3—7 in the region of the œsophagus. Entoderm not drawn in figs. 3, 5, 6.

Fig. 1 of *Epizoanthus danielsseni* (from Spitsb. Exp. St. 42)  $\frac{4}{3}$  <sup>1</sup>.

- 2 - — *norvegicus*, capitular region (Trondhjem Fjord, Östergren)  $\frac{4}{3}$ .
- 3 - — — ( — — — )  $\frac{4}{3}$ .
- 4 of *Epizoanthus erdmanni* (Lyngen, Nordgaard)  $\frac{4}{3}$ .
- 5 - — — var. *aurivilli* (Finmarken, Goës & Malmgren)  $\frac{4}{3}$ .
- 6 - — *roseus*  $\frac{4}{3}$ .
- 7 - — *abyssorum*  $\frac{4}{3}$ .

<sup>1</sup> Cf. PL. III.

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Plate VI.

## Plate VI.

Transverse sections of the body-wall figs. 1, 3, 5 in the region of the œsophagus; figs. 2, 4 in the cnidoglandular tract of the filaments, fig. 6 in the hyposulcus region (Magnification  $\frac{4}{3}$  Reichert's "Austria"; the figures drawn on the level of the microscope's foot; fig. 1 same magnification but with drawn out tube. Entoderm not drawn in figs. 1—4).

Fig. 1 of *Isozoanthus bulbosus* (from Ingolf Exp. St. 104).

- |       |   |   |
|-------|---|---|
| — 2 - | — | <i>arborescens</i> (from Mortsund, Nordgaard).  |
| — 3 - | — | <i>multinsulosus</i> (from Ingolf Exp. St. 51). |
| — 4 - | — | <i>magninsulosus</i> .                          |
| — 5 - | — | —   |
| — 6 - | — | <i>ingolfi</i> (from Ingolf Exp. St. 27).       |
-





Plate VII.

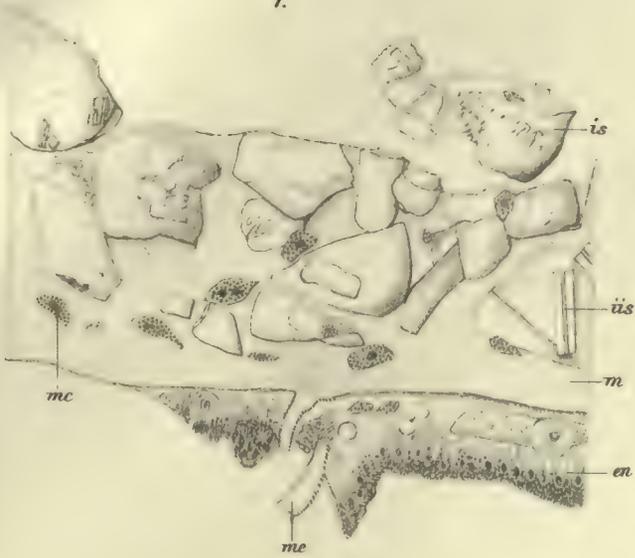
## Plate VII.

Transverse sections through the body-wall in the region of the œsophagus; fig. 5 in the region of the cnido-glandular tract of the filaments, figs. 1—4 magnification  $\frac{2}{7}$  Reichert's "Austria". Figures drawn on a level with the stage of the microscope.

Fig. 1 of *Isozoanthus davisi*.

- 2 - — *islandicus*.
  - 3 - — *dubius*.
  - 4 - — *danicus*.
  - 5 - *Parazoanthus haddoni* (from N. W. of Bergen, Mattson 1880)  $\frac{2}{3}$  with drawn out tube.
  - 6 - — ? (from the Færoes)  $\frac{2}{3}$  with drawn out tube.
-

1.



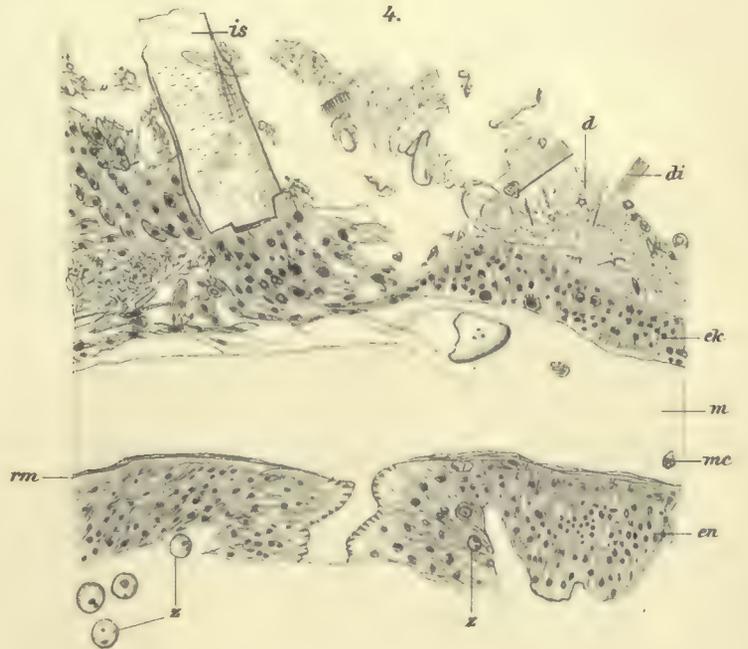
2.



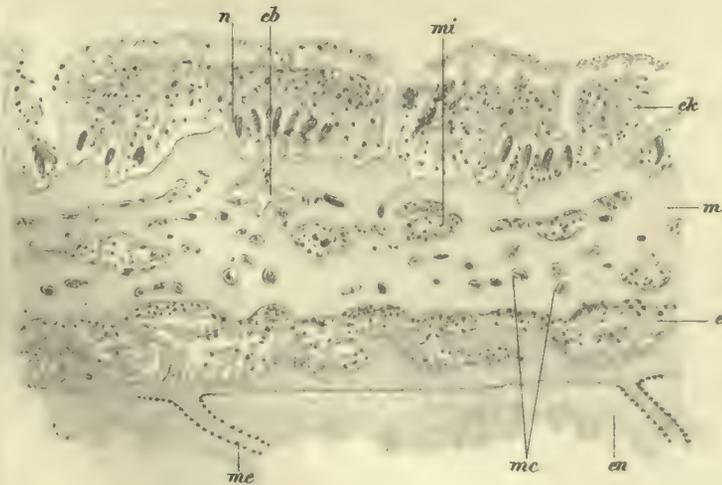
3.



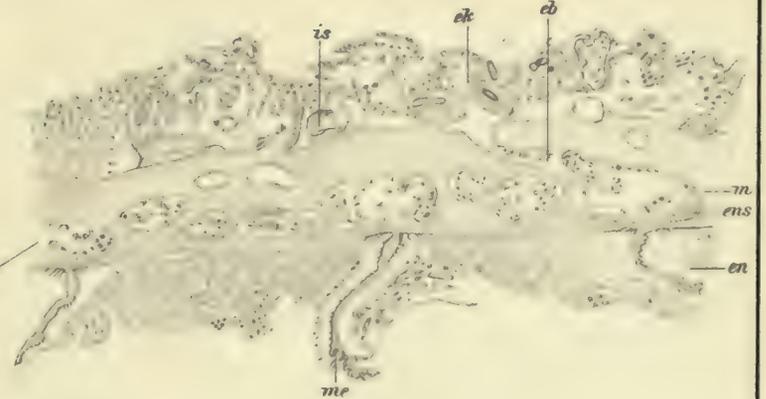
4.



5.



6.





# THE INGOLF-EXPEDITION

1895—1896.

## THE LOCALITIES, DEPTHS, AND BOTTOMTEMPERATURES OF THE STATIONS.

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
1	62° 30'	8° 21'	132	7°2	24	63° 06'	56° 00'	1199	2°4	45	61° 32'	9° 43'	643	4°17
2	63° 04'	9° 22'	262	5°3	25	63° 30'	54° 25'	582	3°3	46	61° 32'	11° 36'	720	2°40
3	63° 35'	10° 24'	272	0°5		63° 51'	53° 03'	136		47	61° 32'	13° 40'	950	3°23
4	64° 07'	11° 12'	237	2°5	26	63° 57'	52° 41'	34	0°6	48	61° 32'	15° 11'	1150	3°17
5	64° 40'	12° 09'	155			64° 37'	54° 24'	109		49	62° 07'	15° 07'	1120	2°91
6	63° 43'	14° 34'	90	7°0	27	64° 54'	55° 10'	393	3°8	50	62° 43'	15° 07'	1020	3°13
7	63° 13'	15° 41'	600	4°5	28	65° 14'	55° 42'	420	3°5	51	64° 15'	14° 22'	68	7°32
8	63° 56'	24° 40'	136	6°0	29	65° 34'	54° 31'	68	0°2	52	63° 57'	13° 32'	420	7°87
9	64° 18'	27° 00'	295	5°8	30	66° 50'	54° 28'	22	1°05	53	63° 15'	15° 07'	795	3°08
10	64° 24'	28° 50'	788	3°5	31	66° 35'	55° 54'	88	1°6	54	63° 08'	15° 40'	691	3°9
11	64° 34'	31° 12'	1300	1°6	32	66° 35'	56° 38'	318	3°9	55	63° 33'	15° 02'	316	5°9
12	64° 38'	32° 37'	1040	0°3	33	67° 57'	55° 30'	35	0°8	56	64° 00'	15° 09'	68	7°57
13	64° 47'	34° 33'	622	3°0	34	65° 17'	54° 17'	53		57	63° 37'	13° 02'	350	3°4
14	64° 45'	35° 05'	176	4°4	35	65° 16'	55° 05'	362	3°6	58	64° 25'	12° 09'	211	0°8
15	66° 18'	25° 59'	330	-0°75	36	61° 50'	56° 21'	1435	1°5	59	65° 00'	11° 16'	310	-0°1
16	65° 43'	26° 58'	250	6°1	37	60° 17'	54° 05'	1715	1°4	60	65° 09'	12° 27'	124	0°9
17	62° 49'	26° 55'	745	3°4	38	59° 12'	51° 05'	1870	1°3	61	65° 03'	13° 06'	55	0°4
18	61° 44'	30° 29'	1135	3°0	39	62° 00'	22° 38'	865	2°9	62	63° 18'	19° 12'	72	7°92
19	60° 29'	34° 14'	1566	2°4	40	62° 00'	21° 36'	845	3°3	63	62° 40'	19° 05'	800	4°0
20	58° 20'	40° 48'	1695	1°5	41	61° 39'	17° 10'	1245	2°0	64	62° 06'	19° 00'	1041	3°1
21	58° 01'	44° 45'	1330	2°4	42	61° 41'	10° 17'	625	0°4	65	61° 33'	19° 00'	1089	3°0
22	58° 10'	48° 25'	1845	1°4	43	61° 42'	10° 11'	645	0°05	66	61° 33'	20° 43'	1128	3°3
23	60° 43'	56° 00'	Only the Plankton-Net used		44	61° 42'	9° 36'	545	4°8	67	61° 30'	22° 30'	975	3°0

Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.	Station Nr.	Lat. N.	Long. W.	Depth in Danish fathoms	Bottom-temp.
68	62° 06'	22° 30'	843	3°4	92	64° 44'	32° 52'	976	1°4	118	68° 27'	8° 20'	1060	-1°0
69	62° 40'	22° 17'	589	3°9	93	64° 24'	35° 14'	767	1°46	119	67° 53'	10° 19'	1010	-1°0
70	63° 09'	22° 05'	134	7°0	94	64° 56'	36° 19'	204	4°1	120	67° 29'	11° 32'	885	-1°0
71	63° 46'	22° 03'	46			65° 31'	30° 45'	213		121	66° 59'	13° 11'	529	-0°7
72	63° 12'	23° 04'	197	6°7	95	65° 14'	30° 39'	752	2°1	122	66° 42'	14° 44'	115	1°8
73	62° 58'	23° 28'	486	5°5	96	65° 24'	29° 00'	735	1°2	123	66° 52'	15° 40'	145	2°0
74	62° 17'	24° 36'	695	4°2	97	65° 28'	27° 39'	450	5°5	124	67° 40'	15° 40'	495	-0°6
	61° 57'	25° 35'	761		98	65° 38'	26° 27'	138	5°9	125	68° 08'	16° 02'	729	-0°8
	61° 28'	25° 06'	829		99	66° 13'	25° 53'	187	6°1	126	67° 19'	15° 52'	293	-0°5
75	61° 28'	26° 25'	780	4°3	100	66° 23'	14° 02'	59	0°4	127	66° 33'	20° 05'	44	5°6
76	60° 50'	26° 50'	806	4°1	101	66° 23'	12° 05'	537	0°7	128	66° 50'	20° 02'	194	0°6
77	60° 10'	26° 59'	951	3°6	102	66° 23'	10° 26'	750	0°9	129	66° 35'	23° 47'	117	6°5
78	60° 37'	27° 52'	799	4°5	103	66° 23'	8° 52'	579	0°6	130	63° 00'	20° 40'	338	6°55
79	60° 52'	28° 58'	653	4°4	104	66° 23'	7° 25'	957	1°1	131	63° 00'	19° 09'	698	4°7
80	61° 02'	29° 32'	935	4°0	105	65° 34'	7° 31'	762	0°8	132	63° 00'	17° 04'	747	4°6
81	61° 44'	27° 00'	485	6°1	106	65° 34'	8° 54'	447	-0°6	133	63° 14'	11° 24'	230	2°2
82	61° 55'	27° 28'	824	4°1		65° 29'	8° 40'	466		134	62° 34'	10° 26'	299	4°1
83	62° 25'	28° 30'	912	3°5	107	65° 33'	10° 28'	492	-0°3	135	62° 48'	9° 48'	270	0°4
	62° 36'	26° 01'	472		108	65° 30'	12° 00'	97	1°1	136	63° 01'	9° 11'	256	4°8
	62° 36'	25° 30'	401		109	65° 29'	13° 25'	38	1°5	137	63° 14'	8° 31'	297	0°6
84	62° 58'	25° 24'	633	4°8	110	66° 44'	11° 33'	781	-0°8	138	63° 26'	7° 56'	471	-0°6
85	63° 21'	25° 21'	170		111	67° 14'	8° 48'	860	-0°9	139	63° 36'	7° 30'	702	-0°6
86	65° 03' <sub>6</sub>	23° 47' <sub>6</sub>	76		112	67° 57'	6° 44'	1267	-1°1	140	63° 29'	6° 57'	780	0°9
87	65° 02' <sub>3</sub>	23° 56' <sub>2</sub>	110		113	69° 31'	7° 06'	1309	-1°0	141	63° 22'	6° 58'	679	-0°6
88	64° 58'	24° 25'	76	6°9	114	70° 36'	7° 29'	773	-1°0	142	63° 07'	7° 05'	587	-0°6
89	64° 45'	27° 20'	310	8°4	115	70° 50'	8° 29'	86	0°1	143	62° 58'	7° 09'	388	0°4
90	64° 45'	29° 06'	568	4°4	116	70° 05'	8° 26'	371	-0°4	144	62° 49'	7° 12'	276	1°6
91	64° 44'	31° 00'	1236	3°1	117	69° 13'	8° 23'	1003	-1°0					





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