Notes on the development and the larval forms of some Scandinavian Echinoderms.

By

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(With 8 text-figures.)

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During a stay at the Swedish Zoological Station at Kristineberg, Fiskebäckskil, in August-September 1918 I had the opportunity of making some observations on the development of some of the Echinoderms occurring there. A renewed visit to the said station from the end of July till the middle of September this year (1919) enabled me to continue these researches. My aim being to acquire a fuller knowledge of the development of the Scandinavian Echinoderms, and especially of the different larval forms, it will need continued researches, which will evidently require visits to different places on the Scandinavian coasts and thus occupy a rather long time. I have therefore deemed it reasonable to publish this preliminary notice of the results hitherto acquired.

I beg to tender my sincere thanks to the authorities of the Swedish Zoological Station, Kristineberg: Professor Hj. Théel and Dr. Hj. Östergren for the cordial hospitality offered me and for their untiring efforts in satisfying my — I fear rather troublesome — needs of material for my researches.

The results were obtained partly by direct rearing of the larvæ in question, partly through combinations of known facts, e. g. the

breeding season and the occurrence of some species in the locality, where the researches were carried out. Thus, when there are found in this place four different species of Spatangoids, the development and the larvæ of two of them being known, the third having its breeding season at another time of the year, while the fourth has its breeding season just at the time in question, it is a logical conclusion that when a larva not belonging to any of the two known forms appears in the plankton, it must belong to the fourth of those species. *Brissopsis lyrifera* represents such a case. In the same way, if some larva of say an Ophiuroid is found to occur in considerable numbers in a place, where only one species of Ophiuroid occurs, it is no less justified to conclude that this larva must then belong to that species of Ophiuroid. Such a case is represented by *Ophiura texturata* in the Limfjord; another quite similar case is that of *Echinocardium cordatum*. MacBride in his memoir on the development of *Echinocardium cordatum* [1]), objects to the latter case, stating that the identification of my specimens as the larvæ of that species „rests on a mere guess because the ground of the identification was the occurrence of the larva in question in the waters of the Limfjord in Denmark on the sandy bottom of which *Echinocardium cordatum* was the only Spatangoid which was found". I must protest against designating that determination as a „mere guess"; *Echinocardium cordatum* being the only Spatangoid occurring in the Limfjord [2]), it is not mere guess to refer a Spatangoid larva normally occuring there to that species. It is a logical conclusion, the correctness of which MacBride could only ascertain. Mere guess work it would be, if I had referred such forms as *Ophiopluteus ramosus* or *O. coronatus* to some definite Ophiuroid, for which reference there would be

[1]) E. W. MacBride. The development of Echinocardium cordatum. Part. I. The external features of the development. Quart. Journ. Micr. Sc. Vol. 59. 1914. p. 472

[2]) Since MacBride (op. cit.) mentions especially the sandy bottom as the condition under which *Echinocardium* occurs in the Limfjord, this might possibly indicate the meaning that other Spatangoids were to be found in places with muddy bottom in the same locality. But, anyhow, there is no foundation for such supposition; as I have stated expressly (Echinodermenlarven d. Plankton-Expedition, p. 103), *Echinocardium cordatum* is the only species of Spatangoids occurring in the Limfjord.

no premises. But that I did not do. Herewith I do not mean to try to justify all the references of Echinoderm larvæ which I have ventured to suggest. The premises may have been wrong in some cases, and then, of course, the conclusions must also be wrong, e. g. in the case of the larva supposed to belong to *Echinometra lucunter*,[1]) — a very singular case which I am as yet unable to explain, the more so as new facts gathered seem to indicate the correctness of the premises that led me to the said conclusion, which I have myself proved to be wrong.[2]) In this case something must, of course, be wrong in the premises; what it is, remains to be disclosed.

I. **Ophiura affinis** Ltk. (?).

One of the first days of August this year I found in the plankton an Ophiuroid-larva, which recalls most strikingly that figured by Joh. Müller in his VI. memoir on Echinoderm larvæ,[3]) Taf. VII, figs. 5—6, which larva was observed by him in the Adriatic Sea in the summer[4]) of 1852. So far as I know this larva has not been observed again till now.

In the general features there is perfect accordance between Müller's larva from the Adriatic and the one observed by me at Kristineberg, and also the skeletal structure appears to be quite the same (— unfortunately I have only a drawing, but no preserved specimens of the larva, which was seen only one day, and I could not there compare it with Müller's figure of the larva, Müller's work being not available at the station —); especially the very characteristic sinuation at the point, where the body rod and postero-lateral rod join, mentioned by Müller, was well marked in the specimens observed by me. Only the coloration was not quite the same.

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[1]) Th. Mortensen. Über die Larve von Echinometra lucunter (L.) (?). Zool. Jahrbücher. Suppl. XV. 1912.

[2]) Th. Mortensen. On the Development of some West Indian Echinoderms. Year Book No. 15 of the Carnegie Institution. Washington. p. 193. 1916.

[3]) Über den allgemeinen Plan in der Entwickelung der Echinodermen. Abhandl. d. Berliner Akad. 1852. (1853).

[4]) The exact time, when it was observed, is not stated by Müller, but it appears to have been in the summer time.

Müller's specimens had the point of the postero-lateral arms red coloured (and, judging from his figure, quite conspicuously so), and the young star also had a big red patch in the middle of the dorsal side; the specimens observed by me had only a faint yellowish tint in the end of the arms and in the middle of the dorsal side of the young star, the larva being otherwise milky white and opaque, so that the skeleton could not be seen distinctly without applying some clearing fluid. This diversity in colour being the only notable difference between the two larvæ it seems justifiable to regard them as identical or, at least, as belonging to two very closely related species. The fact that there were no distinct ciliated bands along the postero-lateral arms, together with the peculiar opaqueness of the larva, would seem to indicate that this larva does not have the full pluteus shape, but belongs to the rudimentary larval forms. This cannot, however, be decided, before larvæ have been observed in which the metamorphosis is less advanced than in those observed till now.

The occurrence of this larval form both in the Adriatic and at the coast of Bohuslän allows a suggestion about the Ophiuroid to which it must belong. The following Ophiuroids are common to the Scandinavian seas and the Adriatic: *Ophiura texturata*, *O. albida*, *O. affinis*, *Amphiura filiformis*, *A. Chiajei*, *Amphipholis squamata*, *Ophiothrix fragilis* and probably also *Ophiocoma nigra*. Of these species one, *Amph. squamata*, is viviparous and thus cannot come into consideration. The larvæ of *Ophiura texturata*, *O. albida*, *Amphiura filiformis* (see below) and *Ophiothrix fragilis* are known, these species being thus also eliminated; likewise *Ophiocoma nigra*, evidently, is out of question.[1]) *Amphiura Chiajei* and *Ophiura affinis* thus alone can come into consideration as species to which this larva could belong. Joh. Müller, in fact, suggested that the larva might possibly belong to *Amphiura Chiajei* (he names it incorrectly *Ophiolepis Sundevalli*; as it is especially noticed that the species has two tentacle scales, it is beyond doubt that the species meant is *Amph. Chiajei*), his reason for this suggestion being that the dorsal side of the disk in this species is red as in

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[1]) Th. Mortensen. On the development of some British Echinoderms. Journ. Mar. Biol. Assoc. N. Ser. X. 1913. p. 12.

the developing star of the larva. This reason, evidently, is of very small weight only, and there is, at least, one fact which appears to show that the larva cannot belong to this Ophiuroid. *Amphiura Chiajei* was found at Kristineberg to have its breeding season only from the middle of September, no specimens with ripe genital products having been observed before that time. But, as stated above, the larvæ were found in the beginning of August, and not later. Everything thus points towards *Ophiura affinis* as the species to which this larva belongs. It is true, the species is not recorded as occurring at Bohuslän [1]), but I found it there in a dredging off „Smedjan" on the 19th August 1918 (together with *Ophiura robusta* Ayres, which was likewise unknown from the coast of Bohuslän). The specimens were noted to contain no ripe sexual products. This fact is also in accordance with the observations on the larvæ, which were all in the metamorphosis stage, so that the breeding season of the species should be about the middle of July.

Provided the reference of this larva to *Ophiura affinis* be correct, this will add considerably to the remarkable diversity among the larvæ of apparently so closely related species as *Ophiura texturata* and *albida*, the difference of these larvæ being so conspicuous that it is hard to understand, how they can belong to the same genus. In case that — as I think there is some reason to suppose — *Ophiopluteus compressus* should prove to belong to *Ophiura Sarsi*, this diversity will be still more remarkable.

The conspicuous difference in regard to colour between the Adriatic specimens of this larva and those from Bohuslän might indicate that the Adriatic form of *Ophiura affinis* differs to some extent from the Scandinavian form. I was therefore very much interested in learning from my friend, Professor Koehler in Lyon, that he was inclined to regard the Adriatic form of *Ophiura affinis* (the *Ophiura Grubei* Heller) as at least a distinct variety; a careful comparison of the single specimen from the Adriatic at my disposal with specimens from the Scandinavian seas convinced me of the correctness of Koehler's view. Indeed, I should be much

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[1]) Hj. Théel. Om utvecklingen af Sveriges Zoologiska Hafstation Kristineberg och om Djurlifvet i angränsande Haf og Fjordar. Arch för Zoologi. Bd. IV. 1907.

more inclined to regard the Adriatic form as a distinct species, though, of course, closely related to *O. affinis*. If this view be correct, the interest connected with this larva would be greatly augmented. We would then here have the first case of the larvæ of two closely related species of the genus *Ophiura* being closely alike, in conformity with what should be expected from the analogy of other Echinoderm larvæ, and the great diversity of e. g. the larvæ of *Ophiura texturata* and *albida* would then be a proof that these Ophiuroids are not really so closely related as hitherto generally supposed, not a proof against the value of the larval characters as tests for the systematic relations of the adult. — Further researches on this wide-bearing problem must be expected with the greatest interest.

II. Amphiura filiformis (O. F. Müller).

The most common of all the Ophiuroid-larvæ occurring at the Zoological Station of Kristineberg, at least from the later part of July until the middle of September, is the form described by me in „Nordisches Plankton" under the name of *Ophiopluteus mancus*. Considering its occurrence in so large numbers it was evident that it must belong to a species of Ophiurid correspondingly abundant in the neighbourhood of the Station. Eliminating those species of which the larvæ were known already, there were hardly any other species to which it could be referred than the two species of *Amphiura*, *A. filiformis* and *Chiajei*. No larva being known hitherto which could with any reasonable degree of probability be referred to *Amphiura*, I was, of course, very anxious to get definite proof of the origin of this larva. Two ways might give the desired result, viz. rearing the larvæ from the egg or rearing the young Ophiurid from the larva till a state sufficiently advanced to recognize it as an *Amphiura*. During the summer of 1918 all efforts to get the Amphiura's to shed their eggs in the aquaria proved in vain, and artificial fertilization did not succeed either, as upon the whole it is next to impossible to get Ophiurid-eggs fertilized, when taken out of an opened female, in the way used with so splendid success in almost all Echinoids, very generally in Asteroids and in many cases also in Holothurians. The other way,

rearing the Ophiurid from the larvæ, on the other hand, proved successful.

Larvæ in all stages of metamorphosis occurred in great numbers. On picking out from the plankton such larvæ, as were in the more advanced stages of metamorphosis and placing them in separate dishes, I had the joy of seeing them go on metamorphosing normally, and almost any number of young Ophiurids could be obtained. The question was now how to arrange for suitable conditions for these young Ophiurids, so that they would feed and grow to the desired size. Some mud from the locality, where the grown Amphiura's abound, was sifted through fine silkgaze in order to avoid all larger organisms, and especially to avoid the presence in it of young Ophiurids the origin of which was not controlled. I put some of this sifted mud in some flat dishes, adding some Nitschia-culture, and the young Ophiurids were placed in the dishes. They at once buried themselves in the mud, and in the course of a few days it was evident that they had grown in size and a new arm joint was about to form. Before leaving the station I put a number of such young Ophiurids, reared from *Ophiopluteus mancus*, into an aquarium with sifted mud and Nitschia culture added. Dr. Östergren kindly promised to take care of them and, at my request, after about four months sifted the mud and sent me what was left of the culture, preserved in alcohol. Examining this material I found that, while some of the young Ophiurids had hardly grown at all, others had grown not inconsiderably having 4 joints in the arms, not counting the terminal joint.

On comparing the young Ophiurids thus reared with young specimens found on sifting the mud from the *Amphiura*-locality, the youngest of which had only 3—4 joints in the arms, it was evident that it was really the young *Amphiura* that had been reared in this way. It is true, the reared specimens had not grown so far as to develop the two infradental papillæ, which represent the most prominent *Amphiura*-character. But among those specimens collected from the mud from the *Amphiura*-locality every transitional stage was found from young specimens not yet having the infradental papillæ developed to such as had the *Amphiura*-characters distinctly developed; and there was the most perfect conformity between the specimens reared in the aquaria and the

younger specimens from the free (e. g. in the very characteristic structure of the disk plates) so that there could be no doubt that the Ophiurid reared from Ophiopluteus mancus was really an Amphiura.

Although the experiment was not carried on until the full result was reached (the appearance of the infradental papillæ) it is evident that here we have a method which may be used with success in the study of the postembryonal development of Ophiurids, and doubtless also of other Echinoderms. Experiments were made likewise with metamorphosing larvæ of *Ophiura albida*; also in this case the metamorphosis went on normally in larvæ kept in separate dishes and the young Ophiurids grew to some size; I did not, however, take special care to carry this experiment further. — It is worth mentioning that in the aquarium with the *Amphiura*-culture there proved to have developed an astonishing number of Foraminifera; also a great number of Nematods had developed.

Though it was thus proved that *Ophiopluteus mancus* is the larva of *Amphiura*, the question still remained undecided to which of the two species *A. filiformis* or *Chiajei* it should be referred, as I found it impossible to distinguish these two species in the very young stages. During my visit to the Station at Kristineberg this summer (1919) I made therefore renewed efforts to solve the question, trying this time especially to get the Amphiuras to shed their eggs in the aquaria and thus to be able to rear the larva from the egg. From the material taken by dredging such specimens were carefully selected which were full of apparently ripe sexual products (in *Amphiura filiformis* with its transparent skin on the ventral side of the disk this is very easily seen) and otherwise unhurt and in good condition. A number of such specimens, the two species kept separately, of course, were put into aquaria with sifted mud from the locality where they were dredged. They lived there excellently, especially *A. filiformis*, lying — in the well known way — buried in the mud with only the points of the arms rising over the surface of the mud, catching eagerly the food (pieces of mussels, Crustaceans) put before them. After two or three days (on August 12th) I had the great satisfaction of seeing them discharge their sexual products. The way in which it was done was rather surprising and deserves a more detailed description.

The normal position of these Ophiurids is, as stated above, this that the disk is completely buried in the mud, lying as in a bed about two—three centimeters below the surface of the mud, only the arm-points rising over the surface. When they want to discharge their sexual products, they rise over the surface of the mud so that the disk is kept about two centimenters above the surface, resting on the five armbases as pillars, the armpoints at the same time disappearing below the surface (Fig. 1.). The disk was generally kept more or less obliquely. While in this position, the sexual products are streaming out of all the bursal slits. The males were the first to discharge their sperm, which spread in the water around them as a white cloud; having finished discharging the sperm they gently sank down into the mud, assuming again their normal position. Very soon after they had disappeared, not more than a few minutes after, some females rose over the surface of the mud exactly in the same way as the males and at once began to shed their eggs, which fell to the bottom, where they formed a distinct red layer; immediately after having discharged the eggs the females went down into the mud again in the same way as the males. It might perhaps be suggested that the oblique position of the disk during the shedding process is of some importance, it being avoided in this way that the eggs are buried in the mud by the sinking body, lying not directly below the disk. However, conditions in the natural surroundings may perhaps afford sufficient safeguard against a burying of the eggs, and I do not venture to maintain that the oblique position of the body is more than quite a casual circumstance.

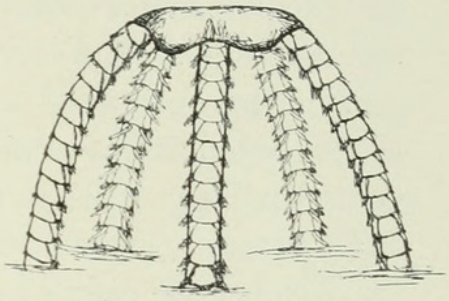

Fig. 1. Sketch of an *Amphiura* in its spawning position.

It was ascertained by examining such specimens which had just discharged their sexual products that they were quite empty, all the sperm and the eggs being discharged at the same time.

Shortly after the eggs had been discharged a number of them were taken up with a pipette and placed in a separate dish in order to trace their development, which could, of course, not be done in the aquaria with the running water. Evidently, I had taken

them away from the aquarium too soon, since it turned out that only comparatively few of them had been fertilized. Moreover a large percentage of those developed abnormally. But fortunately some few of them developed normally. After three days they began to assume the shape of small Plutei with the first rudiments of the skeleton. At the age of 7 days the postoral and posterolateral rods had begun to form, and on the lower part of the latter the small recurrent rod so characteristic of *Ophiopluteus mancus* had appeared. The postoral arms had a prominent red pigment spot in the point. — Although I did not succeed in rearing the larvæ beyond this point, it was hereby definitely ascertained that Ophiopluteus mancus is the larva of Amphiura filiformis.

Wishing, of course, to try to rear the larva of *Amphiura Chiajei* also, I continued the experiment with this species. A closer examination showed that it was not yet ripe at the time, when *Amphiura filiformis* was at the height of its breeding season, in the first part of August. It was only in the beginning of September that its breeding season began. About this time a number of the most ripe specimens to be found were put into an aquarium prepared in the same way as before. On the 9th of September I had then the great pleasure of seeing a pair of males rise above the mud in the same way as *Amphiura filiformis*. I was, however, surprised in seeing that the sperm did not spread as a milky cloud in the water; it sank to the bottom in thick masses. On examining the sperm under the microscope I found that the spermatozoa did not move at all. The reason for this was evident enough. At the time when *Amphiura filiformis* was breeding the salinity of the water used for the aquaria was about 32 ‰; now the salinity was only about 28 ‰. The immobility of the sperm (which I tried in vain to raise by making the water more alkaline) was evidently due to the salinity being too low, and this easily accounts for the fact that no females rose to discharge their eggs, the chemotactic action of the living sperm, which must be supposed otherwise to induce the females to sexual activity, being eliminated in this case.

It is very noteworthy that, in spite of the lover salinity, the Amphiuras themselves lived quite well in the aquaria, taking the

food put before them in the normal way. This has an important bearing on the problems of geographical distribution, showing how some forms may be able to live in places where they cannot normally propagate, the natural conditions being unfavourable to the sexual products.

Since about the middle of September *Amphiura filiformis* had passed its breeding season, while *A. Chiajei* was now just entering into it, it was to be expected that the larvæ of the latter must be found in the plankton towards the end of September and in October in similar abundance as those of *A. filiformis* during the height of its breeding season (towards this time, the middle of September, they were much less abundant). As I could not stay at Kristineberg beyond the middle of September, I asked Dr. Östergren to do me the service to get some good plankton samples for me in the course of October and send them to me preserved in alcohol, which he very kindly did. The examination of these samples was, however, a disappointment to me. They contained all the same larval forms that I had found during August and September, but none which could be referred to *A. Chiajei*. Only one specimen was found of a larva which I had not observed there hitherto, viz. a young specimen agreeing closely with the young larva of *Ophiactis balli*, as described in my paper, quoted above, on the development of some British Echinoderms. *Ophiactis balli* is not known from the coast of Bohuslän, but as it occurs in Skagerak it is not at all surprising that the larva could be brought that distance by the currents. The larva of *Amphiura Chiajei* thus still remains unknown. It is possible that the fairly numerous specimens of *Ophiopluteus mancus* found in these samples really belong to *A. Chiajei*, in which case the larvæ of these two species would be hardly distinguishable. But it is also possible that the larvæ of *A. Chiajei* were not at all present in these samples on account of some unknown reason. Nothing can be stated definitely about these questions, until the larva of *A. Chiajei* has been made known through direct experiments.

The description of *Ophiopluteus mancus* in „Nordisches Plankton" is based only on the younger stages; the fact that none of them had the postero-dorsal arms developed was then naturally explained by their young age. The examination of a very great

number of specimens in all stages of development, however, has revealed the remarkable fact that the posterodorsal arms are entirely absent in this larva, a quite unique feature among Ophiurid larvæ, so far as hitherto known. It is curious that this interesting fact has escaped the observation of H. C. Chadwick, who in his Memoir on Echinoderm Larvæ [1]) describes and carefully figures the metamorphosis stage of this larva. His suggestion that it might prove to be the larva of *Ophiopholis aculeata* seems the more remarkable, since on the next page he mentions the larva referred by me (Echinodermenlarven d. Plankton-Exped. p. 53) to *Ophiopholis aculeata*, without giving any reason at all why that reference should be wrong. It is true, I could not then regard it as a definitely established fact that this larva really belongs to *Ophiopholis aculeata*, but it was pointed out that evidences are for the correctness of this reference. Having now myself (during a stay at the Biological Station at Trondhjem in July 1916) reared the larva of *Ophiopholis aculeata* to a stage corresponding to the youngest of the larvæ figured by Fewkes in his paper „On the development of the calcareous plates of Amphiura," [2]) I have still less doubt that the reference of the said larva to *Ophiopholis aculeata* is correct, although the definite proof is still wanting, the reared larva having not yet developed the characteristic prominences of transverse rods.

III. **Brissopsis lyrifera** (Forbes).

Only four species of Spatangoids are known from the coast of Bohuslän, viz. *Spatangus purpureus*, *Echinocardium cordatum*, *Ech. flavescens* and *Brissopsis lyrifera*. The larvæ of the two former are known, more or less completely.[3]) Chadwick in his

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[1]) L. M. B. Memoirs. XXII. 1914. Proc. & Transact. Liverpool Biol. Soc. Vol. XXVIII.

[2]) Bull. Mus. Comp. Zool. XIII. No. 4. 1887. Pl. I.

[3]) Th. Mortensen. Echinodermenlarven d. Plankton-Expedition. p. 102.
— On the development of some British Echinoderms. Jour. Mar. Biol. Assoc. X. 1913. p. 14.
E. W. Mac Bride. The development of Echinocardium cordatum. Part I. Quart. Journ. Micr. Sc. 59. 1914.

memoir on the Echinoderm larvæ (p. 23. Pl. IX. Figs. 61—64) mentions a Spatangoid larva, found off Port Erin in February—April, which, he thinks, must be referred to *Echinocardium flavescens*. Unfortunately he does not point out which are its characteristic features; judging from the figures it has unfenestrated postoral rods, in marked difference from the other Spatangoid-larvæ known from North-European seas. Only younger stages are figured by Chadwick, with the postero-dorsal arms not yet developed; with a curious selfcontradiction he states not having seen a later stage, although a few lines above he says that in 1914 „numbers of fully developed specimens occurred in the plankton about the middle of April". The reference of this larva to *Echinocardium flavescens* in any case is uncertain; it should also be pointed out that most probably one more species of Spatangoids must occur in the Irish Sea even if not yet found there, viz. *Echinocardium pennatifidum*, the larva of which is also unknown.[1])

During my two sojourns at the Swedish Zoological Station I made all efforts to fill the gap in our knowledge of the development of our Spatangoids. *Echinocardium flavescens* is not at all uncommon, *Brissopsis lyrifera* exceedingly numerous in localities near the station, so that sufficient material of these two species was available. A considerable number of specimens of the former species was examined during the first days of my stay this summer, but the breeding season was past already (end of July), only quite few eggs and a mere trace of sperma still remaining, with which nothing could be done. It could only be ascertained from the character of the eggs, which are very small and quite transparent, that the species must have pelagic larvæ. The interesting question, how far the larva of this species resembles that of *Echinocardium cordatum* in its main features or it is really identical with the larva figured by Chadwick, and thus differing quite markedly from the *Ech. cordatum* larva, remains then to be solved.

[1]) After this paper was sent to the press I received from Dr. Chadwick a slide with some of the larvæ represented in the figures quoted above. I find that the postoral rod is fenestrated in its outer part, as is the case in the *Brissopsis* larva. Unfortunately, the fully developed larvæ mentioned by Chadwick have not been preserved. It cannot, therefore, be decided, whether Chadwick's larvæ belong to *Brissopsis* or perhaps to *Echinocardium flavescens*.

Of *Brissopsis lyrifera* ripe specimens were found already in the middle of August in 1918, though only few females, the great majority of the females being still unripe. In the summer of 1919 I did not succeed in finding a single ripe female before the 3rd of September, while ripe males were found already on the 1st of August; in the later part of August the males, upon the whole, were so full of ripe sperm that one could not help wondering how they could wait the rather long time till the females would become ripe. — I may mention here that on a dredging trip the first of September 1919 to the inner part of the Gullmar Fjord I observed a number of unusually large specimens of Brissopsis in which the genital organs were quite black, without the slightest indication of sexual products. I have no doubt that these large specimens were really quite senile and had passed the age of sexual reproduction; the matter would be worth while a closer investigation.

In the summer of 1918 artificial fertilization of *Brissopsis* was tried several times, but without success. Again in 1919 I repeated the experiment, but always without succes. The fertilization membrane was formed, but there was no cleavage. Evidently this species is exceedingly sensible, in marked contrast to other Echinoids. It may be suggested that it was the somewhat higher temperature in the laboratory which was unfavorable to the development of the eggs. But this can only be ascertained by renewed experiments.

Since it was thus found impossible to rear the larva from the egg under usual laboratory conditions, there was only the hope of finding it in the plankton. The larvæ of *Echinocardium cordatum* and *Spatangus purpureus* being known, that of *Echinocardium flavescens* being eliminated on account of the much earlier breeding season it might be stated with certainty that, if a new Spatangoid larva turned up in the plankton about the middle of September, it could be nothing else than that of *Brissopsis lyrifera*. This was exactly what happened. By this time a young Spatangoid larva different from that of *Ech. cordatum* (the larva of *Spatangus purpureus* was never met with at Kristineberg) appeared in considerable numbers, and soon more advanced specimens were found; larvæ in beginning metamorphosis were found already about the middle of September in 1918 (— in 1919 they were not found in so advanced stages by that time in accordance with the fact

that the breeding season of *Brissopsis* began that year somewhat later than in 1918 —). There cannot be the slightest doubt that we have then here really the larva of *Brissopsis lyrifera*.

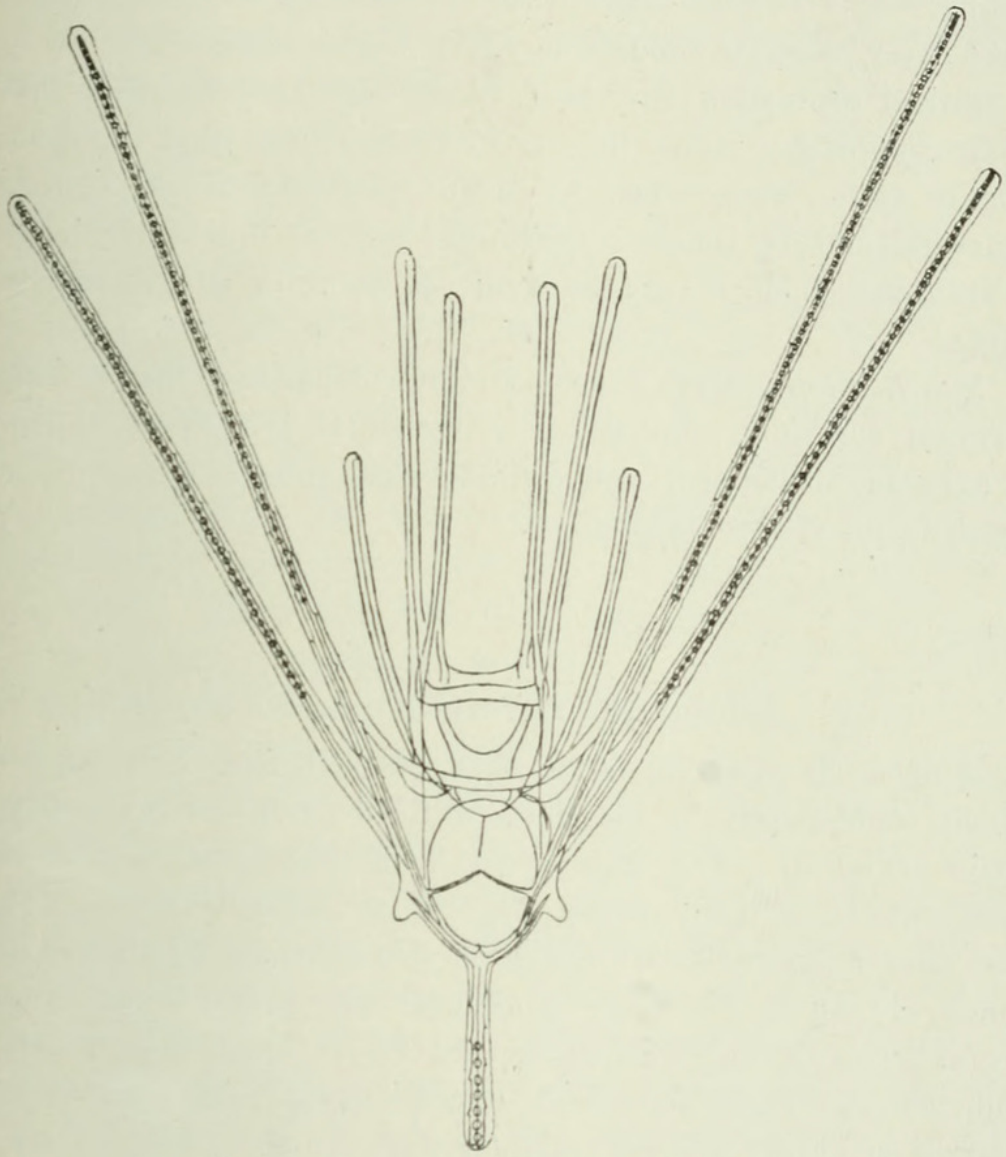

Fig. 2. Larva of *Brissopsis lyrifera*. $^{80}/_{1}$.

The larva is easily distinguished already in its quite young stages from the *Echinocardium* larva by the postoral, postero-dorsal and posterior rods being fenestrated only in the outer part, their basal part remaining unfenestrated; in this character it agrees with the larva of *Spatangus purpureus* and I cannot say at present how to distinguish these two larvæ in the younger stages. The fully formed larva (Fig. 2) is very distinctly characterized by having no postero-lateral arms, only a pair of small ear-

shaped lobes, not supported by a skeletal rod.[1]) (In *Echinocardium* larvæ with the posterolateral arms just beginning to develop and not larger than in the *Brissopsis*-larva, the supporting rod is already distinct, so that they are at once distinguishable). The posterior process is short, hardly as long as the body, in marked distinction from the exceedingly long posterior process of the *Spatangus* larva. (In the *Echinocardium* larva the posterior process varies very much in length, from about body length or somewhat more to quite a diminutive stump; this is not the result of absorption,[2]) as it may be found so short in all different larval stages).

The *Brissopsis* larva is considerably smaller than that of *Echinocardium cordatum*; the colour is the usual: prominent red patches in the ends of the arms and scattered red pigment cells in the body. There is no yellow pigment.

IV. Stichaster roseus (O. Fr. Müller) (?).

Among the Asteroid larvæ observed at Kristineberg was a form which could hardly be identified with any of those previously described (Fig. 3). The fact that it is in beginning metamorphosis shows that it is not a young stage of an *Asterias* larva to develop later into a Brachiolaria form. It is characterized by its processes, which are short, but very contractile and movable like those of the *Asterias* larva. The dorsal and ventral median processes are both well developed and of about equal length; there are no brachiolarian processes and no suctorial disk. All the processes are yel-

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[1]) The same character is found in a Spatangoid larva, which I have from the Gulf of Panama. Further the Spatangoid larva figured by Metschnikoff (Studien über die Entwickelung d. Echinod. u. Nemertinen. Mém. Acad. Imp. St.-Pétersbourg. 7 Sér. XIV. 1869. Taf. VIII) appears to have no postero-lateral arms, not even the small lobes of the skin found in the *Brissopsis*-larva. Metschnikoff refers his larva to *Schizaster canaliferus*. (Cf. Th. Mortensen. Echinodermen-Larven d. Plankton-Exped. p. 107).

[2]) This appears to be the meaning of MacBride (The development of Echinocardium cordatum. Part. I. p. 480).

low in the point and the whole vibratile band is of a faint yellowish tint.

It is perhaps possible to find out to which Asteroid this larva belongs. The Asteroids occurring in the neigbourhood of the Station are the following: *Astropecten irregularis*, *Luidia Sarsi*, *Hippasteria phrygiana*, *Porania pulvillus*, *Solaster papposus*, *S. endeca*, *Henricia sanguinolenta*, *Stichaster roseus*, *Asterias Mülleri*, *glacialis* and *rubens*. Of these are at once out of question: the three *Asterias* species, *Henricia*, the two *Solaster* species, *Porania* and *Luidia*. *Hippasteria* has large and yolk-laden eggs, so that it can be said with certainty that it has no true *Bipinnaria* larva. There are thus left only *Astropecten irregularis* and *Stichaster roseus*. So far as evidence goes the *Astropecten* larva belongs to the type of Bipinnariæ with quite short, not contractile processes. (I have tried to rear the larva but never succeeded in getting suitable material for fertilization). There would then appear to be no other alternative than that we have here the larva of Stichaster roseus. My efforts to try to rear the larva of this species from the egg were in vain,[1]) as I could never get sufficient material of the species, only now and then a single specimen. But at any rate I could ascertain that it has its breeding season at this time (August).

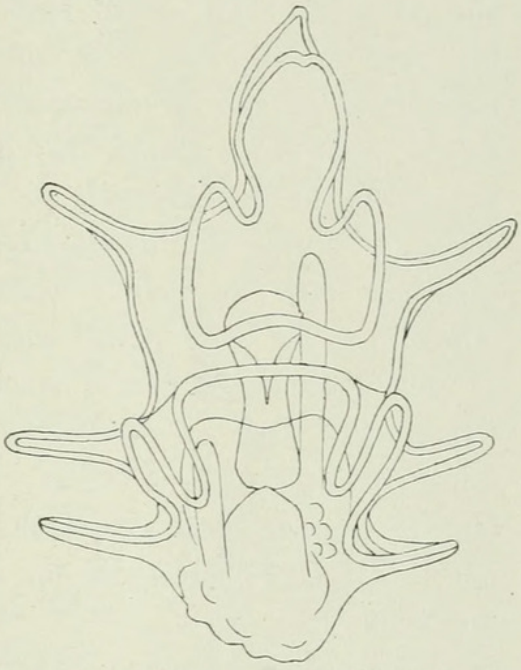

Fig 3. *Bipinnaria* of *Stichaster roseus* (?) $^{60}/_{1}$.

Although thus everything seems to point towards *Stichaster roseus* as the parent species of this larva, nothing definitely can be said about it at present. The rearing of the *Astropecten irregularis* larva would also settle this question.

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[1]) James F. Gemmill has succeeded in rearing the larva from the egg till the young Bipinnaria stage. (Notes on the development of the starfishes *Asterias glacialis* O. F. M.; *Cribrella oculata* (Linck) Forbes; *Solaster endeca* (Retzius) Forbes; *Stichaster roseus* (O. F. M.) Sars. Proc. Zool. Soc. London 1916. p. 562.)

V. Antedon petasus (Düben & Koren).

It might be expected beforehand that the development of this species would present no essential differences from that of its near relatives: *Antedon bifida*, *mediterranea* and *adriatica*, the latter of which species has been so very carefully studied by Seeliger, and is in the text books made the typical representative of Crinoid development upon the whole. Having, however, through my researches on the development of the West Indian Crinoid *Tropiometra carinata*,[1]) found that quite essential differences may occur in regard to development in Comatulids, I thought it well worth while to study the development also of *Antedon petasus* and to ascertain how closely it would agree with the other species of *Antedon* s. str. The result was, indeed, rather suprising.

The breeding season of *Antedon petasus* is mainly in August and September; ripe specimens were, however, found already on the 23rd of July 1919, and that breeding may take place until rather late in the autumn is evident from the fact that I found in January 1910 a Pentacrinoid not yet fully ready to detach itself from the stalk.[2])

I naturally expected to find the eggs and young embryos attached to the pinnules in the same way as in the other species of *Antedon* which have been studied hitherto as regards their development. A great number of specimens were carefully examined, but without success; there was never to be found a specimen with eggs round the genital openings. Although I could hardly believe it possible, I was then forced to the idea that the eggs might be free as in *Tropiometra*. The bottom of the dishes and aquaria in which the specimens were kept was examined and there the eggs were found lying. The surprising fact was thus ascertained (and reascertained many times since) that Antedon

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[1]) A full report on these researches, together with observations on the development of some other Crinoids is given in a memoir: Studies in the development of Crinoids, which will appear in Papers from the Department of Marine Biology of the Carnegie Institution, Washington, Vol. XVI.

[2]) Th. Mortensen. Report on the Echinoderms coll. by the Danmark Expedition at North East Greenland. (Medd. om Grønland. XLV. 1910. p. 250. Pl. X. Fig. 3).

petasus does not carry the fertilized eggs and young embryos on its pinnules, as do the other species of the genus *Antedon* (s. str.) thus far studied as regards their development; the eggs drop at once from the pinnules and fall to the bottom. The fertilization membrane is covered with short spines, almost as a *Callionymus*-egg, very different from the nearly smooth membrane of the other species. Sometimes I have seen the eggs floating in the aquaria and would suggest that in nature the eggs are really not lying on the bottom, the spinous membrane serving as a floating apparatus.

The eggs are ca. 0,15 mm, yellowish-red, opaque. The cleavage is total and regular. After about 20 hours the embryo begins to rotate within the egg membrane, and soon afterwards — generally at the age of about 24 hours — the embryo becomes free, breaking through a hole in the egg membrane (Fig. 4). The empty membranes may easily be found in the dishes and form a very characteristic object.

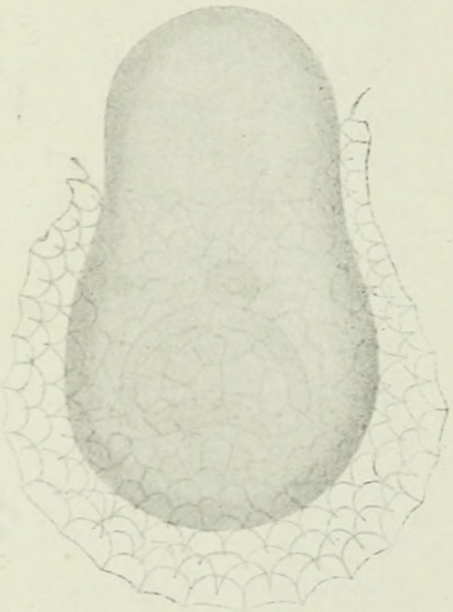

Fig. 4. An embryo of *Antedon petasus* in the act of leaving the egg membrane. 180/1.

The newly hatched embryo is uniformly ciliated, only with a tuft of longer cilia at the anterior end. In the course of the next day the ciliated bands (only 4) are differentiated; the yellow cells appear in considerable numbers, and the larva, seen in diffuse light, forms quite a striking object; the said yellow cells are limited to the interstices between the bands, which appear as broad white lines; only very rarely a yellow cell may be seen lying in one of the bands. The vestibulary invagination appears after about 3 days; it is a wide, shallow deepening, much as in the other *Antedon*-species. No suctorial disk is formed. At the age of 6 days the formation of the skeleton begins.

It was repeatedly observed that the embryos had considerable difficulty in rupturing the egg membrane. I suppose that the lack of movement in the water in the dishes containing the developing eggs is the main cause of this, and this suggestion is supported

by a curious accidental observation, viz. that by sucking the embryos up with a pipette and then squirting them out again with some force they were greatly assisted in rupturing the membrane and becoming free.

A further interesting observation in this connection was made, viz. that those embryos which did not succeed in rupturing the egg membrane did not therefore die at once. On the contrary they continued developing further within the egg, the vibratile bands and the yellow cells appearing at the same age as in the free embryos. In such cases the embryos accordingly reached the same stage within the egg membrane as do the embryos of *Antedon mediterranea* and *bifida* normally before they become free. If not liberated in the way mentioned above they gradually died away, but some of them remained alive even till the age of 6 days.

Although excellent cultures of the larvæ were obtained repeatedly both in 1918 and 1919 I never succeeded in rearing them through metamorphosis. About the time of the beginning formation of the vestibulary invagination they became abnormal, with a median constriction or with the anterior end swollen as if hydrotropic. They might live for many days in this condition, but ultimately died without attaching themselves. Only in comparatively few cases did the vestibulary invagination develop normally, but even such larvæ did not attach themselves; a normal development of the Crinoid skeleton in the larva was not obtained either, only a few calcareous pieces were formed in some cases, which could not be identified with certainty. It could thus not be ascertained in this way, whether infrabasalia are present or not in this species.

As it was thus found impossible to rear the larva through metamorphosis in the aquaria, I made some experiment to obtain the metamorphosis stages by putting the larvæ under more natural conditions. A sort of cage was made of silk gaze just close meshed enough to avoid the passage of the larvæ through the meshes. This cage, containing a good number of larvæ with some Bryozoa and Hydrozoa for eventual attachment, was sunk down to a depth of ca. 25 meters in the neighbourhood of the place where *Antedon* lives in about the same depth. After a week the cage was taken up and the content carefully examined. The result was not much

better than that obtained in the aquaria; not one larva had attached itself, but some of the still surviving larvæ had at least the skeleton much more developed than ever found in the aquaria, though still not quite normal. Although the experiment thus proved a failure, I have little doubt that it must be possible to obtain a good result in this way; probably a much larger size of the cage would be needed. That conditions within the cage were not quite unnatural appears from the fact that the Bryozoa and Hydroids contained in it were found to be in a flourishing condition.

While I was thus unable to get the metamorphosis stages, a fairly complete material of the postlarval stages was obtained. The Pentacrinoids were found attached especially to Hydroids, but also to Bryozoa, worm tubes and other objects from the localities where the adult Antedons abound. It was a rather troublesome work to examine carefully the material from the dredgings, under fairly high power in order not to overlook the important younger stages; but a fairly good series of Pentacrinoids of different stages was the result. It is not the place here to give a detailed description of the Pentacrinoids. It should only be emphasized that a careful study of the younger stages revealed the fact that Infrabasalia are present in this species. On dissolving the calyx of young Pentacrinoids by means of hypochlorite of sodium under the microscope it is seen that there are 3 small, equal-sized infrabasalia, forming a small ring which lies wholly inside the basalia, so that it is impossible to observe it on intact specimens. This fact led me to the wrong statement (Echinoderms of North East Greenland, p. 251) that infrabasalia are not found in this species. The development of the anal plate and the adjoining radial is in full accordance with the observations regarding this point I have made on other Crinoids, as described in the memoir referred to above. The conclusions arrived at there with regard to the question of the alleged homology between the anal plate of Comatulids and the radianal of older Crinoids are thus fully born out by the observations on the Pentacrinoids of the present species also.

Regarding the development and transformation of the inner organs I cannot give a satisfactory account. This species proves to be a most unfavourable object, especially because of the small size of the histological elements and the unusually small content

of chromatin substance in the nuclei, which makes it very troublesome to obtain a satisfactory staining of the sections. To this must be added the difficulty in orientating the embryos by the sectioning; while no orientation at all is possible on embryos still lying within the egg membrane, it is possible, of course, to arrange the sections of the free embryos in transverse or longitudinal direction, but it is only after the formation of the vestibulary invagination that it is possible to direct the longitudinal sections in the sagittal or frontal plane. Considering furthermore the tendency of the larvæ in the aquaria-cultures to grow abnormal, there is only too much reason for the incompleteness of the record of the developmental processes of this larva.

As soon as the blastula is formed, after about 6 hours, the formation of the mesenchyme begins, and the blastocoel cavity is soon filled with a dense mass of mesenchyme cells. The gastrula invagination does not occur till a much later stage, about the time when the embryo is about to leave the egg membrane, and the blastopore — which is very small — does not close until the embryo has become free. The invaginated portion is not a simple sac, but, while still remaining in open connection with the exterior, is flattened in the longitudinal axis. The later subdivisions of the invaginated portion I have been unable to trace with certainty; I would only say that it is intentionally that I do not call the invaginated portion the archenteron, because I am not at all sure that the stomach derives from this part. In fact, there are indications of more than one invagination taking place, in which case probably the enterocoel vesicles alone develop from the invagination mentioned. The enterocoel vesicles do not shift their position in quite the same way as in *Antedon mediterranea* — and the other Crinoids thus far studied (see the authors memoir quoted above) —; at the time when the vestibulary invagination is forming, the two vesicles are still lying in their original position, on the right and left side of the embryo, the mesentery between them being in the posterior midline. Regarding the formation of the hydrocoel, parietal canal etc. I do not venture to put forth any statements.

It is evident already from the few facts recorded here that the development of this species differs so markedly from its supposed

near allies, *Antedon mediterranea*, *adriatica* and *bifida*, that one cannot help suggesting that the relation of *A. petasus* to those species may not be so close after all, and that it may perhaps not rightly be referred to the same genus. This is, however, not the place to discuss this question. — In any case, it has been shown that we have here another instance of unexpected great diversity in fundamental developmental processes in related forms, a striking illustration of the danger in generalizing from a single case, as it has been done especially in the case of Crinoids, *Antedon adriatica* being generally taken to represent the type of the development in Crinoids upon the whole. — A full report on the development of this species would be of the greatest interest. Unfortunately the material available does not suffice for doing so.

While in the normal development the egg undergoes a total, regular cleavage, a curious abnormal modus of development is only too commonly observed in the cultures, viz. that only the nuclei divide, lying free in the egg substance, which does not show any indication of cell limits, forming thus a syncytium. There may be found quite a number of nuclei lying in a fairly regular layer near the surface, and in later stages also some in the inner part of the egg. The development, however, does not go any farther, and the eggs die off.

There can be no doubt that this abnormal development is due to the unnatural conditions of the aquaria and most probably to the too high temperature, so that by future researches it would be advisable to keep the cultures at a lower temperature, corresponding to that normally occurring at the depth, where Antedon lives. A quite analogous case is described for *Cucumaria frondosa* by Des Arts;[1]) moreover it was observed for *Antedon* as well as for *Cucumaria* that a partial disintegration of the egg may take place, the rest developing into a pygmæ larva.

The abnormal development described above recalls that which I have found to occur normally in another Crinoid, *Isometra vivipara*, a detailed description of which will be found in the memoir referred to above. Also in a number of other Echinoderms I have

[1]) Louis des Arts. Über die ersten Entwicklungsstadien von Cucumaria frondosa unter Berücksichtigung einiger anormaler Verhältnisse. Bergens Museums Årbok. 1910. No. 13.

found this modus of development to occur, e. g. in *Cucumaria glacialis*, *Amphiura vivipara* and in some Echinoids, all of them being viviparous, with large yolk-laden eggs. (In the viviparous *Amphipholis squamata*, which has small eggs, the cleavage is total and regular; it is then not the viviparity alone that causes this peculiar modification of the clevage). Des Arts (Op. cit. p. 12) refers to my description of the cleavage stages of *Cucumaria glacialis* and suggests that „es ist nicht unwahrscheinlich, dass die von ihm beschriebenen Fälle ebenfalls auf Syncytienbildung zurückzuführen sind", which must mean that he thinks it an abnormal development, analogous to that found by him to occur in eggs of *Cucumaria frondosa* reared under abnormal conditions in aquaria. Of course, such an interpretation is entirely out of question. The material on which my observations on the development of *Cucumaria glacialis* — as well as that of the other Echinoderms mentioned above with a similar modus of development — rests, does not proceed from aquaria cultures, but was taken directly from specimens found in their natural surroundings. Especially the detailed account of the development of *Isometra vivipara* will afford the proof that this is the normal modus of development for the said forms — but not for *Cucumaria frondosa* and not for *Antedon petasus* either.

VI. On the nervous system of Echinoderm larvæ.

In my work „Die Echinodermenlarven der Plankton-Expedition" I have figured and mentioned (p. 100. Taf. IX. Fig. 3—4) a regular, close series of nuclei lying on each side across the corners of the anal area of the larva of *Echinocyamus pusillus*, from the postoral band down towards the place where the band passes from the side of the anal area out along the postero-dorsal arm. On account of the analogy with the larval nervous system of the *Auricularia* larva, as described especially by Semon, I suggested that it must represent a larval nervous system. As *Echinocyamus*-larvæ were rather plentiful in the Plankton during all the time of my stay at the Swedish Zoological Station, I undertook a closer examination on the living larvæ of the supposed nervous system. The larvæ have the habit of standing very quietly just below the surface of

the water, with the point of the arms resting against the underside of the surface film (— I suppose the fact that the cilia of the arms are directed upwards, as well seen on the figures in Théel's Monograph of the development of *Echiocyamus*, e. g. Pl. VI. Fig. 87 —, accounts for this; the ciliary movement must then evidently produce an upward movement —). They may be found to rest so steadily in this position that it is possible to examine them with the microscope (placing them in a small dish directly under the lens), and I have thus been able not only to examine them from above with a rather high magnifying power, but even to make a camera-drawing thereof. (Fig. 5). The observation of the larva in this position disclosed a peculiar semicircular band of nuclei closely arranged in a regular linear series, lying in the epidermis of the oral area, below the postoral transverse band and proceeding from there on each side in an arc towards the sides of the oral lobe, where it disappears. That this is really a larval nervous system, homologous with that of *Auricularia*, I have no doubt, although I have not histologically demonstrated its nervous character. The general structure is the same as that of the Auricularian nervous system, and as in *Auricularia* it lies in the circumoral area, the main difference being that in the *Echinocyamus* larva it is an unpaired organ, while in the Auricularia's it is a paired structure; also it is formed of a double series of cells in *Auricularia*, of a single series in the *Echinocyamus* larva. The position assigned to this nervous system in the first description, mentioned above, is a mistake, due to the fact that the object was seen from the ventral side; in that view no clear idea could be gained of its true position.

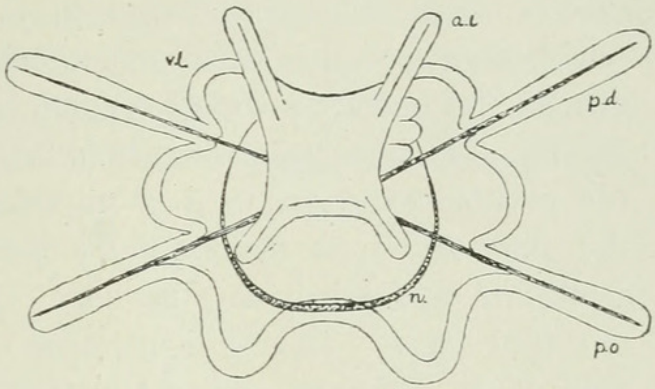

Fig. 5. Larva of *Echinocyamus pusillus*, seen from above. $^{85}/_{1}$. a.l. antero-lateral arms; p.d. postero-dorsal arms; p.o. postoral arms; n. nervous system.

Having found this structure in the *Echinocyamus* larva I naturally looked for it also in the other Echinoid-larvæ available, viz. *Echinus esculentus*, *Psammechinus miliaris* and *Echinocardium cordatum*. In none of them I was able to discover anything cor-

responding to what was found in the *Echinocyamus* larva. In these larvæ a quite different nervous system, lying at the upper side of the oral lobe, was discovered by MacBride.[1]) I regret not having examined the living *Echinocyamus* larva with regard to the possible existence in it of an apical nervous system like that of the other larvæ; in the preserved specimens I have not been able to find it, whereas it may be very distinctly seen in the *Echinocardium* larva. This is a point of no small interest — whether both these different nervous systems may occur together in the same larva or the one excludes the other, and how the matter lies in the different larval forms of Echinoids. Further researches are required to solve this question.

In the Ophiurid larvæ a larval nervous system, homologous with that of the Auricularias, was described by Metschnikoff.[2]) In my memoir on „Die Echinodermenlarven d. deutschen Südpolar-Expedition[3]) I gave a careful description and figures of the nervous system of *Ophiopluteus gracilis* (p. 90—91; Taf. XIII. Fig. 4—6; Textfig. 4). During my stay at the Swedish Zoological Station I took the opportunity of examining this structure on the living larvæ. Like the *Echinocyamus* larva they can easily be examined from above, when standing directly under the surface film; they do not, however, keep so quiet as to allow a camera drawing. The two figures, 6 and 7, represent the larvæ of *Ophiura texturata* and of *Ophiocoma nigra* drawn in this position. The nervous system is seen as a series of nuclei in the bottom of the oral region passing between the corners of the postoral and the preoral band. It is, of course, only the small middle part of the nervous band that can be seen in the view from above. Fig. 8 gives a diagrammatic representation of the arrangement of the two nervous bands in the Ophiurid larvæ.

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[1]) E. W. MacBride. The development of Echinus esculentus, together with some points in the development of E. miliaris and E. acutus. Philos. Transact. Ser. B. Vol. 195. 1903. p. 302.
E. W. MacBride. The development of Echinocardium cordatum. Part. I. The external features of the development. Quart. Journ. Micr. Sc. 59. 1914. p. 480.

[2]) E. Metschnikoff. Embryologische Mitteilungen über Echinodermen. Zoolog. Anzeiger. 1884. p. 47.

[3]) Deutsche Südpolar-Expedition 1901—1903. Zoologie VI. 1913. p. 91.

I found this nervous system in all the typical Ophiurid larvæ which occurred during the time of my visit to the station, viz. besides the two figured, the larvæ of *Ophiura albida*, *Amphiura filiformis*, *Ophiothrix fragilis* and the *Ophiopluteus compressus*.

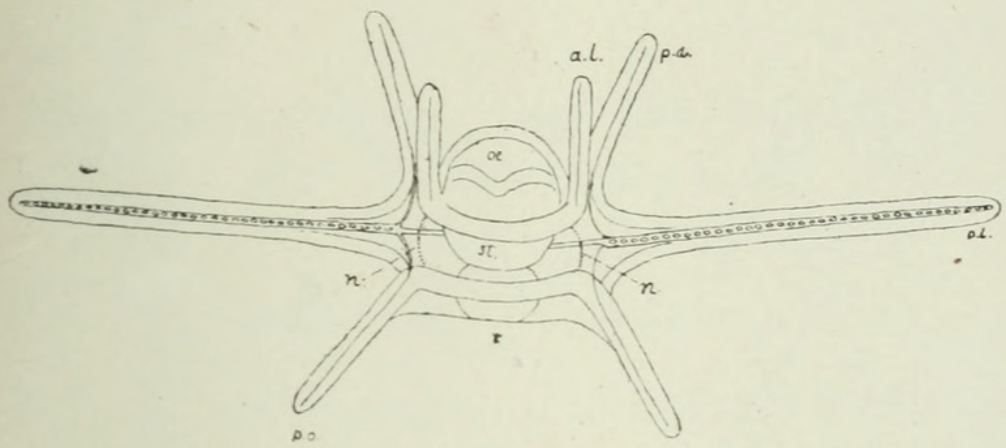

Fig. 6. Larva of *Ophiura texturata*, seen from above.

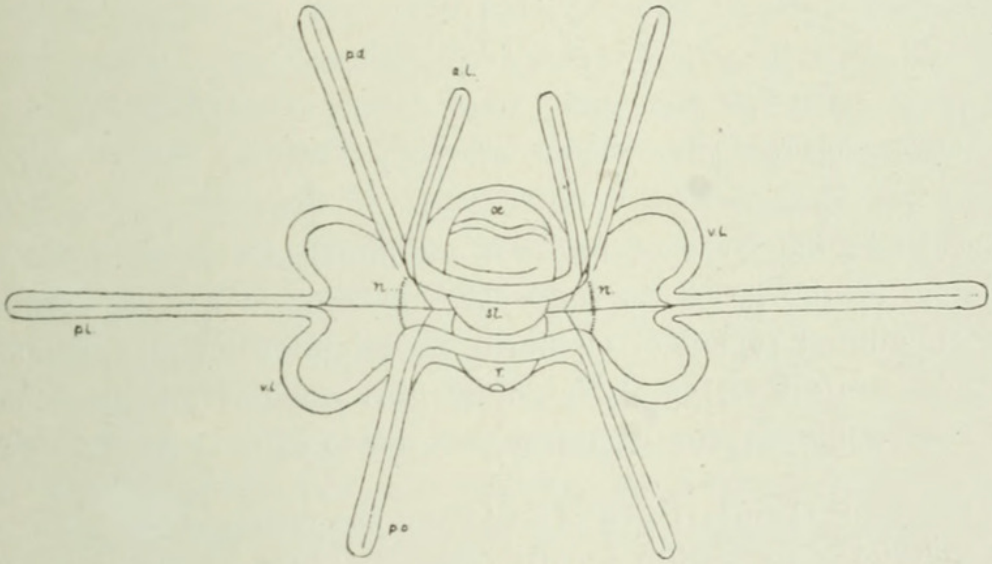

Fig. 7. Larva of *Ophiocoma nigra*, seen from above.
a.l. antero-lateral arms; n. nervous band; oe. oesophagus; p.d. postero-dorsal arms; p.l. postero-lateral arms; p.o. postoral arms; r. rectum; st. stomach; v.l. vibratile lobe.

Further I have found it in a great number of different Ophiurid larvæ in a preserved state, more or less distinctly. I have then no doubt that this is a structure found in all typical Ophiurid larvæ.

It is a very remarkable fact that, while a special larval nervous system is thus developed in both Holothurioid, Echinoid and