CONTRIBUTIONS
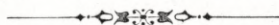
TO

THE STUDY OF THE DEVELOPMENT AND LARVAL FORMS OF ECHINODERMS IV

BY

TH. MORTENSEN

WITH PLATES I—XII

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CONTRIBUTIONS

TO

THE STUDY OF THE DEVELOPMENT AND LARVAL FORMS OF ECHINODERMS

IV

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WITH PLATES I—XII

The present fourth "Contribution to the study of the development and larval forms of Echinoderms"[1] comprises the results of studies carried out from July 1st to September 12th 1937 at the Marine Biological Station of the University of Egypt, at Ghardaqa on the Red Sea Coast, in continuation of the studies made there from April 28th to June 27th 1936.

It is a very agreeable duty to me to renew my sincere thanks to the authorities of the Egyptian University, Cairo, for the hospitality offered me in placing the facilities of this excellent laboratory at my disposal again this summer. In particular I beg to tender my thanks to the authorities of the University for allowing the demonstrator of Zoology of the University, KHALAF EL DEWEINI, B. Sc., to act as my assistant during the whole of my stay. This was of the greatest importance to me, since the cultivation of the many different larvæ requires a great amount of work, much more than is possible for one. KHALAF Eff. proved a very capable and very much interested assistant and companion, and I beg to extend my cordial thanks to him, expressing the hope that he also had some profit of his work with me, and that he may get some opportunity of continuing in the future these studies of the development of the Echinoderms of the Red Sea. Likewise I beg to tender my cordial thanks to the director of the Station, Dr. CYRIL CROSSLAND, who together with Mrs. CROSSLAND made all efforts to help me in every way, and to make my stay at Ghardaqa this year a no less delightful experience than was my stay there in the summer of 1936.

Last, not least, my sincerest thanks are due to the Carlsberg Foundation for the grant which enabled me to undertake this second voyage to the Red Sea.

The fact that last year I found a considerable number of species not to have ripe sexual products even up till the end of June made me expect that I would find these species to have their breeding season in high summer, viz. the months July and August, perhaps also September, so I had to arrange for staying at the station during these months. To a great extent my expectations came true — still, a good number of species were not yet ripe by the time I had to leave the station, September 12th. This holds good of such species as *Brissopsis luzonica* (Gray), *Phyllacanthus imperialis* (Lamarck), *Ophiocoma valenciæ* (Müller & Troschel), and *Ophiothrix hirsuta* Müller & Troschel — the development of all of which I was very anxious to study. They showed signs of becoming ripe by the end of September (probably by full moon), or perhaps not even till October. Other species did become ripe in July or

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[1] "Contributions" I—II were published in 1931 in 9. Ser. Vol. IV. 1, „Contributions" III in 1937 in 9. Ser. VII. 1 of these Memoirs.

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August, but resisted all my efforts to induce them to spawn or to make artificial fertilization of them — as e. g. *Holothuria atra* Jäger, one of the commonest of the Holothurians at Ghardaqa, these large, black sea-cucumbers which occur in great numbers all over the littoral reef-flat, lying almost dry at low tide. I kept them in great numbers in the tanks of the laboratory, also in the large outside-tank, but they would not spawn, although it was their breeding time, and repeated experiments in undertaking artificial fertilization of them all failed, the eggs never ripening in spite of being left at varying lengths of time in the water, with or without the adding of NaOH (or KOH) to the water. As mentioned in my "Contributions" III, p. 9, Hørstadius succeeded in getting a large number of eggs of *Holothuria Poli* D. Ch. fertilized by means of raising the pH of the water, so I was expecting to get similar good results with the Red Sea Holothurians. This was, however, by no means the case. I tried with a number of different species, also some Asteroids, but never found a larger percentage of eggs to have ripened in the dishes with raised pH than in the control dishes to which no NaOH had been added — whereas I found it constantly necessary to raise the pH of the water in order to induce the spermatozoa of Asteroids to move.

Special mention must be made of *Phyllacanthus imperialis* and *Asthenosoma varium*, two species the development. of which I was particularly anxious to study. The fine. large Cidarid *Phyllacanthus imperialis* is quite common on the reefs at Ghardaqa, usually concealed in the crevices between the coral blocks. I have examined great numbers of them as to sexual maturity, last year in May—June, this year in July—September, and never found any of them fully ripe. On the 31st of July I found a single female with the ovaries full of apparently ripe eggs — large, c. 0.5 mm in diameter, yellowish-white, rich in yolk, floating at the surface. Only in one specimen did I find a trace of ripe spermatozoa, which I thought might suffice for fertilizing at least some of the eggs — but no fertilization occurred, very probably because the eggs were not yet fully ripe for fertilization; at least, I thought I could discern the nucleus in the opaque eggs. Later on I never found a single ripe female, and only some few males with some spermatozoa — whether spent or only in beginning maturity I could not make out definitely. In September some specimens had the appearance of being in incipient maturity, so it is likely that by the end of September (at full moon?) a number of specimens would be ripe; but more probably the real breeding season will be in October. Both large and smaller specimens were examined, with the same negative result. It was a great disappointment to me that I could not study the development of this Cidarid. That it will be possible to fertilize the eggs artificially may be concluded from the fact that this was achieved with the closely related Australian species *Phyllacanthus parvispinus* Tenison Woods, which has also large, yolky eggs, which float at the surface. The very remarkable young development stages of this latter species (cf. my "Studies of the Development and Larval forms of Echinoderms". 1921. p. 24, Pl. V. 3—4) indicate that the development of these *Phyllacanthus* species may probably be abbreviated.

Asthenosoma varium Grube, as one of the family of the Echinothurids, in my

opinion the direct descendants of the Palæozoic Lepidocentrids, will no doubt show features of the greatest interest in its development, particularly postembryonally. I was therefore very anxious to study the development of this species — but here again all my efforts were in vain. The eggs are large, c. 0.8 mm, red, and quite intransparent, on account of their rich content of yolk, for which reason they also float at the surface like the eggs of *Phyllacanthus*. Females with apparently ripe eggs were found repeatedly during the whole time of my stay this summer, as also specimens with quite young eggs, and such as were evidently spent, so that the species appears to have no definite breeding season. Specimens with ripe spermatozoa were also found most of the time, but only a small amount of sperma; not till the 10th of September did I find a single male with the testes full of ripe spermatozoa, which might indicate that *Asthenosoma* breeds mainly towards the end of the summer, September—October. Fertilization was tried many times, but always without success. The trouble is, with this species as with all those species with large, yolky, intransparent eggs, that it is impossible to see whether the eggs are ripe for fertilization or not. Sections of supposed ripe eggs show the presence of a large distinct nucleus, which explains why no fertilization took place. I have also tried to keep the eggs for varying lengths of time, up to 24 hours, in the water before adding sperma, and in water with added KOH, but always without success. I think it will be found that for obtaining fertilization of this species it is necessary that the eggs are shed by the female itself, not taken out of the ovary. There is here again the difficulty that *Asthenosoma* is very hard to keep alive in the tanks; most specimens are found more or less

Fig. 1. Spermatozoa of *Asthenosoma varium* Grube. × 850.

injured in the trawl, and such will remain alive for only a few hours; but even specimens in fine condition I have been unable to keep alive in the tanks for more than one day. The only possibility for getting normally shed eggs of *Asthenosoma* would seem to be that intact specimens might spawn directly when put from the trawl into a container with water — as I have repeatedly found it to occur with various species of Holothurians.

It is of no small interest that the spermatozoa of *Asthenosoma varium* have a very long and slender head (fig. 1), thus differing considerably from the usual type of spermatozoa of Echinoderms. Also the spermatozoa of *Phyllacanthus imperialis* are somewhat elongate, but not nearly so much as those of *Asthenosoma*.

Besides *Phyllacanthus* and *Asthenosoma* there was quite a number of other species the development of which I failed to get; some of them for want of sufficient material, others because they would not spawn, artificial fertilization being impossible. The latter was the case with a small Comasterid, *Comissia Hartmeyeri* A. H. Clark[1], common on *Lobophyllia*, on the reefs off the laboratory. The specimens were ripe, and lived perfectly well for more than a month in the tank under running

[1] Identification due to Professor GISLÉN, Lund, Sweden, for which I beg to thank.

water, even regenerating lost parts of arms; but they would not spawn — a very regrettable fact, since till now the embryonal development is not known of any Comasterid.

The small Ophiuran *Ophiura Kinbergi* Ljungman is quite common off Abu Sadaf on sandy bottom at a depth of c. 5—10 fathoms. I tried repeatedly to keep it alive in dishes with sand on the bottom and thus induce it to spawn, ripe specimens being found both in July and August; but whereas *Ophiolepis cincta* did spawn under similar conditions, *Ophiura Kinbergi* would not, to my great regret, both because it would be of the greatest interest to learn to know the larvæ of other species of the great genus *Ophiura* than the few species of the North Atlantic the larvæ of which are known till now, and also because the eggs of this species, unique (so far as known till now) by having a small red spot, almost like an oildrop, would seem to indicate its development to be of unusual interest. — Another Ophiurid, *Ophionereis dubia* (Müll. & Troschel) likewise would not spawn, though it lived quite well in the dishes for a long time.

The giant Synaptid *Synapta maculata* Chamisso & Eysenhardt, up to c. 5 metres long, I tried repeatedly to keep alive for spawning in the tanks. At first it did not live well in the tanks, because it does not tolerate it well to be hurt and lose a large part of its body, as does *Opheodesoma grisea*, — and because of its huge, disgustingly adhesive anchors it is quite difficult to extricate the specimens undamaged from one another when (— as is usually the case —) brought home by the sailors in an almost inextricable bunch. At length I succeeded in getting a small number of complete specimens, which then lived very well in the tank for some weeks, their long snake-like bodies creeping over one another without becoming entangled. They offered a glorious sight — but did not spawn, very naturally, since when I opened them in the beginning of September I found them to be quite unripe — probably spent long ago. Their breeding season must be either in June—July or late in September—October. Now that it is known how they can be kept alive in the tank, it will probably be possible to induce them to spawn. The study of the development of this species will be of great interest, especially in view of its possible relation to the remarkable *Auricularia nudibranchiata* (cf. "Contributions" III. p. 54). The species does not seem to be hermaphrodite as is *Opheodesoma grisea*.

Holothuria curiosa Ludwig is fairly common at Ghardaqa, particularly on grass-bottom at a depth of a few fathoms. Repeatedly I had a number of specimens standing in large dishes for eventual spawning. Twice they did spawn, but only the males, the females kept together with them happening to be either spent or unripe. Another time all the specimens happened to be females — there being no means of ascertaining the sex of the intact specimens. Artificial feritilization I could not try, never having a ripe female and a ripe male at the same time. — This species is remarkable for its Cuvierian organs; only a single thread is thrown out at a time, but it is very long, about one meter at least, and unusually thick, c. 1 mm in diameter. It is evidently a very effective means of defence.

Another Holothurian which I kept in vain in the tanks for spawning was *Holo-*

thuria edulis Lesson; as the specimens were all rather small, scarcely more than c. 15 cm long, they may have been too young (none of them were found to contain ripe sexual products). They, however, afforded an opportunity for an interesting observation. They would be seen rising perpendicularly from the bottom, standing on the posterior tip of the body, and then turning slowly round, quite gracefully, as if they were dancing. No doubt the meaning of this was to find some new place of support. They may even release their hold on the bottom and float freely at the surface of the water, moving quite slowly, not actively swimming. I am not aware that such a way of moving has till now been observed in this or any other Holothurian[1].

A Holothurian the development of which it would have been of great interest to study is *Holothuria pleuripus* Haacke. This peculiar small, white Holothurian, which resembles, indeed, much more a naked land-snail, like *Vaginulus*, than a *Holothuria*, is rather commonly found attached to the underside of stones on the littoral reef-flat at Ghardaqa. I kept a considerable number of them in a dish under a water-tap, where they lived very well for quite a long time, but no spawning took place. In the several specimens which I opened I found no ripe sexual products, thus apparently August, at least, is not its breeding time.

Of *Labidodemas semperianum* Selenka only very few specimens were found, and only one at a time, so there was no possibility of studying the development of this very interesting Holothurian.

Once on the reef at the small islet Fanadir, a few miles from the station, I got two specimens of the beautiful seastar *Mithrodia clavigera* (Lamarck). They proved to be ripe, but both of them males. They were kept alive in the tank for more than a month, in the hope that a third, possibly female, specimen might be found. But no more specimens were found. — Another day a fine large specimen of *Leiaster Leachi* (Gray) was brought home by the sailors, likewise from Fanadir. It was a ripe female, and it was likewise kept quite a while in the tanks waiting for a hoped for male — but no more specimens of this species turned up.

From all the difficulties thus met with it was evident that the number of species, the development of which could be studied, could not possibly reach the record number of 30 species of last summer's researches. It is only surprising that it did amount to 18 species (two of them partly studied already last year). The total number of species of Echinoderms studied as regards their development during my two visits to Ghardaqa thus amounts to no less than 46. It may well be said that nowhere in the world has so large a percentage of the local Echinoderm fauna been made known in regard to the development as that of the Northern part of the Red Sea, a fact bearing radiant witness to the excellent conditions for such studies offered by the Ghardaqa laboratory.

The species, the development of which was studied this summer (1937) are the following:

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[1] I am indebted to KHALAF Eff. for calling my attention to this curious habit of *Holothuria edulis*. The tank in which the specimens were kept was in another room than that in which I was working, so that if he had not seen it, I should probably have missed making this interesting observation.

1. *Prionocidaris baculosa* (Lamarck). Reared through metamorphosis.
2. *Laganum depressum* L. Agassiz. Reared through metamorphosis.
3. *Echinodiscus auritus* Leske. Reared through metamorphosis; larvæ reared till nearly full size last year.
4. *Luidia Savignyi* (Audouin). Reared through metamorphosis.
5. *Fromia ghardaqana* Mrtsn. (n. sp.) Reared through metamorphosis.
6. *Pentaceraster mammillatus* (Audouin) Reared through metamorphosis.
7. *Linckia multifora* (Lamarck). Reared to metamorphosis.
8. *Echinaster purpureus* (Gray). Reared to metamorphosis.
9. *Ophiothrix Savignyi* (Müll. & Troschel). Reared through metamorphosis.
10. *Ophiolepis cincta* (Müll. & Troschel). Reared through metamorphosis.
11. *Synaptula vittata* (Forskål). Reared through metamorphosis. Young larva reared last summer.
12. *Opheodesoma grisea* (Semper). Reared to near metamorphosis.
13. *Holothuria impatiens* (Forskål). Reared through metamorphosis.
14. *Holothuria pardalis* Selenka. Reared to full larval shape.
15. *Holothuria papillifera* Heding (n. sp.). Reared to full larval shape.
16. *Holothuria difficilis* Semper. Reared through metamorphosis.
17. *Holothuria* (*Microthele*) *nobilis* (Selenka). Reared to young larva.
18. *Heterometra Savignyi* (Joh. Müller). Reared to young Pentacrinoid.

I am indebted to Mr. S. G. Heding for the identification of the Holothurians.

Foremost among these species, in regard to the importance of the results achieved easily ranks *Prionocidaris baculosa*, the first Cidarid reared through metamorphosis. Especially the fact now disclosed that the young Cidarid actually passes through an *Archæocidaris* stage, having a pluricolumnar interambulacrum, is of the highest importance, raising beyond doubt the suggestion of *Archæocidaris* being the ancestor of the Cidarids s. str.; that it is in direct opposition to the theory of *Bothriocidaris* being the ancestor of the Echinoids need hardly be pointed out.

That the *Prionocidaris* larva closely resembles the other Cidarid larvæ known till now, thus corroborating the result reached through last year's researches ("Contributions" III) that the Cidarid family has a larval type of its own, is, of course, a fact of considerable importance. Of great interest is also the observation of the active movements of its long arms, and the complicate muscular system that makes these movements possible. Further the rather common normal occurrence of one-egged twins in this species is an embryological fact of quite unusual interest, being a rather unique case of nature itself making embryological experiments.

Among the Asteroids studied *Luidia Savignyi* and *Fromia ghardaqana* are of particular interest, the former in supporting the assumption that the family of the Luidiids has a larval type of its own, but at the same time showing that within this larval type there is a marked gradation from a primitive form of small size, the larval body of which is resorbed on metamorphosis, to the highest specialized form (the larva of *Luidia Sarsi*), which grows to a very large size, the larval body being thrown off, not resorbed, on metamorphosis.

Fromia ghardaqana is very interesting in being a protandric hermaphrodite, a rather rare case among Asteroids, and in having abbreviated development, the larva being a rudimentary Brachiolaria. Also in regard to the cleavage it is of unusual interest, belonging to the type in which the nuclei are at first scattered irregularly in the undivided yolk-mass. This type of cleavage, which was not hitherto known in Asteroids, has now been proved to exist in all Echinoderm classes: in the Holothurian *Cucumaria glacialis* Ljungman, in the Ophiuran *Amphiura vivipara* H. L. Clark (= *Amphiura Stimpsoni* Lütken), in the Echinoids *Hypsiechinus coronatus* Mrtsn., *Amphipneustes Koehleri* Mrtsn., and *Abatus cavernosus* (Philippi), and in the Crinoid *Isometra vivipara* Mrtsn.[1] All these forms have large eggs, rich in yolk — which fact does not, however, mean that all Echinoderms with large, yolky eggs have this type of cleavage. Thus e. g. *Echinaster purpureus* Gray, with large, yolky, black eggs, has total and regular cleavage.

Among the Holothurians the giant Synaptid *Opheodesoma grisea* (Semper) is particularly interesting in being a hermaphrodite and capable of self-fertilization. The various *Holothuria* larvæ described here corroborate the result reached last summer ("Contributions" III) that the formation of elastic balls at metamorphosis is a feature common to all these larvæ, and that the general shape of the larvæ within the family of the Holothuriidæ is so similar in all of them that specific characters hardly exist, except in the shape of the calcareous bodies in the posterior end of the larva. These latter, however, appear to afford important systematic characters, as evinced e. g. by the fact that the larva of *Microthele nobilis* differs conspicuously herein from that of *Holothuria difficilis*, likewise referred to the genus *Microthele* on account of the character of its spicules, but in spite of the fact that in general appearance it differs so strikingly from *M. nobilis* that anybody who has had an opportunity of seeing the two species alive together would protest against the idea that they could be congeneric — and the character of their larval spicules is in full agreement therewith.

The duration of the larval life, mind well within one and the same species, may be subject to great variation, as pointed out in my "Contributions" I. p. 23—24, and III. p. 32—33, with regard especially to *Tripneustes gratilla* and *Echinometra Mathæi*. It was found e. g. that at Mauritius the larva of *Tripneustes gratilla* was only about to begin to reach the second larval stage at the age of 30 days, whereas at Ghardaqa it was in beginning metamorphosis at the age of 18 days. Similarly the larva of *Echinometra Mathæi* was found by ONODA (1936) to take 40 days from fertilization to metamorphosis in Japan, whereas I found the same species at Ghardaqa to reach its full larval shape in about 18 days, thus in only about half the time

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[1] Cf. the author's papers "Zur Anatomie und Entwicklung von *Cucumaria glacialis* (Ljungman)" (Zeitschr. f. wiss. Zool. LVII. 1894); "Studies in the development of Crinoids" (Papers from the Department of Marine Biology, Carnegie Inst. XVI. 1920. p. 32 and 34. Pl. XlV); "Studies of the development and larval forms of the Echinoderms". 1921. p. 177. Pl. XXXI. 7—8; and my Report on the Echinoidea of the Swedish S. Polar Expedition. 1910. p. 75.

it took in Japan. I suggested ("Contributions" III, loc. cit.) that temperature and the amount of food available to the larvæ might account for this great difference in the duration of the larval life (cf. also my "Studies of the development and larval forms of the Echinoderms". 1921. p. 245).

The observations recorded in the present report, particularly on *Holothuria impatiens* and *difficilis*, (cf. pp. 53—54 and p. 56), prove that in these cases the reason for the prolonged duration of the larval life cannot possibly be sought in temperature, which remained the same all the time, it can only be due to lack of food, as also evidenced by the fact that, when the food supply (in the case of *Holothuria impatiens*) again became normal, metamorphosis promptly occurred. This does not imply that temperature may not play the same rôle, as would seem beyond doubt in the case of *Echinometra*.

But in other cases neither temperature nor scarcity of food can be the reason for the prolonged duration of the larval life. This applies to the *Prionocidaris* larvæ, which were constantly carefully attended to, the water being shifted every day, and further to such cases where the larva does not feed, but subsists on the yolk-substance of the egg, e. g. *Fromia ghardaqana* and *Heterometra Savignyi* (and apparently all Comatulids with free-swimming larvæ). As mentioned on p. 39, some of the *Fromia* larvæ metamorphosed at the age of 16 days, while others went on swimming for 2—4 weeks more before attaching themselves and metamorphosing. In *Heterometra* a number of the larvæ attached themselves and metamorphosed into Pentacrinoids already at the age of 2 days, others not attaching themselves till about 1—2 weeks later. Even a good number of larvæ of both these two species would not attach themselves at all for metamorphosing, but went on swimming, gradually deteriorating and perishing. In these cases the reason for the failing metamorphosis of the larvæ can hardly be anything but that they did not find any place to their liking for attaching themselves to.

These observations have an important bearing on the very interesting problem: do these larvæ all find a suitable place to attach themselves to for metamorphosis under natural conditions? Considering the immense number of eggs shed by a single female specimen, one would expect to find both adults and young specimens to be exceedingly common; but even though the said species are fairly common, particularly *Heterometra*, their number is nothing in comparison with the number of the eggs. That many of such conspicuous eggs and embryos as those of *Fromia* and *Heterometra* are eaten by young fishes and other organisms can scarcely be doubted; but it would seem equally probable that great numbers perish because they cannot find a suitable place to attach themselves to — especially, of course, if they are carried out with the currents to the open sea. — The latter case, of course, holds good of all larvæ which are carried so far out to sea by the currents that when metamorphosing and sinking to the bottom they do not find suitable conditions (depth, kind of bottom etc.) for living in such places.

These observations together with those on the *Prionocidaris* larva mentioned below, p. 18, are in conformity with the highly interesting results reached by

DOUGL. P. WILSON & DAY in their studies on the relation of the substratum to the metamorphosis of *Scolecolepis fuliginosa* and by DOUGL. P. WILSON in his researches on the influence of the substratum on the metamorphosis of the *Notomastus* larvæ (J. Mar. Biol. Assoc. XIX, 1934 and XXII, 1937).

The scarcity of the adults in comparison with the immense numbers of eggs produced cannot, however, in many cases at least, be explained either by the larvæ not finding a place to attach themselves, or not finding suitable conditions when sinking to the bottom after metamorphosing, or by great numbers of them being eaten by other organisms. With the millions of eggs produced e. g. by each specimen of *Diadema*, it is an extraordinary fact that young specimens are as a rule a great rarity (though the adult Diademas are common and conspicuous enough, usually living in large flocks). *Luidia ciliaris* (Philippi) especially affords a very striking case. In my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X. 1913) I have stated that the number of eggs produced by a single adult specimen amounts to c. 200 millions. When in spite of this the species is apparently nowhere very common, none of the above named causes will explain this scarcity in a satisfactory way. I think that in this and many other cases the main reason is that a v e r y g r e a t p e r c e n t a g e o f t h e e g g s f a i l t o b e f e r t i l i z e d. In cases where some species occurs in great numbers in a locality, there is of course no risk of the eggs failing to be fertilized, but in all such cases where specimens are scarce, and do not collect for breeding purpose (and, of course, where no copulation takes place), I think it beyond doubt that lack of fertilization of the eggs is a main reason for the number of specimens not increasing.

The faculty of the larvæ to continue life as larvæ for a long period beyond the normal duration of larval life, be it on account of insufficient food, or because they do not find a suitable place for attaching themselves, must be of material importance for the dispersal of such species; this means chances for the larvæ of being carried a long way from the place where they came into existence, and they may thus be able to colonize places where the species did not hitherto occur.

A few words may still be said about the l u n a r p e r i o d i c i t y in reproduction, as discussed by H. MUNRO FOX (Proc. Royal Soc. B. Vol. 95. 1923). He finds a pronounced lunar periodicity in *Diadema setosum* at Suez, whereas no such periodicity exists in the Mediterranean Echinoid *Paracentrotus lividus*, against the common belief in the Mediterranean countries. (I might suggest that it would be worth while to examine in this regard a couple of other Echinoids much used for food in the Mediterranean countries, viz. *Sphærechinus granularis*, *Echinus acutus*, and *Ech. melo*, perhaps these might form the basis for the general belief in the lunar periodicity in these countries).

As regards *Diadema setosum* it seems that at Ghardaqa this species agrees in the main with the observations of Fox. But as for the other Echinoderms studied, there is not much support for a lunar periodicity. Of some species ripe specimens may be found during a longer, continuous period e. g. *Laganum depressum;* many species appear to have only one breeding season during the summer — which may

very well for many species coincide with a full moon (e. g. probably *Brissopsis luzonica*), but other species I have found ripe at new moon, or any time. I must emphasize, however, that I have not made special researches regarding this problem, but my general impression is that lunar periodicity in the reproduction of the Echinoderms at Ghardaqa is a rare exception.

Whether other marine forms of the Red Sea show any distinct lunar periodicity I am not aware; but since a distinct lunar periodicity, in reproduction or otherwise, occurs in various Molluscs, Polychætes (— "Palolo" —), and Crustaceans, (I must refrain from quoting the extensive literature relating to this subject — I will mention only the names of Amirthalingham, Battle, Orton, and Wheeler), it is probable that similar observations could be made also at Ghardaqa. And whatever the result would be, proving or disproving the existence of lunar periodicity, regularly continued observations would be sure to be of great value.

My observations on the breeding seasons of the Echinoderms at Ghardaqa also have an important bearing on the question whether the tropical marine animals breed continuously throughout the year, as has been maintained by Semper and Orton (cf. my "Studies of the development and larval forms of Echinoderms", 1921, pp. 245—246). As pointed out already, pp. 3—4, several species did not become ripe at all till July or August, or even September. Such species evidently breed only once or twice, possibly three times a year. It is probable that such species as were found ripe already in April—May, e. g. *Echinometra Mathæi* and *Tripneustes gratilla*, will breed continuously (every full moon?) throughout the summer — but I did not pay attention to this problem. It should be pointed out, however, that, although the northern part of the Red Sea must be regarded as tropical in spite of its higher latitude (Ghardaqa lies at 27° 13′ N.), it has a distinct winter-season, during which the temperature of the sea water may fall as much as 10° C. This, of course, must have some influence on the breeding of the marine animals. It is quite probable that species which breed here only once or twice a year may breed more often, perhaps continuously, in the properly tropical seas, where no distinct winter season lowers the temperature. It may be recalled here that Gopala Aiyar (Early development and metamorphosis of Salmacis bicolor. Proc. Ind. Acad. Sc. I. 1935, p. 726) found *Salmacis bicolor* ripe at all times of the year. Direct researches into this problem are much required.

I may take the opportunity here of correcting an erroneous statement in my "Contributions" III, p. 9. It is said there that "by means of keeping a number of specimens in a live-box Selenka succeeded in getting good cultures of *Holothuria nigra*". This is a rather curious slip of the pen. The species thus reared by Selenka was *Holothuria tubulosa* — as evident already from the title of his paper quoted four lines above! And *Holothuria nigra* was reared not by Selenka, but by myself, as described in my paper "On the development of some British Echinoderms" (J. Mar. Biol. Ass. X. 1913. p. 17).

Echinoidea.

1. **Prionocidaris baculosa** (Lamarck).

Pls. I—III.

This species does not actually occur in the neighbourhood of Ghardaqa. During the dredging trip in the Egyptian research steamer "Mabahiss" to the Gulf of Suez in May 1936 (mentioned on p. 3 of my "Contributions" III) I got a great number of specimens — about 250 specimens in a single haul! — off Ashrafi Light, at a depth of 40 fathoms, on hard bottom with a rich growth of algæ. These I carried alive to the station, hoping to be able to study their development. As they were, however, far from being mature, part of them were kept alive in the tanks of the station (where they lived excellently, feeding on algæ that were put with them into the tank), others were set out at the pier and on the reef-flat near the station, where they could easily be found again. But even by the end of June, when I had to leave the station, they did not show any sign of becoming ripe in a very near future.

It was one of my ardent hopes this year to find again some of these specimens of *Prionocidaris baculosa* liberated near the station last year, and thus to be able to study the development of this species — a hope which was to be fulfilled. On July 28th Dr. CROSSLAND brought home some specimens found at the pier in the very place where they were liberated last year. They proved to have ripe sexual products, and artificial fertilization was undertaken. The first experiment, however, gave no result. Although the fertilization membrane had been formed, no cleavage followed, and the following morning the eggs were found lying dead on the bottom of the dishes. A new fertilization was then undertaken, and most of the fertilized eggs put into a fine plankton-net suspended in the tank so as to hang in running sea-water, a smaller part of them only being left in the usual dishes. This time it was a perfect success, cleavage going on normally, not only of the eggs in the plankton-net, but also of those lying on the bottom of the dishes. The reason for the failure of the first fertilization, where the eggs were lying on the bottom of the dishes, remains unknown, all the usual precautions having, of course, been taken.

The eggs are of the usual small size, c. 0.15 mm in diameter, perfectly clear and transparent; the fertilization membrane stands widely off from the egg. The cleavage is total and perfectly regular, the two first cells lying perfectly isolated from one another (Pl. I, Fig. 2), so that I could not help wondering, how they would be able to join into a normal single blastula on further development. The 4- and 8-cells stages seemed more of the usual form, but in the 16—32-cells stages the cells were arranged in a rather unusual way, forming a two-layer plate, leaving a rather large empty space on both sides of it within the membrane (Pl. I. Fig. 4). Ultimately the cells, on further development, arranged themselves so as to form a normal blastula of perfectly spherical shape (Pl. I. Fig. 5) — i. e. in the majority of the eggs. But a large percentage of the embryos were of a more or less irregular shape (Pl. I. Fig. 6), evidently due to the original isolation of the two first blastomeres, showing that actu-

ally the cells originating from the two first halves of the egg had difficulty in uniting into a single embryo, as it was my first impression that they would perhaps have. Moreover, quite a number of the embryos proved to be double, there being two separate blastulæ within the membrane, sometimes, indeed, even three of them (Pl. I. Figs. 7—8), proof that in these cases the cells originating from the first two blastomeres had actually been unable to join together to form a single, normal embryo. We have thus here the very unusual, but highly interesting case of normal one-egged twins, and even one-egged triplets. (I did not observe any case of quadruplets, but that such may occur also there is hardly reason to doubt). Nature itself thus makes here the experiment of isolating the first blastomeres, as has so often been done artificially by experimental biologists. And as has been found experimentally, the isolated blastomeres develop into normal larvæ, only of half size. Although I did not isolate the twins, the much smaller size of some of the larvæ was proof enough that the twins develop into normal larvæ; these small larvæ reached full shape, identical in all their characters with the normal, full-sized larvæ, differing from them only in their much smaller size. That they would also metamorphose I cannot have the slightest doubt, though I have not definitely ascertained it. Of course, I quite realized that it would have been of the greatest interest to have the twin-larvæ isolated and observed throughout their development and through metamorphosis, but there was simply no time to do so, the work with the divers other cultures of Echinoderm larvæ occupying all my time. But it is clear that this Cidarid would be a marvellous object for experimental researches on its development.

So far as known to me the only other case known of one-egged twins (viz. quadruplets) occurring normally is that of the armadillo, *Tatusia*. That exceptionally one-egged twins may occur in several animal forms, man included, is a different matter. The polyembryony of some parasitic Hymenoptera may be recalled, but this is scarcely comparable to the case of *Prionocidaris baculosa*. Likewise the twin-embryos of the earth-worm *Lumbricus trapezoides* (cf. Kleinenberg. Development of the Earthworm Lumbricus trapezoides. Quart. Journ. Micr. Sc. 19. 1879. p. 206. Pls. IX—XI) are something different, being a secondary division of the embryo in a later stage of development. It should further be emphasized that the *Prionocidaris*-twins are something quite different from the so-called twin larvæ of Echinoderms, with double hydrocoel or double alimentary canal, artificially produced or occurring casually in normal cultures of Echinoderm larvæ (cf. e. g. Newth. The early development of *Astropecten irregularis*, with remarks on duplicity in Echinoderm larvæ. Qu. Journ. Micr. Sc. 69. 1925). Such larvæ are monsters, whereas the twins of *Prionocidaris* are perfectly normal larvæ. More similar to the case of the *Prionocidaris* twins is that of one-egged twins in *Arbacia lixula* ("*pustulosa*") quite recently described by P. E. Lindahl ("Über eineiige Zwillinge aus Doppeleiern". Biol. Zentralblatt. 57. 1937. p. 389). But here it is an abnormal formation of the polar bodies, resulting in the polar body sometimes being as big as the egg itself. Each of the two are ferti-

lized and apparently develop normally, so that twin blastulæ within the same membrane become the result. Still, this is principally different from the case of *Prionocidaris*, it being here a parallel development of twin eggs, not twins developing from one and the same egg.

The first development stages take a very short time, the blastulæ beginning to rotate within the egg-membrane only 6 hours after fertilization (Pl. I. Fig. 5); immediately afterwards the egg-membrane dissolves and the embryos become free-swimming. They are rather thick-walled, the cells not being large and flat as is the case in *Eucidaris metularia*, and the cell-mosaic not nearly as large and conspicuous as in the latter (cf. "Contributions" III. Pl. I. 4). 9 hours old the embryos had assumed the shape of elongate gastrulæ, without apical thickening of the ectoderm (Pl. I. Figs. 9—10). — The gastrulæ developing from such "half-twins" as Pl. I. Fig. 6 were observed to be more or less irregular, according to the degree of irregularity of the blastulæ. Whether they would ultimately develop into normally shaped embryos, I do not know, as I had no time to isolate such irregular gastrulæ and follow their further fate.

In embryos 26 hours old the first traces of the skeleton were already found, viz. the future postoral rods, situated in the lower corners of the embryo, the shape of which is, on the whole, much more slender than that of *Eucidaris metularia*, in which latter the young gastrula is almost spherical, at the beginning differentiation of the archenteron almost triangular (Pl. I. Figs. 9—10 to compare with Pl. I. Figs. 5—6 of "Contributions" III, which represent the corresponding stages of *Eucidaris metularia*). Also in regard to the first appearance of the skeleton the *Prionocidaris* embryo differs markedly from that of *Eucidaris*, the first rudiments of the skeleton appearing only at the age of four days in the latter, against scarcely more than one day in *Prionocidaris*. The formation of the enterocoel-pouches was not followed in details.

As is apparently the rule in Cidarid embryos the postoral rods are from the first directed outwards, or, indeed, a little backwards (Pl. I. Fig. 10), but very soon they are turned obliquely upwards, the young larva having a fairly normal Echinopluteus shape (Pl. I. Fig. 11). In this stage — the figure represents a larva $2^1/_4$ days old — the larva differs from the *Eucidaris* larva of the corresponding stage in the oral lobe being much broader and the posterior part of the body much smaller (comp. Pl. I. 8. of "Contributions" III). The *Eucidaris* larva of the corresponding stage is 9 days old, against the $2^1/_4$ days of *Prionocidaris* — an enormous difference in the rate of the developmental processes of these two species, the more remarkable as the two larvæ in their full shape are so very closely alike; apparently the difference is due to the somewhat smaller size of the eggs in *Eucidaris* and therewith probably a smaller amount of nutrient material in these latter.

The skeleton of the young larva is, on the whole, very much like that of the *Eucidaris*-larva, only the body rods are somewhat more developed, almost joining in the posterior end of the body, and the postoral rods are fenestrated throughout (Fig. 2), whereas there are no holes in the basal part of this rod in *Eucidaris*.

The larva in this stage has already the pigment well developed (— the very first traces of pigment are observable already in the gastrula with the first rudiments of the skeleton —), a good number of carmine spots along the vibratile band, more densely accumulated at the ends of the postoral arms, and a few scattered spots in the posterior end of the body.

In larvæ four days old the posterodorsal rods have appeared. At the age of 10 days the larva is nearly fully formed (Pl. I. Fig. 12), the posterior transverse rod and the dorsal arch and the divers lobes developed, the larva being at this age a good deal more advanced than the 22 days old *Eucidaris* larva ("Contributions"
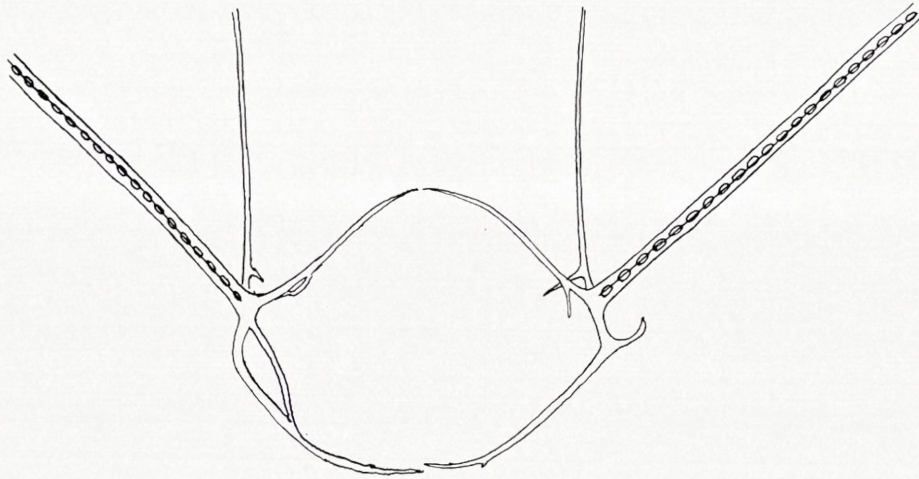
Fig. 2. Skeleton of young larva, $2^1/_4$ days old, of *Prionocidaris baculosa* (Lamk.). $\times$ 300.

III. Pl. I. 9). The full larval shape was reached in the course of another week, the posterodorsal arms being now as long as the postoral ones, the anterolateral and preoral arms being more slender and elongate, and all the divers lobes fully developed (Pls. II—III). The larva now so closely resembles the *Eucidaris* larva ("Contributions" III. Pl. II) that they are hardly to be distinguished from one another. It is an exceedingly beautiful microscopical object, with its long, slender arms and its five pairs of large vibratile lobes, bordered by the vibratile band, decorated with delicate carmine spots.

A very interesting fact is that the larva is able to move its four long arms very actively, not only from a normally forward directed to a horizontal position, but even to a straight backward position (Pl. II. Figs. 1—2). The movement of the arms from the forward to the backward position is very quick; usually the movement is repeated two to three times in quickly succeeding strokes, after which the arms are held quiet in a horizontal position. It is evidently not a normal swimming movement, but an averting movement, occurring only when something touches the larva (— thus always when I sucked them up with a pipette). Of course, there must be quite a powerful and complicate muscular system for making such

active movements possible. Such a one also exists, as shown in figs. 3—4; it consists of two pairs of straight horizontal muscles connecting the bases of the postoral and posterodorsal rods of both sides with one another, one straight dorsoventral muscle on each side, connecting the bases of the postoral and the posterodorsal rods of the same side, and four muscles going obliquely from the bases of the four main rods to the middle of the posterior transverse rod.

There can be no doubt that the *Eucidaris* larva moves its four main arms in the same way as does the *Prionocidaris* larva. In figures 2—4, p. 16—17 of "Contributions" III, representing the basal part of the skeleton of the fully formed *Euci-*
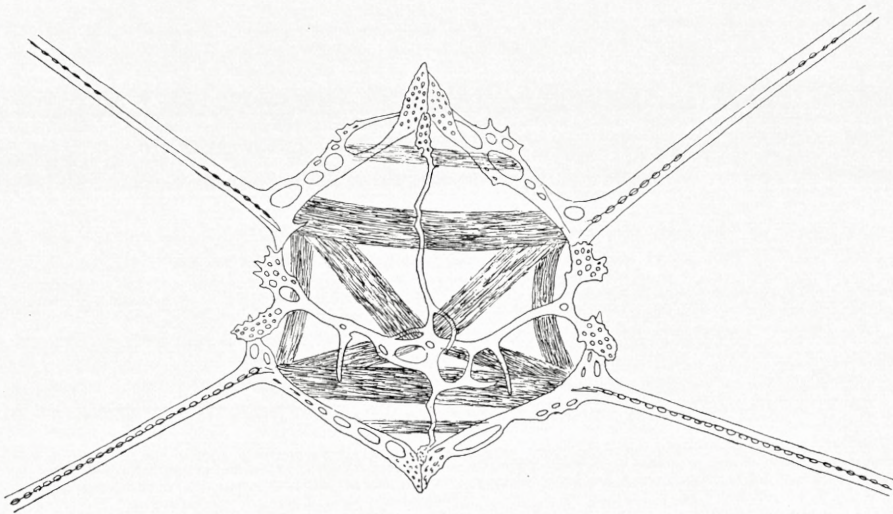
Fig. 3. Skeleton and muscular system of the fully formed larva of *Prionocidaris baculosa* (Lamk.). Seen obliquely from behind. The oral side is turning upwards. × 200.

daris larva, both straight and oblique muscles are shown — but not the complete muscular system, the small outer horizontal muscles having been overlooked; not at that time knowing anything of the peculiar movements of the arms, I was, of course, not intent on seeking the complete muscular system on which such movements depend. On a re-examination of the *Eucidaris* larva I find, however, the muscular system to be in full accordance with that of the *Prionocidaris* larva.

The skeleton of the fully formed larva (figs. 3—4) very closely resembles that of the *Eucidaris* larva, particularly in the highly characteristic shape of the posterior transverse rod, with its long dorsal and ventral median processes, which reach up to the transverse rods from the postoral and posterodorsal rods. These latter are quite smooth, fenestrated rods, as in the *Eucidaris* larva, the only difference being that here they are fenestrated from the base, whereas in the *Eucidaris* larva the fenestration only begins a good distance out. It is, however, an interesting fact that in the larva about to metamorphose the posterodorsal rods usually show stretches near

the base where the fenestration has disappeared (fig. 3); but this is no constant feature, both being sometimes fenestrated throughout (fig. 4), while sometimes only one of the rods is partly unfenestrated. This may have something to do with the pre-paration for metamorphosis.

The beginning metamorphosis, indicated by the presence of pedicellariæ and embryonal spines, was not observed till the age of 25 days, and the first metamor-phosed young sea-urchins were found exactly a month after fertilization. So far as I have been able to ascertain the four long rods of the larva are not wholly resorbed
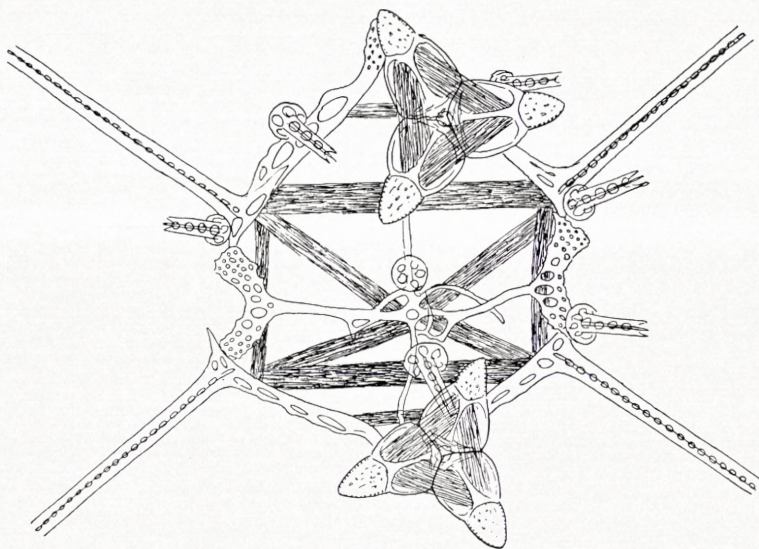
Fig. 4. Skeleton of larva of *Prionocidaris baculosa* (Lamk.) in beginning metamorphosis. Two pedicel-lariæ and some spines have appeared. Seen from behind, so as to show also the muscular system. The oral side turning upwards. × 200.

on metamorphosis, but only their proximal part, the distal part being dropped after the skin has retracted therefrom. The vibratile lobes were observed to be gradually resorbed.

Whereas the first metamorphosed sea-urchins were found by the end of August, many of the larvæ kept on swimming for another two weeks, till I left Ghardaqa, and would quite evidently have remained unmetamorphosed for a still longer time. When the first larvæ showed distinct signs of metamorphosis, they were put into a separate dish containing some algæ to which the young sea-urchins might attach themselves. Though I did not find any of these directly on the algæ, it seemed evident that the presence of the algæ in the dish accelerated the metamorphosis (— probably by the larvæ on swimming coming into touch with the algæ —); at least all the larvæ transferred to this dish metamorphosed in the course of one or two days, whereas the larvæ not transferred, though apparently in the same advanced stage, did not metamorphose until much later.

The larvæ are good swimmers, and do not lie on the bottom of the dishes, as so many other Echinoid larvæ do when near metamorphosis; on the contrary, they were often swimming close under the surface, which caused a good number of them to be caught in the surface film and thus killed. A more remarkable fact was that not a few of the larvæ metamorphosed at the surface, the young sea-urchins being found floating directly under the surface film. A good number of the young, newly metamorphosed Cidarids were found attached to the sides of the dish, others on the bottom.

In the dish with the algæ the young Cidarids lived very well, the algæ affording
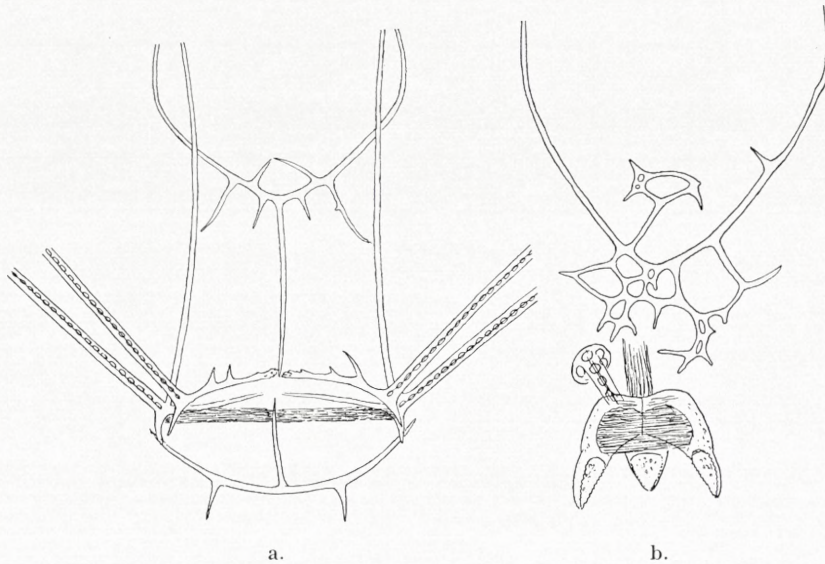
Fig. 5. a. Skeleton of a 10 days old larva of *Prionocidaris baculosa* (Lamk.); b. dorsal arch of a larva of same in beginning metamorphosis. A pedicellaria and an embryonal spine have developed on the dorsal arch. × 200.

both the necessary oxygen and food, mainly by the numerous diatoms and other microscopical organisms living on them and propagating actively — a whole microcosmus gradually developing in the dish, in which the young Cidarids were living and growing very well. When I had to leave, most of the young Cidarids were preserved; the rest of them Dr. CROSSLAND very kindly looked after till the beginning of October, when they were preserved and sent me. They had, however, not grown noteworthily beyond the size of the most advanced of the specimens preserved on September the 10th. They had then been kept in a small dish, without change of water, for more than a month! In larger dishes, and with some changing of water and algæ, it would evidently be quite easy to rear the young Cidarids to a much larger size — but that is for those, who have access to undertake such experiments.

The first sign of metamorphosis is the appearance of pedicellariæ, three of them appearing almost simultaneously, viz. on the left ventral and dorsal transverse

3*

rods, and on the dorsal arch, one on each of these parts of the larval skeleton (figs. 4 and 5 b); on the young sea-urchin these three pedicellariæ are found again, attached to three of the ocular plates, the origin of which from the said parts of the larval
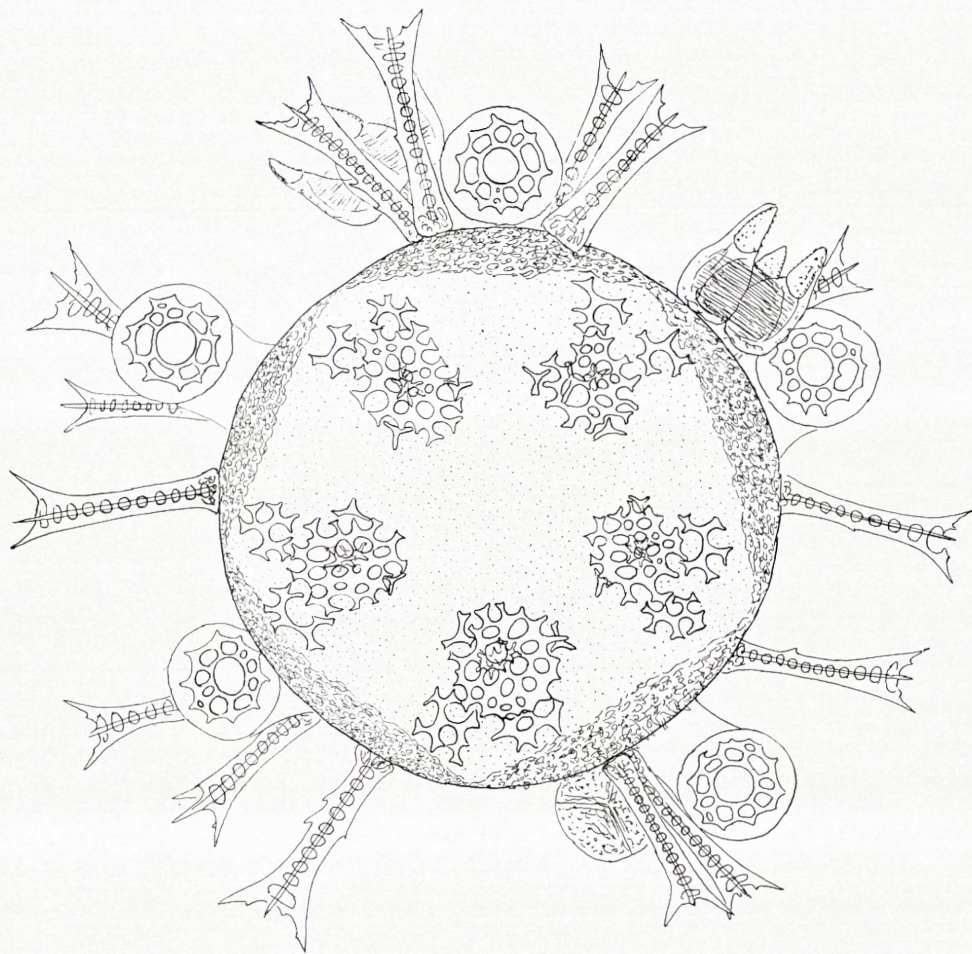

Fig. 6. Newly metamorphosed *Prionocidaris baculosa* (Lamk.), from the oral side. Showing the interambulacral plates 1—3, and under the adoral edge of I. A. 1 (the primary interambulacral plate) the first rudiments of the buccal plates; corresponding to the ocular plates (the five dense marginal plates) are seen the embryonal spines, the primary tubefeet and the three pedicellariæ, the one on the lower right hand side seen from its base. × 200.

skeleton being thereby ascertained. (The exact parts of the larval skeleton from which the two other ocular plates originate, or whether they represent new, independent formations, I have been unable to ascertain).

Figs. 6—7 represent the newly metamorphosed sea-urchin, from the oral and the aboral side. On the buccal membrane, which is continuous, without mouth-opening, are seen the five primary interambulacral plates, the first pair of inter-

ambulacral plates, near the edge, and the buccal plates, still quite small and partly concealed under the primary interambulacral plates. On the aboral side (fig. 7) are seen the five genital plates, one of them developed from the posterior transverse rod, another from the right (dorsal?) transverse rod; a third one shows an indication of being developed from the dorsal arch, which latter would then form the origin
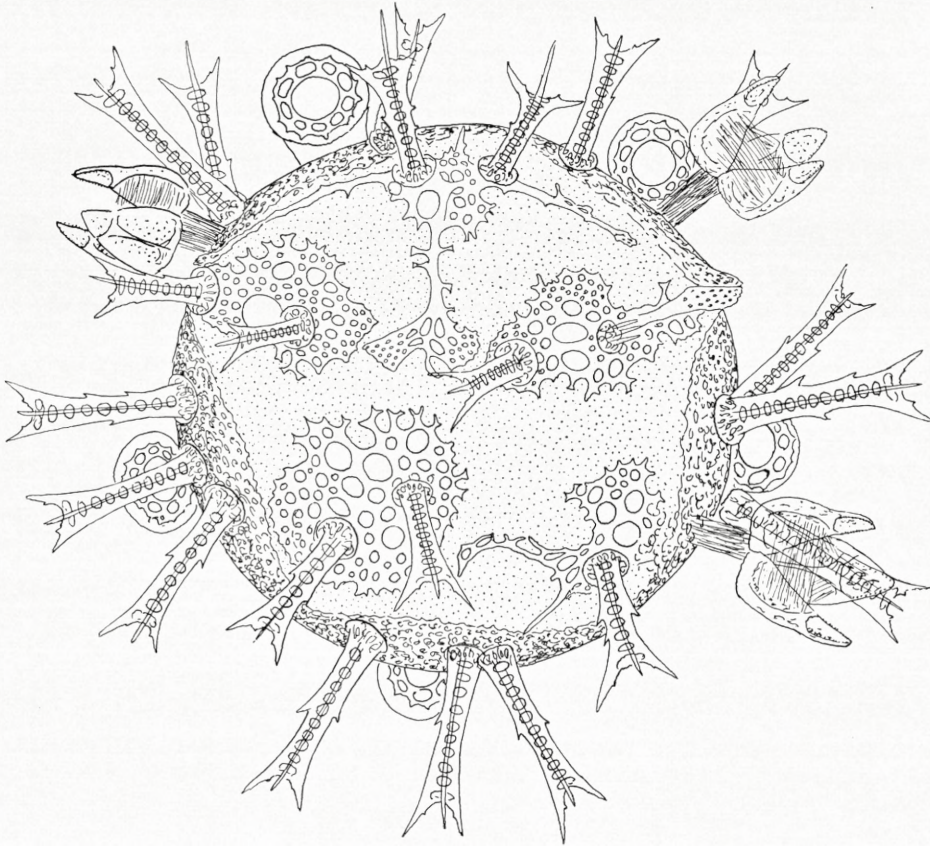

Fig. 7. Same as fig. 6, seen from the aboral side. Showing the young genital plates, the one on the upper side of the figure developing from the posterior transverse rod, the one on the right side from one of the transverse rods, the one on the lower right hand side apparently developing from the dorsal arch. × 200.

partly of an ocular plate, partly of a genital plate — but I have been unable to ascertain this definitely.

In this young stage all the spines are of the embryonal type, terminating in three diverging points; there are three to four to each ocular plate, one or two on each genital plate. The primary tubefoot is large and has a fine ring-shaped plate in the sucking disk.

Fig. 8 represents the oral side of a more advanced stage. The buccal plates have grown considerably, forming a nearly closed ring, in the center of which is

an indication of the future mouth. The buccal tubefeet are about to appear, all at about the same time, as evident from the size of the holes for them in the buccal plates. Below the adoral end of the buccal plates are seen the first rudiments of the
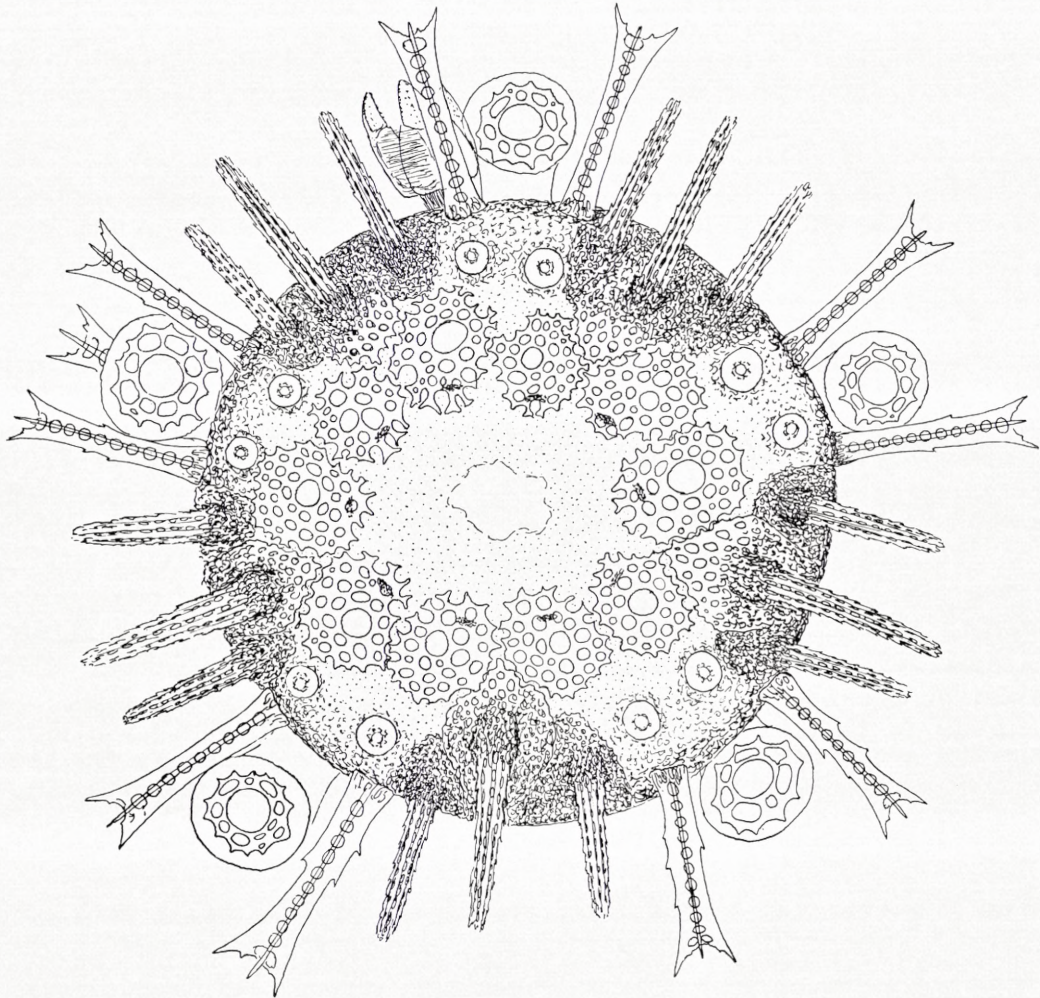

Fig. 8. More advanced stage of *Prionocidaris baculosa* (Lamk.), from the oral side. The plates arranged in a ring in the middle are the buccal plates, under the adoral edge of which are seen the first rudiments of the dental apparatus. The three first interambulacral plates carry young spines, not yet fully formed. The first pair of tubefeet have appeared. × 200.

dental apparatus. The primary and the first pair of interambulacral plates have grown very considerably and the primary spine of each of them is already fairly developed, though not yet fully formed; they are quite different in shape from the three-pointed embryonal spines found on the ocular plates. The first pair of tube-feet have appeared; they are much smaller than the primary tubefoot, and their

sucking disk very small and indistinct. The corresponding ambulacral plates could not be made out distinctly.

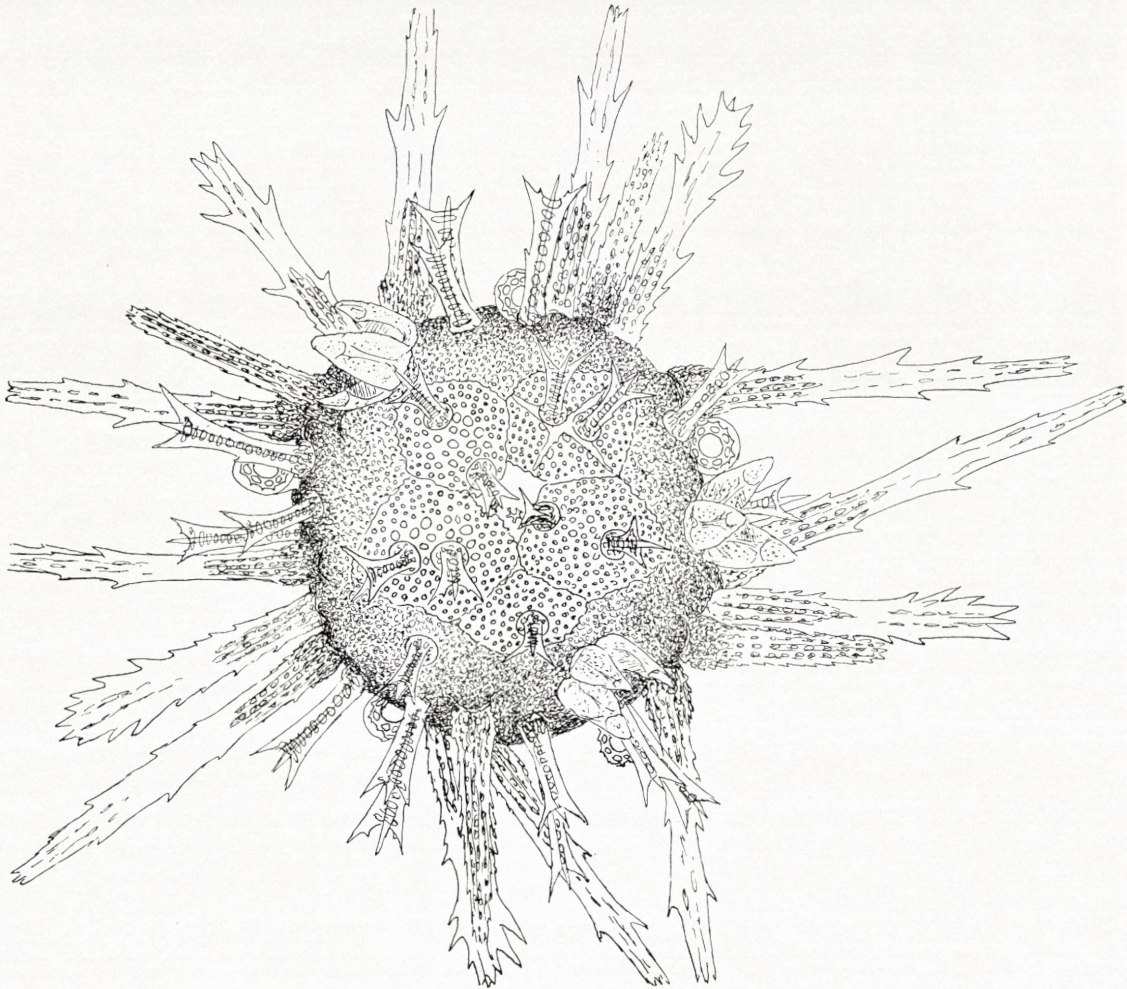In fig. 9 is shown the aboral side of the most advanced stage reached. Here

Fig. 9. Aboral side of more advanced stage of *Prionocidaris baculosa* (Lamk.). The genital plates form a closed ring, leaving a central space, in which are seen the first rudiments of two anal plates. The inter-ambulacral spines partly fully formed. $\times$ 105.

the genital plates have joined so as to form a rosette enclosing a small central membranous area, the future periproct. Two small plates have just appeared therein, the first of the future anal plates, which are thus seen to develop separately and gradually, the five plates in the radial corners of the periproct of adult specimens having no separate preponderance or morphological value, and there is, of course, no sign of a central plate originally covering the periproct. One of the genital plates

lags a little behind, not reaching the edge of the periproct; another of them still shows traces of the part of the larval skeleton (evidently the posterior transverse rod) from which it originated. The primary spines of the first two or three interambulacral plates are fully developed and with colour bands already indicated. These spines are very characteristic by their strong thorns, especially the one on the primary interambulacral plate, which makes it easy to recognize them with certainty in the following growth-stages (cf. my description of the young *Eucidaris metularia* in my paper "On the postlarval development of some Cidarids". Mem. Acad. Copenhague. 8. Sér. XI. 1927).

In this stage the buccal tubefeet have appeared, and a spine has appeared on the adoral edge of each buccal plate. The mouth has opened and the teeth have been formed. These latter are, however, still in an embryonal stage, of a very curious shape, with the point coarsely serrate and the aboral end in the shape of an irregular fenestrated plate (fig. 10 a). How this is transformed into the definite form, with the new lamellæ constantly forming at the aboral end, would seem rather difficult to understand. I have, however, succeeded in finding in a very young specimen of *Eucidaris metularia* from Banda a slightly more advanced stage in the development of the teeth, which seems to show that the lamellæ begin to appear outside the fenestrated part of the young tooth, this fenestrated part not being directly transformed into lamellæ (fig. 10 b). But it seems that the fenestrated part of the young *Eucidaris* tooth is rather different from that of *Prionocidaris* and occupies a much larger part of the tooth than in the latter, a difference which makes the conclusion as to the transformation of the young tooth into that of the adult form a little uncertain.

a.   b.

Fig. 10. Tooth of young *Prionocidaris baculosa* (Lamk.) (a.), and of *Eucidaris metularia* (Lamk.) (b.). a. × 410; b. × 150.

These peculiar serrate young teeth recall the remarkable serrate teeth of *Meekechinus*, figured on Pl. 76, fig. 7 of Jackson's "Phylogeny of the Echini". In my Monograph of the Echinoidea, II. p. 79 I suggested that the serration of the teeth of *Meekechinus* may perhaps rather be due to fracture. The character of the teeth of *Prionocidaris* (and evidently also of *Eucidaris*) does not lend support to this suggestion.

A point of the greatest morphological importance is the appearance of the interambulacral plates 4—6. As shown in fig. 11, plate No 4 lies nearly in the midline of the interradius, plate 5 and the — still quite young — plate 6 lying to the sides of plate 4, so that we have here a transverse series of three plates. This means that we have in this young stage a pluriserial interambulacrum, exactly like what is found in palæozoic Echinoids. In *Archæocidaris* the basal part of the corona is resorbed during growth (just as it is in recent Cidarids), so we do

not actually find these first interambulacral plates; but there cannot be the slightest doubt that they must have been there, arranged as shown by JACKSON in the theoretical restoration Pl. 9 fig. 8 of his "Phylogeny of the Echini". A comparison of fig. 11 with the said figure in JACKSON's work, as well as with the quite similar figure of an interambulacrum of the Lepidocentrid *Hyattechinus elegans* Jackson
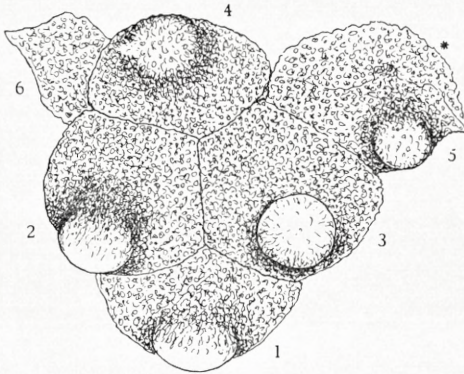

Fig. 11.

Fig. 11. Interambulacrum of young *Prionocidaris baculosa* (Lamk.). At the asterisc on the upper right side the limit between the interambulacral plate 5 and the adjoining ocular plate could not be made out distinctly. × 225.

Fig. 12. Interambulacrum of *Hyattechinus elegans* (Jackson) (a.) and of *Archæocidaris wortheni* (Hall) (b.). Adapted from JACKSON's »Palæozoic Echini of Belgium", fig. 5, p. 25 (a.), and from the same author's "Phylogeny of the Echini" Pl. 9. 6 (b.).
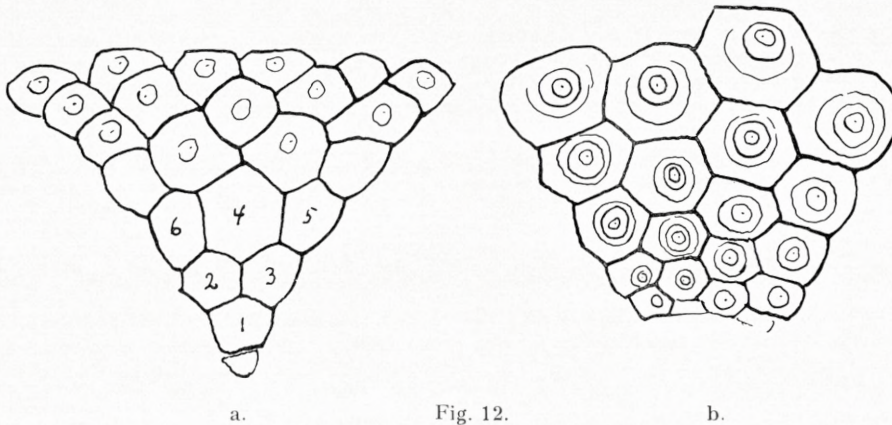

a.   Fig. 12.   b.

(fig. 12 a) shows the arrangement of the first 6 interambulacral plates to be exactly the same (that JACKSON's numeration of the plates differs from mine does not alter this fact). We may thus say that the young *Prionocidaris* (and probably all recent Cidarids) passes through an *Archæocidaris* stage, a fact decidedly indicating the correctness of seeing in *Archæocidaris* the ancestor of the Cidarids. — That not the slightest support of the *Bothriocidaris* theory is to be found in the Cidarid development need hardly be mentioned.

The knowledge of the *Prionocidaris* larva now obtained shows it to be in complete accordance with the other Cidarid larvæ thus far known (cf. "Contributions" III. p. 18—20) and makes it practically certain that there is a special larval type peculiar to the Cidarid family, characterised by the very long, smooth, fenestrated

postoral and posterodorsal rods, by the posterior transverse rod being provided with a very long and slender ventral and dorsal median process, and by the very strong development of the ciliated lobes. No doubt also the strongly developed larval muscular system, enabling the two pairs of long arms to be moved straight back-wards, is a common character of the Cidarid larval type.

2. **Laganum depressum** (L. Agassiz).

Pl. IV. Fig. 1.

This species, which is very common at depths of c. 5—25 fathoms on a sandy or muddy bottom off Abu Sadaf, a little outside the laboratory, was found partly ripe in the beginning of July (most of the specimens were still unripe at that time);

a.   b.
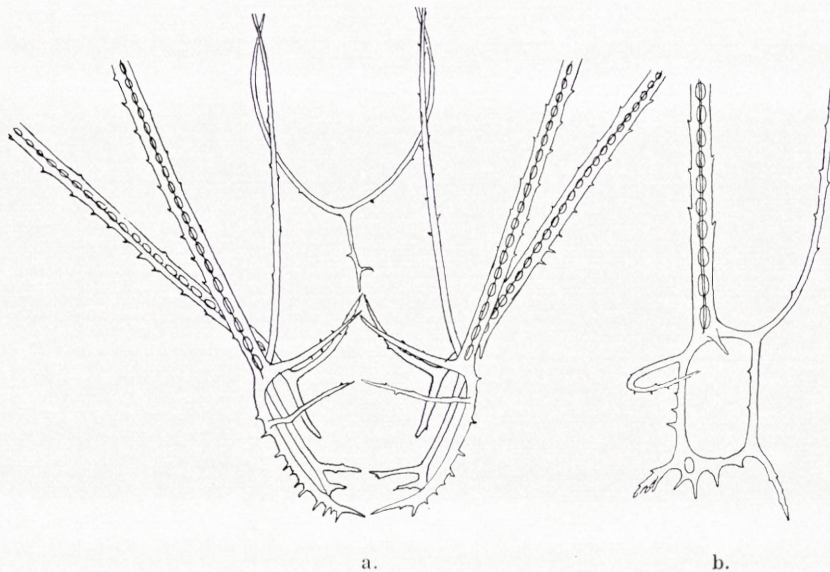
Fig. 13. a. Skeleton of fully formed larva of *Laganum depressum* (L. Agassiz). a. Front view, from the oral side. b. Half of skeleton of a younger larva, seen from the inside. × 200.

fertilization was undertaken on July the 2nd and proved successful. The larvæ of this culture having died before metamorphosis, a new culture was started on June the 24th, the larvæ of this latter culture being carried successfully through meta-morphosis.

The eggs are small, c. 0.1 mm in diameter, perfectly transparent, without any pigmented mucilaginous coat, such as occurs e. g. in *Echinodiscus auritus*. The cleavage is perfectly regular and does not offer any specially noteworthy features. 18 hours after fertilization the embryos were beautiful, a little elongate, transparent blastulæ, containing a varying number of free mesenchyme cells; some of the blastulæ showed a beginning of the gastrula invagination. Two days old the embryos had assumed

the shape of young plutei, with a rather strongly thorny skeleton, and without pigment. At the age of 6 days they showed the first rudiments of the posterodorsal rods, which are fenestrated like the postoral rods; still no pigment. At the age of 10 days the larvæ showed the first signs of metamorphosis, viz. the formation of the amnion;
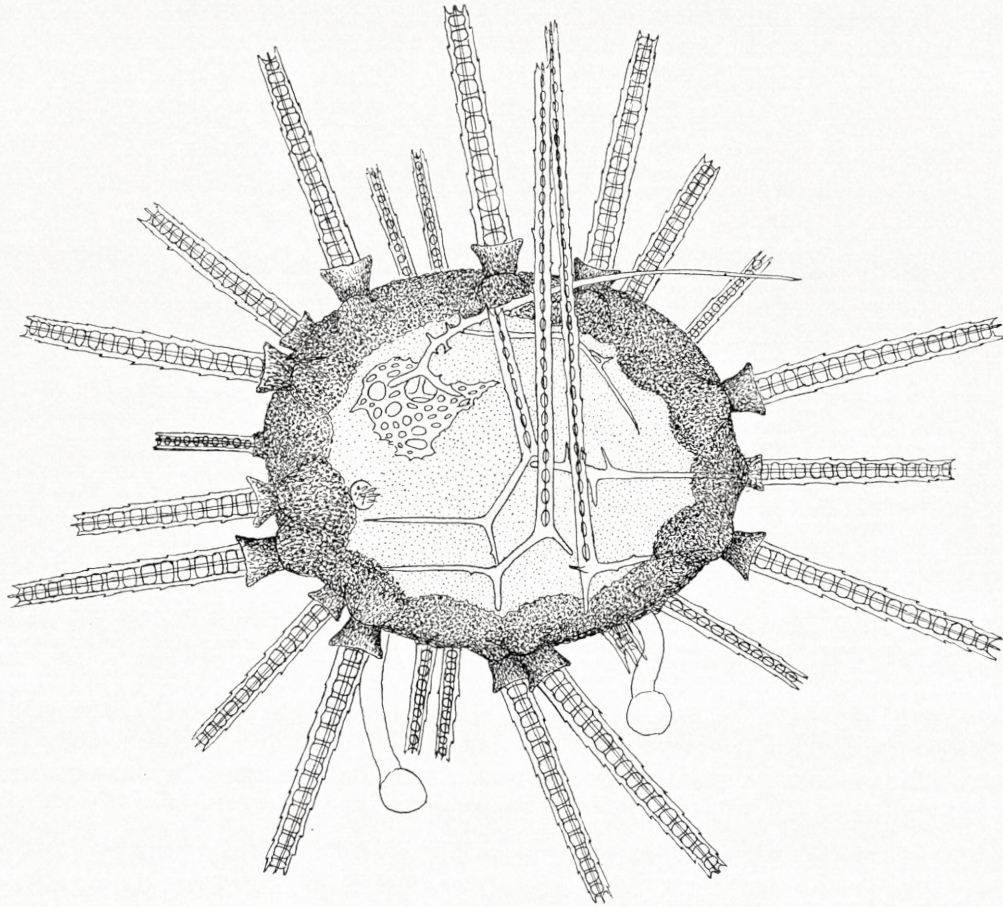

Fig. 14. Newly metamorphosed *Laganum depressum* (L. Agassiz). Aboral side; showing the main parts of the larval skeleton beginning to transform into the apical skeleton of the sea-urchin. × 200.

and now also some scattered yellowish pigment spots had appeared. Beyond this stage the larvæ of the first culture did not develop.

In the second culture the development proceeded at about the same rate, the larvæ having metamorphosed at the age of about two weeks.

The fully formed larva (Pl. IV. Fig. 1) has rather long, slender arms, with only a very slight terminal widening. The lateral lobes are small and inconspicuous; the postoral band forms a small lobe on the transition to the postoral arms. The pigmentation is very inconspicuous, consisting only in a few small yellowish spots

scattered in the vibratile band and over the body. There is no distinct accumulation of these spots at the end of the arms, only an exceedingly faint yellowish tinge.

The skeleton of the larva (fig. 13) is of the usual Clypeastroid type, the body skeleton forming the typical basket structure; but it does not develop into a large fenestrated plate in the posterior end, as is the case in *Echinodiscus*. At metamorphosis the basket is partly resorbed, and the remaining part of the body rod, as well as the posterior prolongation of the posterodorsal rods are connected by horizontal muscles enabling an active movement of the four arms.

The young, newly metamorphosed sea-urchin shows the transformation of the basal part of the four main rods and of the dorsal arch into the apical system of the sea-urchin (fig. 14). There is herein such complete accordance with what obtains in *Echinocyamus pusillus*, so admirably described by Théel in his paper of 1892, that I find it superfluous to give a detailed description and figures of the postembryonal metamorphosis of the present species.

3. Echinodiscus auritus (Leske).

Pl. IV. Fig. 2.

As I did not succeed last year in rearing the larva of this species through metamorphosis, I made an attempt to do so again this year and succeeded. Artificial fertilization was undertaken on July the 7th and on the 21st some specimens had metamorphosed.

The larva figured on Pl. VII. Fig. 2 of "Contributions" III has not quite reached the full larval shape, the arms being not yet of full length. I therefore give a new figure of the larva, in beginning metamorphosis (the amnion formed), from which it will appear that the arms are a good deal longer than shown in the figure from last year; they are slightly curved towards the point, which may be a little widened.

The ciliated band forms a somewhat more prominent lateral lobe than in the figure quoted and the postoral band also forms a fairly conspicuous lobe at the base of the postoral arms, and there is a corresponding lobe on the dorsal side. The colour consists of isolated spots of a faint reddish-carmine tint; only at the point of the postoral (not the posterodorsal) arms is there a slightly more conspicuous reddish spot.

In its general features the young sea-urchin agrees so closely with the young *Laganum* that I think it superfluous to figure it. Also the larval skeleton forms the base of the apical skeleton of the sea-urchin in the same way as in the young *Laganum*, cf. fig. 14. I may only mention specially that the complicate fenestrated plate occupying the posterior end of the larva is actually dissolved before metamorphosis, not incorporated into the final skeleton — a fact which I was unable to ascertain from the non-metamorphosing larvæ from last year's culture.

It would have been of very great interest to have reared the young sea-urchins till the beginning formation of the slits in the test. In order to try to rear them so far I put them into a dish with some coarse sand at the bottom; but they did not develop

any further. And as only very few adult specimens were found on the only locality in the neighbourhood of the station (Abu Mingar), where the species occurs (on the very beach, lying dry at low tide), it was hopeless to try to find the quite young stages in the sand there.

Asteroidea.

4. Luidia Savignyi (Audouin).

Pl. V. Figs 2—5.

As mentioned on p. 8 of "Contributions" III, I did not succeed last year in getting any fertilization of this *Luidia* species, artificial or natural, in spite of repeated attempts. This year I made a fresh attempt, thinking it of great interest eventually to compare the larva of this species with that of the two other species, the larvæ of which are known so far, viz. the two European species, the 5-armed *Luidia Sarsi* and the 7-armed *Luidia ciliaris*. The species *L. Savignyi* not being of common occurrence at Ghardaqa I had some trouble in getting the necessary material, the single specimens brought home now and then by the sailors all being males; finally on August the 3rd they brought home 6 specimens, among which one ripe female, the rest of them males. I then tried to make artificial fertilization. Although some of the eggs showed no nucleus, fertilization seemed as unsuccessful as in last year's attempts. Still, after 6 hours I found a very few apparently normal cleavage stages, from which I got the next morning about 20 normal gastrulæ. Another attempt was then made (the female specimen having been kept alive in the tank; only two of its arms were used at the first attempt, and the loss of a couple of arms does not, of course, matter to a *Luidia*, which practises autotomy on the least bit of rough treatment, and regenerates the lost parts with great ease). The eggs were left in the sea-water about 3 hours, before the sperma (activated by adding a drop of KOH to the water) was added. This attempt gave a somewhat better result — some 200 blastulæ. So far as I could ascertain (by the evening light) the wall of the blastulæ was folded, as usual in Asteroids. From the two attempts together I got in all c. 45 young larvæ, which had at the age of two days assumed the shape of young Bipinnariæ.

Pl. V. Fig. 2 represents the young larva, 5 days old. It is rather remarkably short, the anterior part not at all elongate, as was to be expected from our knowledge of the young *Luidia ciliaris* larva (cf. fig. 9, p. 7 of my paper "On the development of some British Echinoderms" J. Mar. Biol. Ass. X. 1913). At the age of about a week the larvæ began, however, to become more elongate in the anterior part of the body, viz. the median lobes, as seen best in Pl. V. Fig. 4 representing a fully formed larva in side view. The two median lobes are movable, but only slowly, and they are by no means used actively in swimming, as is the case in *L. Sarsi* and *ciliaris*. This accords with the fact that there is no trace of the strongly developed muscular system found in the anterior lobe of the two latter species, as described and figured by TATTERSALL & SHEPPARD, in their paper "Observations on the Bipinnaria of the

Asteroid genus *Luidia*" (James Johnstone memorial volume. Liverpool 1934. p. 44—48).

The larvæ represented in Pl. V. Figs. 3—4 are only 12 days old, but already in beginning metamorphosis and have thus reached their full shape. They are entirely transparent, without any trace of colour, whereas the young, newly metamorphosed sea-star is faintly yellowish, with the stomach orange-coloured.

The larva of this *Luidia* species accordingly differs very conspicuously from the two European *Luidia* larvæ, remains so to say in a much more embryonal stage. The elongation of the anterior part of the body, though distinct, is very much smaller than in the latter; also the paired arms are much shorter and not transformed into ciliated, food-collecting channels, as so excellently described particularly by Tattersall & Sheppard. Another, very noteworthy, difference is that the anterodorsal arms remain simple, not becoming double (or even triple), as they are in the fully developed larvæ of *L. Sarsi* and *ciliaris* — whereas in the younger stages of the said larvæ the anterodorsal arms are still simple as in the *L. Savignyi* larva.

From the relatively small size of the *L. Savignyi* larva it was to be expected that the larval body would be resorbed on metamorphosis, not thrown off, as is the case in the *L. Sarsi* larva. It took me some time to ascertain this. Repeatedly, in the evening, I put some larvæ near metamorphosis, but with the larval body still in perfect form, into a separate dish, expecting then early next morning to find either the resorption stages or the thrown off larval bodies; but I found only the completely metamorphosed young sea-stars, without any trace of the larval body attached, and no free, thrown off larval bodies. Finally, observing some metamorphosing larvæ from hour to hour under the microscope, I succeeded in following the resorption of the larval body (Pl. V. Fig. 5). The whole process takes only a couple of hours, and it thus became clear why I could not see anything of the process in metamorphosing larvæ, which had been kept the night over.

It is in accordance with the small size of the larva, only c. 1.5 mm full length, that the development takes so much shorter a time — only c. 12—15 days — than in the much larger European larvæ, *L. ciliaris* c. 7 mm, *L. Sarsi* c. 30 mm (according to Tattersall & Sheppard only 15—18 mm). It is true, we do not know exactly the time the development of the two latter larvæ requires; but the young larva of *L. ciliaris* figured on p. 8 of my paper of 1913 quoted above, with the arms still quite short and simple, and evidently far from metamorphosis, is 5 weeks old[1] — proof enough that this larva will require at least a couple of months for completing its development, and the much larger *L. Sarsi* larva probably a much longer time.

Knowing now the larva of *L. Savignyi*, we are able to form a better judgment

[1] Tattersall & Sheppard, Op. cit. p. 44, say that I described the early stages of the *L. ciliaris* larva "from material collected at Plymouth". This seems to indicate that they overlooked the fact that I reared the young larvæ from artificially fertilized eggs. I did not "collect" these young larvæ; if collected from pelagic material it would have been impossible to identify them with certainty as the *L. ciliaris* larva.

of the real characteristics of the *Luidia* larva in general, than was possible from the knowledge of the two European species alone. These latter are now seen to be a highly specialized form of the *Luidia* larva. The general characters of the *Luidia* larva are: the more or less pronounced elongation of the anterior part, viz. the median lobes; further the total absence of Brachiolaria arms and sucking disk. In the latter character they agree with the larvæ of Astropectinids, from which they differ only in the more developed arms and the elongation of the median lobes. The larvæ of the two families of the Astropectinidæ and the Luidiidæ would seem, according to our present stage of knowledge of the Asterid larvæ, to stand apart from all the other Asterid larvæ, these latter having all, so far as is known, a Brachiolaria-stage (much reduced, but still recognizable, in those which have direct development). It would be of very great interest to learn whether the third family of the *Paxillosa*, the Porcellanasterids, agree with the Astropectinids and Luidiids in having no Brachiolaria-stage. Judging from the embryo of *Ctenodiscus australis* figured by LIEBERKIND ("Ctenodiscus australis Ltk., a brood-protecting Asteroid". Vid. Medd. Dansk Naturhist. Foren. 82. 1926, p. 193, fig. 6) there seems to be no trace of a Brachiolaria stage in this species.

Of the three *Luidia* larvæ known till now the *L. Savignyi* larva is much the simplest; the *L. ciliaris* and *Sarsi* larvæ, with the much more elongate median lobes, forming even active swimming organs, with the paired arms developed into ciliated channels, and the anterodorsal arms divided from the base into two (or three) equally developed branches, are much more specialized, particularly the *L. Sarsi* larva, which grows to such an excessive size that, as pointed out by TATTERSALL & SHEPPARD, the larval body has become too big for being resorbed on metamorphosis, and is simply thrown off, remaining free-swimming for some time, even for months! It is in accordance herewith that the young sea-star of the *L. Sarsi* larva grows to a much larger size, before the larval body is thrown off, than that of *L. ciliaris*, the larva of which reaches only a smaller size and is resorbed, not thrown off at metamorphosis (cf. TATTERSALL & SHEPPARD, Op. cit.).

The newly metamorphosed sea-star of *L. Savignyi* is at first rather amoeboid, changing its shape, being usually somewhat elongate (fig. 15), and only gradually assuming the final circular shape (fig. 16). At metamorphosis it has only the two first pairs of tubefeet developed[1] — whereas the newly metamorphosed *L. ciliaris* has 5 pairs[2], the newly liberated *L. Sarsi* no less than 10 pairs; the relative size of the young sea-stars of the three species is in accordance therewith.

[1] In fig. 15 a. only one pair of tubefeet is shown, the second pair not being discernible in the unstained specimens (which show the skeleton distinctly, and therefore were used for drawing), but in stained specimens the second pair of tubefeet also is seen to be present.

[2] According to TATTERSALL & SHEPPARD (Op. cit. p. 57, fig. 7 c.) the young sea-star of *L. ciliaris* has only 5 pairs of tubefeet at metamorphosis. GEMMILL (On a new brachiate Asteroid larva and on the advanced Bipinnaria of *Luidia ciliaris* (Philippi) Gray. Proc. R. Phys. Soc. Edinburgh. XIX. 1915, p. 197), however, states that the young sea-star has 12 pairs of tubefeet in each arm. I am unable to account for this discrepancy; but it would seem probable that the statement of TATTERSALL & SHEPPARD is the correct one.

The young sea-stars were put into a dish with some sand from the locality
where the adults were found; they lived very well in it, and after about four weeks
had reached the stage shown in fig. 16, with two pairs of tubefeet distinct. I shall
not enter on a detailed description of the development of the skeleton — it appears
plainly enough from a comparison of the figures — I would only point out the peculiar
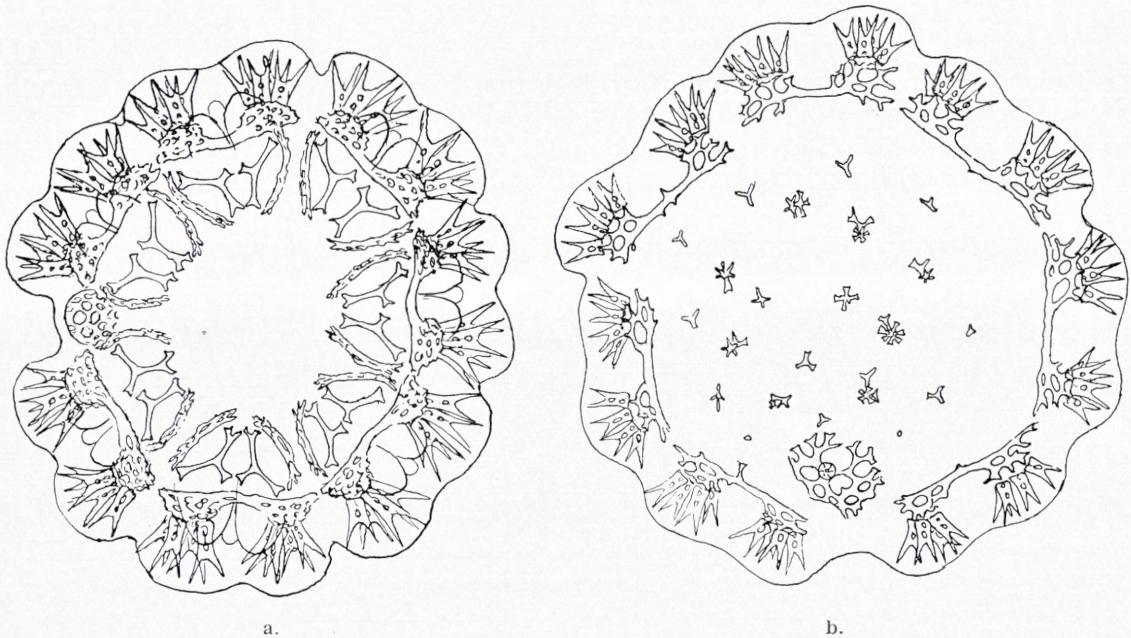shape of the terminal plates, each carrying two bundles of two-pointed spines; fur-

a.   b.

Fig. 15. Newly metamorphosed *Luidia Savignyi* (Audouin). a. Oral side, showing the first pair of am-
bulacral and adambulacral plates; b. aboral side, showing the beginning formation of the dorsal skeletal
plates. The larger plate at the lower edge is the madreporite. $\times$ 135.

ther the fact should be noted that the dorsal skeleton shows no regular arrangement,
and especially that there is no central plate (figs. 15, b; 16).

According to *Hörstadius* (Embryologische Beobachtungen über Luidia ciliaris
Phil., L. Sarsi Düb. & Kor. und Phyllophorus urna Grube. Arkiv för Zoologi, Bd. 18.
B. 1926) the hydrocoel of *L. ciliaris* at first only develops 5 radial pouches, the 6th
and 7th appearing later, after the hydrocoel has closed into a ring. I regret very much
not to have followed the formation of the radial pouches in the live larvæ; in the
preserved larvæ all the 7 radial pouches are formed, and in an equally advanced
stage. But it is an important fact that the young ambulacral and adambulacral plates
of the 7 radii are all of exactly the same size and equally advanced in their development
— which, however, says nothing about the time of the appearance of the 6th and
7th radial pouch, the ambulacral skeleton not appearing till after the hydrocoel
has formed the 7 radial pouches.

The fact that the *L. Savignyi* larva differs so strikingly from the larvæ of *L. ciliaris* and *Sarsi*, being so much more primitive than these latter, makes it rather urgent to study the development of other *Luidia* species also. DÖDERLEIN, in his excellent Monograph of the great genus *Luidia* ("Siboga" Exped. Monogr. XLVI. b. 1920) came to the result that the *ciliaris*-group, to which the species *Sarsi* and *ciliaris* belong
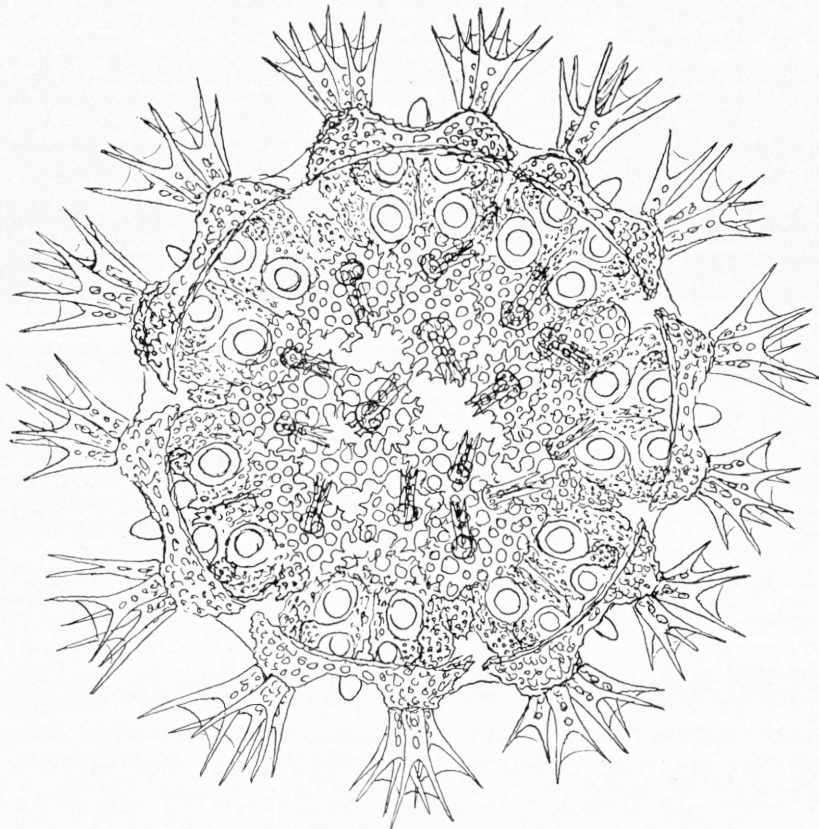

Fig. 16. Young *Luidia Savignyi* (Audouin), 5 weeks old. Aboral side. Two pairs of tubefeet developed. ×135.

(subgenus *Hemicnemis* Müll. & Troschel) is the most specialised of all the Luidiids, whereas the group to which *L. Savignyi* belongs, the *alternata*-group (subgenus *Maculaster* Döderlein) represents a less specialised type (although not the most primitive of all). The shape of the larvæ of the three said species is in full accordance with the results reached by DÖDERLEIN from a comparative study of the characters of the adult; even the fact that the *Sarsi* larva is more highly specialised than the *ciliaris* larva is in accordance with the result of DÖDERLEIN that within the genus *Luidia* the many-armed forms are the more primitive, the 5-armed the more specialised. It would now be of the greatest interest to learn whether the other species of the *ciliaris*-group have the same highly specialised larval type as *ciliaris* and *Sarsi*

(— it is of interest in this connection that a *"Bipinnaria asterigera"* is recorded from off Celebes in the "Summary of the Scientific Results of the "Challenger" p. 836; as I pointed out in my "Echinodermenlarven d. Plankton-Expedition" (1898), p. 39, this cannot, of course, be identical with the *"Bipinnaria asterigera"* of SARS, which is the *Luidia Sarsi* larva, but must belong to another *Luidia* species —). It will be equally interesting to learn whether the other species of the *alternata*-group, or even those of the *clathrata*-group, the most primitive of all the Luidias, have a similar primitive larva to that of *L. Savignyi*.

5. Pentaceraster mammillatus (Audouin).
Pl. V. Figs. 6—7.

On the 15th of July the sailors brought home from Abu Mingar, a few miles South of the station (in the immediate neighbourhood of which this species does not occur), 10 specimens of *Pentaceraster mammillatus*, 8 of which proved to be ripe males, 2 females, one of which had ripe eggs, the other being unripe. Artificial fertilization was undertaken (late afternoon) and proved in some degree successful, although the sperma was very little movable (not treated with KOH).

The eggs are small, c. 0.1 mm, quite transparent. The cleavage was regular and very beautiful; the 32-cell stage was reached after three hours. The next morning I could isolate c. 200 fine gastrulæ, which after 2 days had developed into normal young Bipinnariæ. 12 days old the larvæ had the shape shown in Pl. V. Fig. 6; the enterocoel pouches have grown forwards and have joined in the preoral lobe. At the age of 16 days the larvæ showed the first indication of Brachiolaria arms and sucking disk, and three weeks old they had developed into typical Brachiolarias and showed the first signs of metamorphosis. On the 7th of August, thus after 24 days, I found the first larvæ about to metamorphose.

The larvæ are, as usual among Asteroids, very active swimmers; but they did not keep near the surface, and did not swim horizontally, as I found it to be the case last year with the *Astropecten* larvæ, and especially the larvæ of *Asterope carinifera*. Whereas up till the beginning metamorphosis the larvæ had been very healthy, scarcely a single one having been lost, now suddenly a strong mortality set in — probably because of some sort of infection. But a few metamorphosed successfully and, having been transferred to a dish with some small pebbles and shells on the bottom, grew a good deal in size, as appears from figs. 17, a, b, representing a newly metamorphosed and an 8 weeks old specimen.

Concerning the larva, represented in its young and its final shape in Pl. V. Figs. 6—7 it is to be mentioned that the arms, particularly in the fully formed larva, are rather strongly movable, but not contractile. The ventral median lobe varies considerably in length, especially in the fully formed larva, may even be conspicuously longer than the dorsal median lobe. The Brachiolaria is of the type with a series of papillæ along each side of the ventral lobe and a short series of papillæ along the

Brachiolaria arms, much as in the *Porania* larva, not with a terminal crown of papillæ as in the *Asterias* larva. The colour is very faint; only the oesophagus is fairly distinctly yellowish, and, mainly in the fully formed larva, there is the merest indication of yellowish colour on the preoral and postoral transverse band; otherwise it is colourless.

The young sea-star does not call for a more detailed description, the figures giving the necessary information. In comparison with the young Luidias it is re-

a.   b.
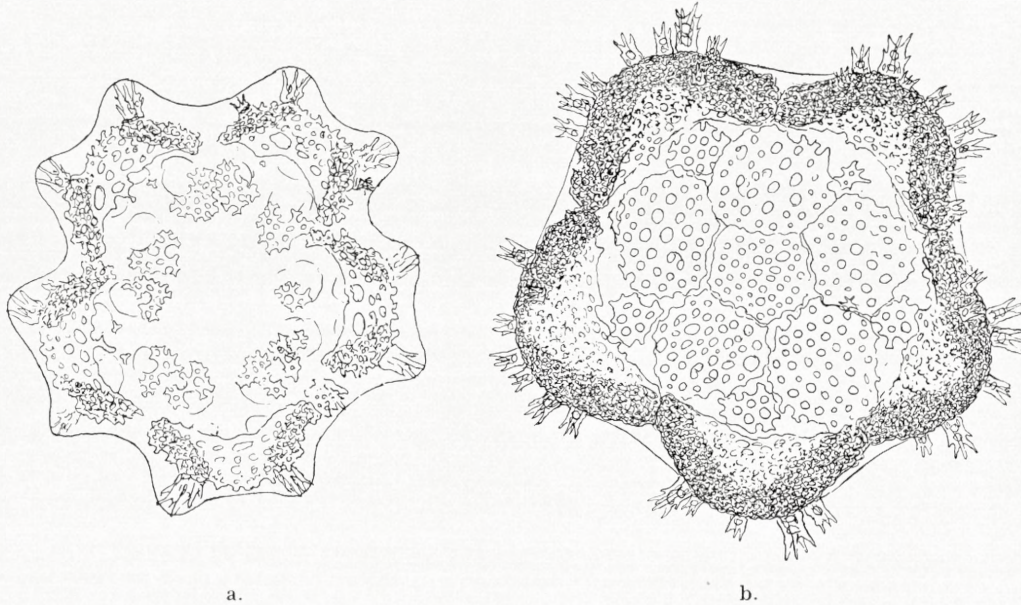
Fig. 17. *Pentaceraster mammillatus* (Audouin). a. Newly metamorphosed, from the oral side: b. 8 weeks old specimen, from the dorsal side. × 105.

markably strongly built, the plates being rather heavy, in conformity with the strong build of the adult *Pentaceraster*. The perfectly regular dorsal skeleton is in strong contrast to that of the young *Luidia*.

6. Linckia multifora (Lamarck).

Pl. IV. Figs. 3—4.

This species, the "kaf Mirjam" (hand of the Virgin Mary) of the natives, has specialised to such a high degree in the propagation by autotomy that one could scarcely help being a little surprised to find it to propagate in the normal way also, by means of eggs and pelagic larvæ. And it was the more surprising to find the small, dividing specimens to contain ripe sexual products, as it appears that it is mainly in young age it propagates by autotomy; larger specimens — and it grows to a large size, I have specimens of all intermediate sizes up to 170 mm arm-length — do not appear to practise autotomy, and it might therefore be expected that young specimens propagated by autotomy alone, adult specimens by eggs and pela-

gic larvæ alone. But such then is not the case. However, it is evident that the propagation by autotomy is by far the dominant in the young specimens. The gonads — which are serial — were found developed only in the larger arms, usually very irregularly, only in one or two arms, and usually only few of the gonads, now one at the base on one side of the arm, now a few farther out on the other side of the arm. In the smaller regenerating arms I never found gonads developed — but in such arms that had thrown off the distal part of the arm and were about to regenerate it. Specimens with ripe sexual products could be found most of the time from about the middle of May (last year) to September. I did not succeed in getting ripe specimens of both sexes at the same time last year, although they may be kept alive very easily for quite a long time in the tanks of the station. But this year I got some ripe specimens of both sexes on July the 23rd and then tried to undertake artificial fertilization. Only rather few eggs were obtained, the gonads being small and few, and as moreover only a very small percentage of the eggs would ripen for fertilization, even after being kept some hours in the water before the sperma was added, it is no wonder that the result of the fertilization was very poor. After two days I had in all 9 gastrulæ, most of them apparently not quite normal. After five days I had 5 young Bipinnariæ left. After two weeks I had only two larvæ left, one of them not even quite normal, its left anterodorsal lobe being undeveloped.

These two larvæ, however, went on developing normally, the incomplete one even ultimately developing a quite normal anterodorsal arm. On the 9th of August, at the age of 17 days, the enterocoel pouches had united above the oesophagus, not prolonged into a long point but simply rounded above the oesophagus. Three weeks old the larvæ showed the first indication of Brachiolaria arms, and 27 days old they were near metamorphosis and had assumed full Brachiolaria shape. As, in order to have them figured correctly, it was necessary to narcotise them (— which proved to be very difficult; both sulphate of magnesia and alcohol, added dropwise, had to be used —) they were now preserved. Thus I did not get the young, metamorphosed sea-star, but the full larval stage was obtained in spite of the very scarse material.

The fully formed larva, not the young one, proved to be exceedingly sensible; at the slightest touch — thus when sucked up in a pipette for being transferred to fresh sea-water — it would fold all its arms tightly up around the body and remain so for quite a long while before unfolding its arms again to begin swimming.

In the young stage the larva so closely resembles the young *Luidia* larva, as represented in Pl. V. Fig. 2, that I did not think it advisable (or necessary) to sacrifice one of my few larvæ for making a camera drawing of it. The only difference from the young *Luidia* larva, I could find, was that the dorsal median lobe of the *Linckia* larva is narrower than the ventral one, and with perfectly straight sides. The fully formed larva (Pl. IV. Figs. 3—4) has moderately long arms, very movable, as explained above, though not used actively for swimming; they are not distinctly contractile. The posterolateral arms are usually bent forwards. The Brachiolaria arms are as in the *Pentaceraster* larva, the median lobe with a series of papillæ along each

side, and the paired arms with a short series of papillæ at the tip. The ventral median lobe usually bends down towards the paired Brachiolaria arms; the dorsal median lobe, which is somewhat longer than the ventral one, is usually bent dorsalwards, as shown in Pl. IV. Fig. 4.

The colour of the fully formed larva is a very faint, diffuse yellowish, the stomach dark, almost black, in young larvæ more reddish-violet.

The skeletal plates of the beginning sea-star do not present any specially characteristic features, as is the case with the young *Fromia*.

7. **Fromia ghardaqana** Mrtsn. (n. sp.)[1].
Pls. VI. 1—4; VII.

In the report on my researches of last year ("Contributions" III, p. 8) it was mentioned, under the name of *Fromia monilis*(?), that I had found it to be a protandric hermaphrodite, but that I did not succeed in studying its development; artificial fertilization was impossible because of the eggs being large and full of yolk, and although I kept a number of specimens alive in the tank for a long time no spawning took place. This year (1937) I was more successful, getting its complete development. Also the statement of its being a protandric hermaphrodite was verified.

Having put a good number of specimens together into a dish, I had the pleasure of seeing them spawning on July the 8th, in the afternoon at about 3 o'clock. On the following days again some specimens were spawning, always at about 3 o'clock in the afternoon. On the 14th of July the last spawning took place (fresh material having repeatedly been brought in from the reef). Later on no spawning occurred, though I repeatedly had fresh material brought in.

The spawning specimens always came up along the sides of the dish to the surface of the water, sometimes with an arm stretched out horizontally under the surface film. Always some males would start, the sperma coming out in a white stream from each of the genital pores, which lie on the dorsal side, two in each interradius, a little distant from the edge. Soon the water became quite milky, and then the spawning of the females would begin. The female genital pores are likewise situated on the dorsal side, two in each interradius. The pores being quite small,

[1] This new species of the genus *Fromia* belongs to the group with relatively long and slender arms (cf. H. L. CLARK. Echinoderms of the Torres Strait. 1921. p. 39) and appears to be the nearest related to *Fr. pacifica* H. L. Clark, from which it differs, however, especially in having a series of enlarged plates (blue in life) along the dorsal midline of the arms; further the granular covering is different, not nearly so close in *pacifica*, in which also the granules are pointed, so that the surface feels rough, whereas in the present species the granules are not pointed and the surface is smooth, according to kind information from H. L. CLARK, who has compared a specimen of the Red Sea species with the type of *Fr. pacifica*.

It is this species which was mentioned under the name of *Fromia monilis*(?) on p. 8 of "Contributions" III, and apparently it is also the same species which TORTONESE (Echinodermi del Mar Rosso. Ann. Mus. Civico Storia Nat. Genova. LIX. p. 213) mentions as *Fromia monilis* Perrier. I have had an opportunity of comparing the Red Sea species with the type of *Fr. monilis* in the Paris Museum and found them to be quite different.

and the eggs large, c. 1 mm in diameter, this necessitates the eggs coming out slowly, one by one, and pressed into the shape of long, thin sausages. After being liberated they gradually assume, more or less completely, the normal spherical shape, but they often remain elongate, elliptical. On account of the rich content of yolk they do not sink to the bottom, but float freely in the water or, more generally, directly under the surface of the water. Gradually there would be at the surface of such dishes with spawning Fromias a dense layer of these large, intensely high-red eggs. Apparently they were fertilized immediately after liberation, which, however, was not easy to ascertain, owing to the fact that the fertilization membrane lies close to the egg-surface.

The first lot of eggs, simply removed to a dish with fresh sea-water, did not seem to develop normally; those spawned the following day were then put into a plankton-net in the tank, under a very faint stream from a tap. The following day only a very few of them were left, the rest of them dissolved, evidently smashed by that gentle stream of water; the eggs are, indeed, exceedingly brittle, on account of the great amount of yolk contained in them. The eggs spawned the following days were then put partly into the tank itself, with only a very faint stream through, and the outlet so secured that the floating eggs could not pass through, partly into a plankton-net suspended in the tank, with the stream from the tap outside the net, so that the eggs could not be hurt by it. With these precautions I succeeded in getting the normal development of the eggs.

What makes it especially difficult to see whether the eggs are developing normally is the fact that the cleavage is not externally observable. Only when the cilia have developed, and the embryo is beginning to rotate within the egg-membrane, which stage is reached after about 18 hours, does it become clear that the development has proceeded normally. At the age of c. $1^3/_4$ days the embryo leaves the egg-membrane,

The young free-swimming embryo is a simple, thick, oval, perfectly intransparent, red lump (Pl. VI. Fig. 1). At the age of three days they are assuming their full larval shape — a uniformly ciliated round or oval body, with a pair of short, thick lobes and an unpaired, somewhat longer one, usually bending a little downwards towards the two shorter lobes. It is beautifully high-red, perfectly intransparent (Pl. VI. Figs. 1—4). Later on a thickening becomes apparent at the base of the unpaired process; this, of course, corresponds to the sucking disk of a Brachiolaria, and the three processes accordingly represent the Brachiolaria arms. It is thus proved that *Fromia* has a rudimentary Brachiolaria-stage, corresponding to what is found in other Asteroids with direct development, e. g. *Asterina*, *Solaster*, *Asterias Mülleri*. Pl. VI. Fig. 3 represents a larva with a pair of smaller inner lobes, evidently an anomaly.

The larva swims with the round end forwards, the lobes directed posteriorly; it seems never to use the sucking disk for attaching itself, before it metamorphoses.

At the age of 6—7 days the larvæ began to become flattened, or rather compressed, in the broad main part of the body, and indistinctly pentagonal, indication of the approaching metamorphosis, but not till the age of 16 days did any of the larvæ complete metamorphosis. In the course of the following 2—4 weeks several

more larvæ metamorphosed; but a great percentage of them went on swimming, without showing signs of completing metamorphosis. And still at the end of my stay at the laboratory I found a pair of apparently normal, free-swimming larvæ, while a good number of other, not metamorphosed, larvæ were more or less reduced in size, having of course subsisted that long time upon the rich yolk content of the egg.

Owing to intransparency of the eggs the cleavage and the developmental processes could only be studied by means of sections, a number of which, representing divers developmental stages, are represented on Pl. VII.

No direct cleavage of the egg takes place. The nuclei alone divide and are scattered irregularly in the yolk-mass, as shown in Pl. VII. Fig. 1, which is a section of an embryo 3 hours old. The yolk is very distinctly vesicular, more finely in the central, more coarsely in the peripheral part. At the age of 5—6 hours the nuclei are beginning to wander out towards the surface of the egg (Pl. VII. Fig. 2), where gradually they arrange themselves in a single layer. But the nuclei gradually become much too numerous for forming a regular single layer, so that a most peculiar folding must take place. The nuclear layer, in order to find room, is pressed inwards as irregular strands (Pl. VII, Fig. 3), the embryo in this stage (c. 15 hours old) rather recalling a miniature walnut. The yolk vesicules arrange themselves in such a way that the larger of them in the main follow the strands of nuclei. While still enclosed in the egg-membrane the nuclei gradually again wander out towards the surface, but now in a thick layer, as necessary on account of their great number, and form now a definitely limited, thick ectoderm (Pl. VII. Fig. 4, from an embryo 28 hours old). At the same time the gastrula invagination takes place; the space between the ectoderm and the archenteron is filled out by a rather coarsely vesicular yolk with scattered nuclei, the mesenchyme. One cannot help wondering how the nuclei can know where they have got to go — and as a matter of fact the process sometimes does not happen in quite the typical way — as in the embryo represented in Pl. VII. Fig. 5. Here the nuclei have not got to the surface of the egg, but have collected to form the ectoderm layer some way inside the yolk, leaving a large portion of the yolk outside, so as not to participate in the embryo-formation. Such embryos, of course, become a good deal smaller than normal; I have observed some such smaller embryos among the larger normal ones, but I regret not having isolated them for following their further fate, so I cannot say definitely whether they can develop through metamorphosis like the normal embryos; my impression is, however, that none of these smaller embryos reached metamorphosis.

It may not be superfluous to point out that the fact of the gastrula invagination being in the embryo represented in Pl. VII. Fig. 4 on the broader side, in that shown in Pl. VII. Fig. 8 at the posterior end, has no morphological significance. The apparent difference is due to the simple fact that the eggs do not all assume the normal spherical shape after having been pressed out through the small genital pores — and there is, of course, no guarantee that the long axis of the elongate eggs corresponds with the future longitudinal axis of the embryo.

The further development of the embryo, from the gastrula stage through meta-morphosis, is exceedingly difficult to follow. Whereas the ectoderm remains a very distinctly limited epithelial structure, this is not the case with the entoderm and its derivates, the enterocoel and the hydrocoel. They are very distinctly limited against the mesenchyme, but they show no epithelial structure, and they have no distinctly limited cavities, these being more or less completely filled by yolk-substance, which leaves, at most, only irregular free cavities. It is merely the arrangement of the nuclei which makes it possible to distinguish the archenteron and the enterocoel and hydro-coel derived from it. To work out the whole process of transformation from the gastrula to the young sea-star would require an enormous amount of work — recon-structions from the divers series of sections — and a great number of figures. I have not thought this worth while, as also I could not very well spare the time for such work, so I have had to content myself with giving figures 6—12, Pl. VII, to illu-strate these later stages of the embryonal development, from which it appears that in the main features there is a general agreement with what is known from Master-man's report on the development of *Cribrella oculata* (= *Henricia sanguinolenta* (O. Fr. Müller)), the eggs of which latter are large and full of yolk like those of *Fromia ghardaqana*.

In Pl. VII. Fig. 8 is seen the beginning separation of the entero-hydrocoel from the archenteron; the latter still remains in connection with the ectoderm through the gastrula invagination which is, evidently, about to undergo resorption. (The cavity seen at the upper side of this figure is an artefact, due to preservation. Normally the whole space between ectoderm and entoderm is completely filled with mesenchyme, of the usual vesicular structure). This embryo is $2^1/_4$ days old. In Pl. VII. Fig. 7, from an embryo $1^3/_4$ days old, the division of the archenteron is only beginning. The section is not median, therefore does not show the gastrula invagination; on the other hand the pouch to the left at the upper end of the archenteron may probably represent the incipient formation of the hydropore. Pl. VII. Fig. 9, which is a medial sagittal section of an embryo $3^3/_4$ days old, shows the very well developed sucking disk of the Brachiolaria. In Pl. VII. Fig. 10, which is from the same series of sections, but more laterally, the hydropore is seen distinctly; the large cavity from which it proceeds can only be the combined hydro-enterocoel vesicle. That the latter is not yet entirely separated from the entoderm vesicle appears from Pl. VII. Fig. 12, which is a frontal longitudinal section of an embryo 4 days old. Pl. VII. Fig. 11, which re-presents a transverse section through another embryo 4 days old, shows the hydro-pore distinctly; in the following sections of the same series the hydropore is seen to connect with the lobed vesicle seen below it in the figure. This accordingly is the hydrocoel; the central vesicle is the entoderm, that to the left in the figure the entero-coel. But, as said above I cannot go into further details of the transformation of the Brachiolaria into the young sea-star.

It should be pointed out that a similar walnut-like folding of the young embryo as shown in Pl. VII. Fig. 3, was found by Masterman to occur also in *Henricia sang-*

uinolenta (cf. MASTERMAN. "The early development of Cribrella oculata (Forbes)." Trans. R. Soc. Edinb. XL. 1902, Pl. I. Figs. 5, 16—17). But it is evidently only an exaggeration of a feature commonly found in embryos of Asteroids, also such as have small eggs and normal, total cleavage, the blastula having the wall irregularly folded, and only assuming the normal regular shape when the embryo leaves the egg-membrane. It seems beyond doubt that it is lack of space within the egg-mem-

Fig. 18. Embryos of *Fromia ghardaqana* Mrtsn. a. $6^1/_4$ days old; oral side; showing the first rudiments of the ambulacral skeleton. b. 12 days old; dorsal side; showing the 5 terminal plates, and the primary dorsal plates. $\times$ 72.

brane which necessitates this folding of the skin, and the embryo, when it has straightened its skin after leaving the egg-membrane, is at once much larger, in contradistinction to other Echinoderms, in which no such folding of the skin of the blastula occurs.

The development of the skeleton may be studied on larvæ made transparent in Canada balsam. The first rudiments of skeletal plates are found in larvæ about $3^3/_4$ days old, having just assumed the Brachiolaria shape (Pl. VI. Fig. 2). A great number of small crystals are seen there, strewn without any apparent order over the posterior end of the body, both on the dorsal and the ventral side. Any direct interpretation of these young plates is impossible, but evidently they all represent plates of the dermal skeleton, especially the small plates occurring in varying numbers in the later stages between the primary skeletal plates (fig. 18).

The first ambulacral plates are seen in fig. 18, a, from a larva $6^1/_4$ days old;

Fig. 19. Radial (a.) and terminal plate (b.) of embryo of *Fromia ghardaqana* Mrtsn. 8 days old. × 225.

also the terminal plates and the first plates of the dorsal skeleton are laid down here, but are shown somewhat more developed in fig. 18 b, from a larva 12 days old. They are of a very unusual, highly characteristic structure, irregularly star-shaped (fig. 19), and only gradually do they assume the usual shape of fenestrated plates, as seen in fig. 20, representing the dorsal side of a newly metamorphosed sea-star, 16 days old. Between the main plates are seen a number of quite small plates, each carrying a spine. It is noteworthy that the first circle of dorsal plates are placed interradially, though very early some irregul-
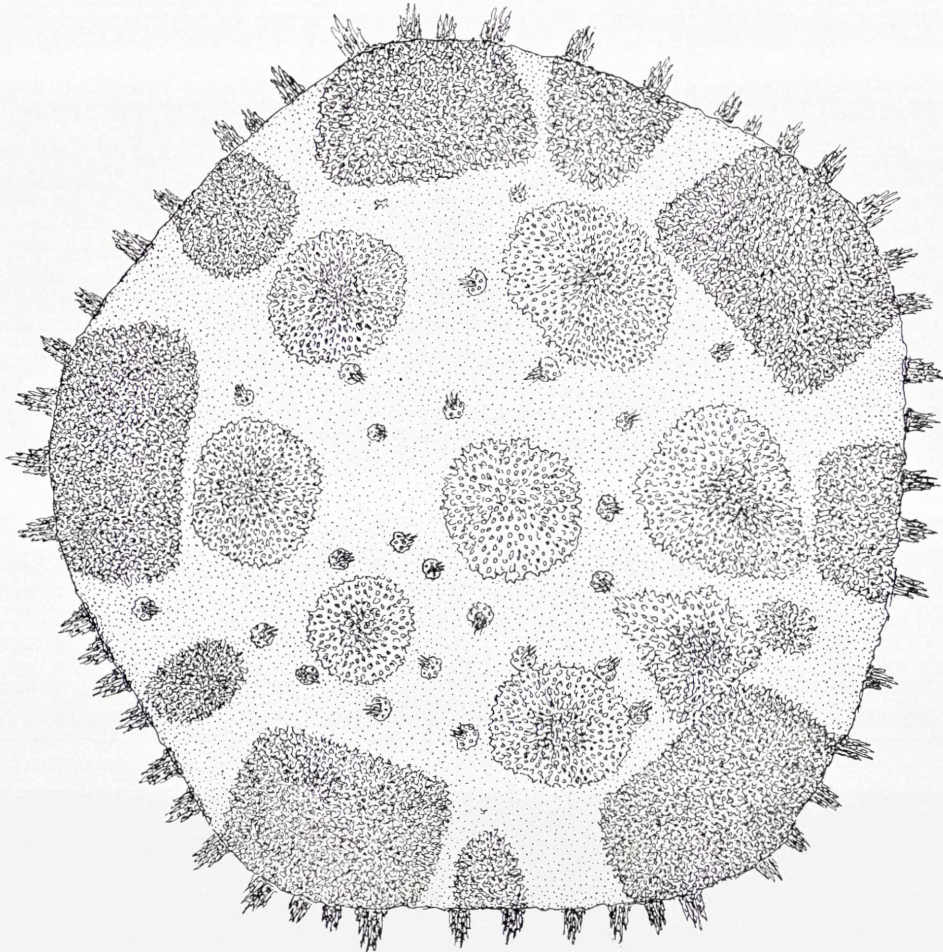
Fig. 20. Young sea-star of *Fromia ghardaqana* Mrtsn. 16 days old. Dorsal side. × 100.

arity appears in their arrangement (figs. 18 b and 20). The most advanced stage obtained, two months old, is represented in fig. 21, in which two pairs of tubefeet have developed. Very noteworthy is the large size of the terminal plates (with their ventral furrow for the terminal tentacle), which join in the interradial midline, no trace of marginal plates having appeared as yet. The ambulacral armature has begun to form, as well as the mouth-spines. Very noteworthy is also the fringe of marginal spines, such not being found in the adult sea-star. The dorsal side is wholly covered by skeletal plates, among which the central plate is the most conspicuous; the other plates are so closely packed that their identification is scarcely possible.

A few words may still be added concerning the hermaphroditism of *Fromia ghardaqana*. On gonads of the live specimens the hermaphrodite character is very easily ascertained directly under the microscope, the red eggs showing very distinctly in the whitish testicular tissue, and especially against the white mass of sperma-
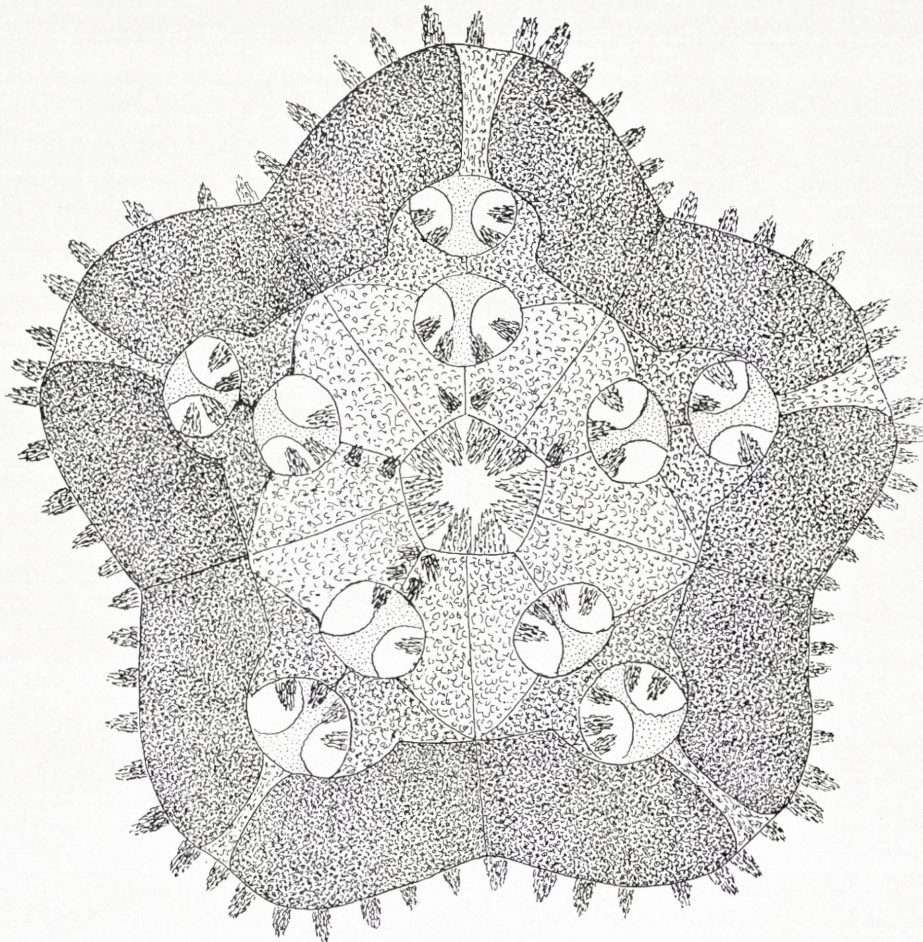
Fig. 21. Young sea-star of *Fromia ghardaqana* Mrtsn. Two months old. Oral side. × 65.

tozoa. Fig. 22 shows part of a section of a gonad from a specimen of only 10 mm arm-length (R). The young specimens I have constantly found to be almost pure males, but with a few, scattered eggs in the gonad walls. With age more eggs develop, and large specimens usually are almost pure females, with only rather insignificant traces
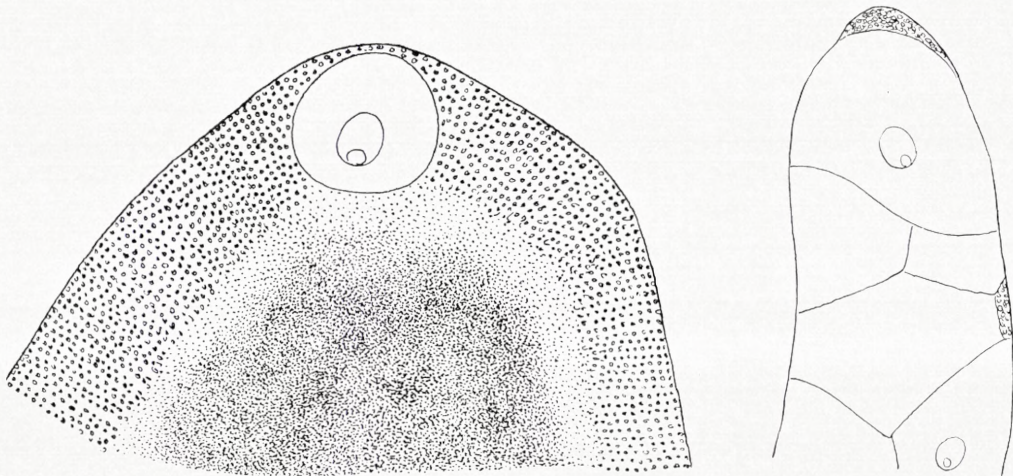
Fig. 22.   Fig. 23.

Fig. 22. Part of transverse section of gonad of *Fromia ghardaqana* Mrtsn., from a specimen of 10 mm. R. In the testicular mass is seen a single young egg. Fig. 23. Longitudinal section through the end of a gonad branch of an adult female *Fromia ghardaqana*. Indistinct remnants of testicular tissue are seen. 22×300; 23×40.

of sperma or testicular structure (Fig. 23). Still, also some adult specimens are functional males, but then always with a fair number of eggs in the gonads.

As pointed out in my "Contributions" III, p. 8, the only other Asteroid known to be a normal protandric hermaphrodite is *Asterina gibbosa* (Penn.), so the demonstration of *Fromia ghardaqana* being a protandric hermaphrodite is of considerable interest.

8. Echinaster purpureus (Gray).

Pl. VI. Fig. 5.

During my stay at Ghardaqa in 1936 I tried repeatedly, but in vain, to get material for studying the development of this sea-star, by artificial fertilization or through voluntary spawning of specimens kept in the tank. The large, almost black eggs, like other eggs full of yolk, resist artificial fertilization, and no spawning took place, though a great number of specimens were kept alive in the tank for a long time.

This year I again kept a good number of specimens in the tank of the laboratory, and on the morning of July the 11th I had the pleasure of finding that some spawning had taken place during the night. Unfortunately no precaution had been taken to prevent the eggs, which float at the surface like those of *Fromia*, from being carried

away with the water flowing out through the outlet of the tank; the result was that I could secure only 10 eggs in all from this spawning. They were put into the plankton-net in the tank, together with the red *Fromia* eggs, the two species being, of course, very easily distinguished by their colour.

For the following nights all precautions were made to prevent eventual new eggs from being carried away with the water — but no new spawning took place, now or later, although a considerable number of specimens were kept the whole time till my departure in September.

The very scant material obtained was, of course, quite insufficient for a detailed study of the development of this species — the more so as after a couple of days only two embryos were left. But these two were taken great care of, and they developed normally till near metamorphosis, when they were preserved.

It was observed that the cleavage, in spite of the great yolk-content of the eggs, is total and regular; but only the 2- and 4-cell-stages were observed, and no drawings were made, as I was expecting to get new material the following days and therefore would not risk losing the few eggs I had. The young larvæ were very like the *Fromia* larvæ, differing from the latter only in their dark, blackish colour; but in contra-distinction to the *Fromia* larvæ they attached themselves to the bottom of the dish by means of their sucking disk. At the age of four days they showed signs of metamor-phosis, the young sea-star being indicated.

A characteristic feature of the *Echinaster* larva is the large size of the anterior Brachiolaria-arm, the paired Brachiolaria-arms remaining quite small (Pl. VI. Fig. 5). There is a rather large sucking disk at the base of the large Brachiolaria-arm (not very distinct in the figure, which represents the larva in half side view). — The ske-leton of the young sea-star at this stage is represented only by a number of quite small crystals, which cannot be identified with certainty, so I refrain from giving a figure thereof.

The development of *Echinaster purpureus*, as far as known, agrees very closely with that of the Mediterranean *Echinaster sepositus*, as described by NACHTSHEIM (Über die Entwicklung von Echinaster sepositus (Gray). Zool. Anzeiger. XLIV. 1914). Here, too, the larva is a reduced (red) Brachiolaria with a very large anterior arm. In the preserved *Ech. purpureus* larva the shape of this lobe is, in its somewhat con-tracted shape, even rather exactly as shown in NACHTSHEIM's fig. 6, p. 604 (Op. cit.). — I shall not enter on a criticism of NACHTSHEIM's paper, but confine myself to pointing out that what he regards as the mouth of the larva is the sucking disk of the Bra-chiolaria.

Ophiuroidea.

9. **Ophiothrix Savignyi** (Müller & Troschel).

Pl. V. Fig. 1.

On the very first day of my stay at Ghardaqa this summer, July the 1st, I got some specimens of this species, from a large sponge taken by dredging. They proved to be ripe, and on being put into a dish with water taken from off the pier, which was a good deal warmer than that in which they had at first been kept, they immediately spawned. During spawning they moved one or two arms at a time with rapid, snake-like movements (— much as a swimming *Nereis* —), at the same time raising

a.   b.
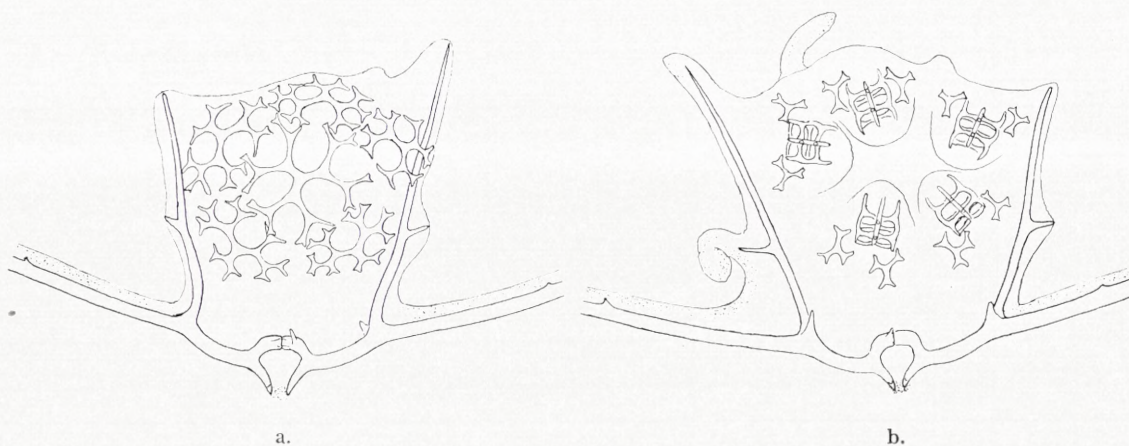
Fig. 24. Skeleton of larva of *Ophiothrix Savignyi* (Müll. & Troschel), in beginning metamorphosis. a. Dorsal side, showing the central and radial plates; b. oral side, showing the terminals and the first pair of lateral plates. $\times$ 105.

the corresponding part of the disk, shedding the genital products. (I have not observed such spawning movements in any other Ophiuroid).

The eggs are whitish, intransparent, c. 0.1 mm in diameter. The fertilization membrane lies close to the surface of the egg. The cleavage (the 2-cell stage reached one hour after fertilization) is regular, the cleavage-cells with a very distinct, transparent outer layer. The next morning, 14 hours after fertilization, the embryos were dense, transverse-oval gastrulæ, without apical crest, and with the first rudiments of the skeleton already formed. At the age of 22 hours they had the shape of young plutei.

The fully formed larva, two weeks old, is of the typical *Ophiothrix*-shape, distinguishable from the *Ophiothrix triloba* larva ("Contributions" III. Pl. IX. 2—3) only by its colour: 3—4 yellowish gray bands on the posterolateral arms; no black spots on the body. The stomach is a very faint yellowish-gray (Pl. V. Fig. 1).

At the age of three weeks the larvæ were in metamorphosis. I have been unable to ascertain definitely whether the hydrocoel grows round above the oesophagus; evidently the hydrocoel-development proceeds at great speed, which may account

for the lack of the intermediate stages. Otherwise, the metamorphosis is as typical of *Ophiothrix*, the long arms remaining unresorbed as floating organs of the young brittle-star, to be thrown off when the metamorphosis is completed.

Figs. 24, a—b show a developmental stage, where the main parts of the skeleton have been laid down, figs. 25, a—b the young brittle-star, with the first arm-spines of the characteristic hook-shape. Very characteristic is the central plate, with its unusually large holes. A conspicuous feature is also the large size of the first ventral plate.

a.   b.
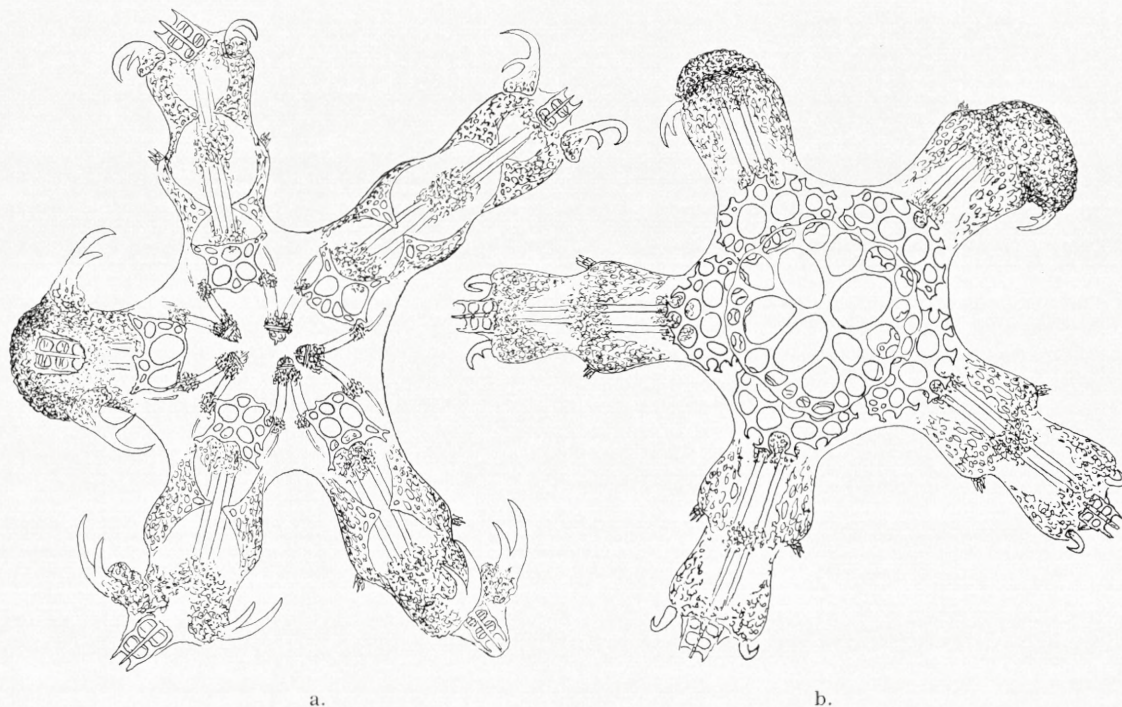
Fig. 25. Newly metamorphosed brittle-star of *Ophiothrix Savignyi* (Müll. & Troschel). a. Oral side, showing the mouth-skeleton, the first ventral plate, and the first two pairs of ambulacral plates (vertebræ); b. dorsal side, showing the remarkably developed central plate and the radial plates. $\times$ 105.

It may be mentioned that I found fully ripe specimens of this species again in September, so that it must have at least two spawning seasons; but as I did not continually pay attention to the state of maturity of this species, I cannot say anything more definite about its spawning, but the facts available rather tend to indicate a monthly breeding during the summer time.

10. Ophiolepis cincta Müller & Troschel.
Pl. VI. Figs. 6—9.

A number of specimens of this species (which is rather common under coral blocks on the reefs and on the shore-flat at Ghardaqa) were put together into a dish

on July 23rd, and were found the next morning to have spawned during the night. The eggs were reddish-brown, intransparent, 0.3 mm in diameter. They were found, as it were. attached to the armspines nearly to the tip of the arms.

Nothing of the cleavage process could be observed, partly because of the intransparency of the eggs, partly because the cleavage had taken place in the course of the night. In the morning, when c. 12 hours old, the embryos, still enclosed in the egg-membrane, were blastulæ, showing the beginning gastrula formation (Pl. VI. Fig. 7). In the afternoon the embryos were free-swimming elongate, flattened gastrulæ,

a.   b.   c.   d.
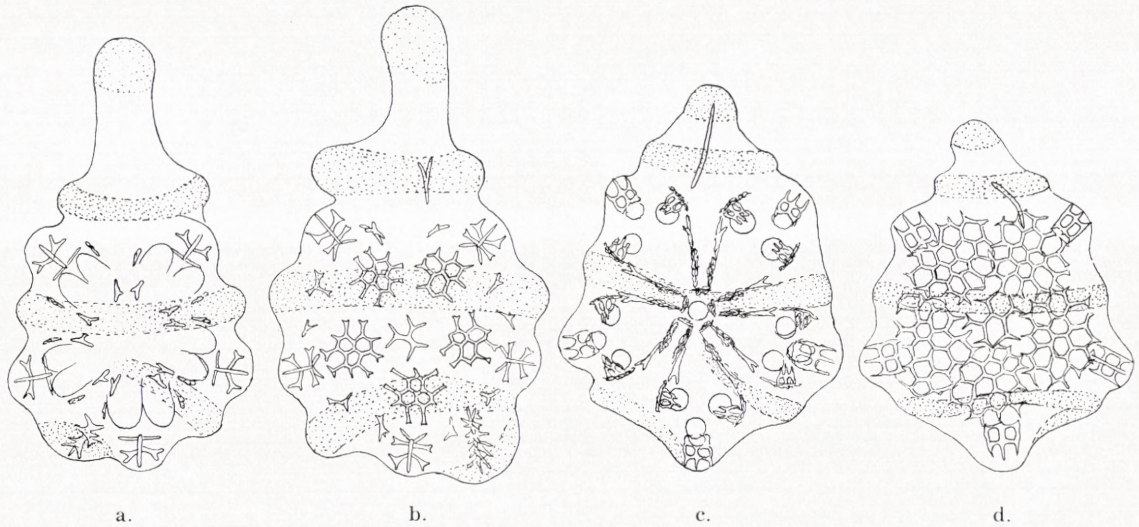
Fig. 26. Two stages in the development of *Ophiolepis cincta* Müll. & Troschel. a. and c. from the oral side, b. and d. from the aboral side. In figs. b.—d. is seen the rudimentary larval skeleton in the anterior end, in figs. a. and b. the complicate skeletal rod in the posterior end. × 135.

which collected at the surface, close to the edge of the dish, forming, as it were, a string of beads. In Pl. VI. Fig. 8 is represented a section of the gastrula stage, c. 18 hours, showing no distinct archenteron or blastocoel cavities. Pl. VI. Fig. 9 is a sagittal section of an embryo c. $1^1/_2$ days old. The notch on the left side probably represents an incipient larval mouth, which however, does not develop any farther.

About $2^1/_2$ days old the embryos were already in beginning metamorphosis, the development being direct, without an Ophiopluteus stage. The shape of the larva (Pl. VI. Fig. 6) is triangular, with a narrow anterior lobe, surrounded at its base with a ciliated band, and with an apical ciliated tuft; the main part of the body is pentagonal, on account of the developing young brittle-star. There is a median ciliated band, nearly complete, and two incomplete bands in the lower part. The colour of the larva is uniformly reddish (in transmitted light; in reflected light it is more redbrown). The edges of the ciliated bands are dark.

A very interesting fact is that there is a rudimentary larval skeleton in

this larva: usually, but not constantly, a slender rod, simple or branched, in the anterior lobe and an unsymmetrically placed, irregular, very complicate, branched rod in the posterior end (figs. 26, a—b). In figs. 26, a—d are represented two stages in the development of the skeleton of the brittle-star; a detailed description seems to me superfluous, the figures giving directly all the information available. Note-worthy is the small size of the central plate, which lags far behind the radials in its development. The details of the ambulacral (oral) skeleton in the more advanced stage are rather difficult to make out, the divers plates mainly standing on edge. The presence of the first arm-spine makes the interpretation of the plate to which it is attached as the first lateral (adambulacral) plate certain.

The young brittle-stars, after the complete resorption of the larval body, were put into a dish with sand on the bottom, in the hope that they would go on growing; but evidently they did not find conditions suitable, and I did not succeed in getting them any farther in their development.

The development of *Ophiolepis cincta* agrees very closely with that of the West Indian *Ophionereis squamulosa* Koehler, as described and figured in my "Studies of the development and larval forms of Echinoderms" (1921), p. 171—177, Pl. XXXI. 1—6. I gave there a detailed discussion of the literature relating to Ophiuroids with direct development, without an Ophiopluteus larva, to which it may suffice to refer.

Holothurioidea.

11. **Synaptula vittata** (Forskål).

Pl. IX. Figs. 1—3.

In my researches of last year (1936) I did not succeed in rearing to metamor-phosis the larva of this species, so very common on the littoral reef-flat at Ghardaqa. The larva was figured on Pl. X. 7 and XI. 6 of my "Contributions" III, but I stated (Op. cit. p. 54) my expectation that the larva in its later stages would prove to be a good deal more complicate. I was therefore anxious to try again this summer (1937) to rear this larva through metamorphosis — in which I succeeded. Some specimens put into the tank of the laboratory on July the 10th spawned during the night. The embryos were distributed in three dishes, all dealt with in the same way, being put into fresh sea-water every day. After 12 days the larvæ in one of the dishes were near metamorphosis, those of the two other dishes being in poor condition or having died already, as it happened last year. But the one dish with the larvæ in good con-dition was enough to secure success, the larvæ herein not only reaching their full shape and size, but also metamorphosing.

The fully formed larva, c. 12 days old, is rather complicately lobed, and full of wheels all over (Pl. IX. Fig. 1). It is perfectly transparent, without any pigment. When two weeks old. some of the larvæ were metamorphosing, having assumed the typical barrel-shape (Pl. IX. Fig. 2), so well known especially from SEMON's beautiful

figures (Die Entwicklung der Synapta digitata. Jenaische Zeitschr. XXII. 1888, Taf. VI—VII), with the ciliated band transformed into closed rings. Whereas the larva swims quietly along, it begins, when about to transform into the barrel-shaped "pupa" (or *Doliolaria*), to whirl round, and when it has assumed the barrel-shape it whirls round and round, always to the right, in a quite frantic hurry, standing, generally, upright in the water.

The young, fully metamorphosed Synaptula is, as usual, much reduced in size, much smaller than the larva and the pupa. I tried to keep them for further growth, putting them into a dish with a few small stones and algæ from the localities where the adults were common, and succeeded to some extent. The most advanced specimen, 5 weeks old, represented in Pl. IX. Fig. 3, has still only 5 simple tentacles; but both the radial and interradial pieces of the calcareous ring have been laid down. The body wall is full of wheels, the shape of which is given more enlarged in fig. 27 b; they are very small, only c. 0.005 mm. Anchors have begun to appear, lying transversally; they are simple, without knobs on the vertex; the anchor-plates are still of quite irregular shape. In the tentacles rosettes have begun to appear — and in the posterior end the balls of the larva are still lying undissolved. The young *Synaptula* is able to crawl along on the bottom by means of its tentacles, on which some small papillæ are found; it is also able to attach itself quite firmly to the bottom, so that it requires quite a strong jet from a pipette to remove it.

I regret very much having omitted to look for the statocysts in the live specimens; in the preserved ones I cannot find them.

Some of the larvæ did not metamorphose till 4—5 weeks old.

Fig. 27. Anchor (a.), wheel (b.), and rosettes (c.) of the young *Synaptula vittata* (Forskål). Wheel of *Opheodesoma grisea* (Semper) (d.). a.—c. × 540; d. × 850.

12. **Opheodesoma grisea** (Semper).
Pls. VIII. Figs. 1—18; IX. Fig. 4.

This large, fine, reddish-mottled Synaptid (up to 2—3 metres long), which occurs in good numbers near the station, especially at Abu Sadaf, — together with the still larger, up to 5 metres long, grey *Synapta maculata* (Chamisso & Eysenhardt) — was found (like the latter) to live very well in the tanks of the laboratory; even if quite a large part of the body had been lost, the anterior part would live quite well

(— and, no doubt, under natural conditions, would regenerate the lost part —). Although kept for nearly a month, a good number of specimens together, they did not, however, spawn, so I thought it advisable to try artificial fertilization, even though I hardly expected any success.

When opening some specimens, on August the 28th, I was very much surprised on finding this species to be a hermaphrodite. It was clear that the specimens were in the main either males or females, but in the male gonads always a varying number of eggs were found, and in the female gonads always some sperma. Sections of the gonads fully verified the observations made on the living material (fig. 28). Still more surprising was the fact that within the gonads a small number of embryos in the gastrula-stage were present. which means that self-fertilization may take place. (Also I found that when I kept pieces of gonads of a "female" separately, a good number of the outstreaming eggs would become fertilized and start normal cleavage). On isolating some of the gastrulæ from within the gonads I saw them develop into young Auriculariæ, and there is

Fig. 28. Part of section of hermaphrodite gonad of *Opheodesoma grisea* (Semper). $\times$ 165.

no reason to doubt that they would be able to go on developing and metamorphosing. Still, it is clear that this species does not normally propagate by self-fertilization, but by cross-fertilization in the usual way.

The eggs of the opened "females" were found to be, for the greater part, ripe for fertilization, no nucleus being visible, and fertilization, with sperma from a "male" specimen, succeeded completely, The eggs are c. 0.1 mm in diameter, quite clear and transparent. The young cleavage-stages, exceedingly beautiful ("like a diagram" I have said in my notebook), up to the 32-cell stage, were observable after two hours. Four hours old the embryos were in the blastula-stage, eight hours old the gastrula invagination was beginning to form, the embryo still lying within the fertilization membrane; but immediately after the formation of the gastrula invagination the membrane dissolves, and the embryo becomes free-swimming. (Pl. VIII. Figs. 1—10). The gastrula now becomes more and more elongate, and at the age af 15 hours it is very elongate and slender (Pl. VIII. Figs. 11—13), the remarkably long and slender gastrula invagination beginning to curve towards the future ventral side (for the formation of the larval mouth); a number of mesenchyme cells have wandered into the blastocoel cavity from the upper end of the invaginated part. The formation of the enterocoel pouches I have not followed in details; Pl. VIII. Fig. 13 apparently represents a stage in their formation; they seem to be attached to the ectoderm wall,

7*

much as I found it to be the case in the gastrula of *Temnotrema scillæ* (Mazetti) ("Contributions" III, Pl. X. 1).

At the age of c. 1³/₄ days the embryos had assumed the shape of young Auriculariæ, perfectly transparent, still without indication of wheels (Pl. VIII. Figs. 14—15). Three days old they showed the beginning formation of calcareous balls in the left, sometimes also in the right, posterolateral lobe (Pl. VIII. Figs. 16—17), and in larvæ 7 days old the first formation of wheels was observed (Pl. VIII. Fig. 18), sometimes in the left, sometimes in the right posterolateral lobe.

At the age of 11 days (September the 9th) the most advanced larvæ (Pl. IX. Fig. 4) were, evidently, near metamorphosis, as indicated by the fact that the left enterocoel had grown so much as to reach the end of the stomach, the right enterocoel also beginning to grow (in the previous stages both enterocoel and hydrocoel vesicles were so small as to be exceedingly difficult to distinguish). The hydrocoel also had grown somewhat, but was still unlobed. There was still only one wheel in each posterolateral lobe, but some small cell-groups here, and also in the anterior end of the larva, seemed to indicate that a few more wheels would be present in the metamorphosing larva.

The larva at this age (Pl. IX. Fig. 4) — which is perfectly clear, without any trace of colour — must be very nearly fully formed, which means that the *Opheodesoma* larva is scarcely more complicate than the *Synaptula* larva, both of them being very far from reaching the exceedingly complicate shape and large size of the famous *Auricularia nudibranchiata*. The rather more complicate Synaptid larva mentioned on p. 54 of "Contributions" III can, according to the observations here recorded, hardly have been an *Opheodesoma* larva; it may have been the *Synapta maculata* larva, which is still unknown.

When I left Ghardaqa, September the 12th, only a very few larvæ of *Opheodesoma* were still alive; as there was evidently no hope of keeping them till metamorphosis, they were then preserved.

It may be added that the *Opheodesoma serpentina* mentioned on p. 54 of "Contributions" III should be *Opheodesoma grisea*, which is the common *Opheodesoma* species found at Ghardaqa. *O. serpentina* is much more rare, usually found only in single specimens on the outer reefs, and I never had specimens enough of this species for keeping them in the tanks for eventual spawning.

13. Holothuria impatiens (Forskål).

Pl. X. Figs. 1—6.

During my stay at Ghardaqa last summer (1936) I had kept a good number of this species, so common under stones on the reef-flat close to the station, in a big dish with stones on the bottom for nearly two months, May—June, in the hope that they would spawn. Although apparently ripe they did not, however, spawn. On my arrival at the station this summer, July 1st, 1937, I at once again put a number of

specimens into a big dish with stones, and now I had the pleasure of finding them to have spawned during the night of the 2nd—3rd July, the dish containing on the morning of the third numerous, not yet swimming, blastulæ. Towards the evening, thus about 18 hours old, they were fine gastrulæ. Two days old the embryos had assumed Auricularia-shape, with a rather distinct yellowish pigment, but still without any skeletal elements. At the age of 5 days the larvæ had formed a calcareous ball in the posterior end of the body, often lying asymetrically; more rarely there were two balls (Pl. X. Figs. 1—2). Usually the posterior end of the body is simply drawn out, the ball not lying in a slender prominence, as is often the case in Auriculariæ, e. g. in that of *Holothuria scabra* ("Contributions" III. Pl. XII. 1); in the more advanced larva there is, however, a fairly distinct prominence from the posterior end, in which the ball is situated. The ball is covered with low, spiny prominences or warts (fig. 29, b).
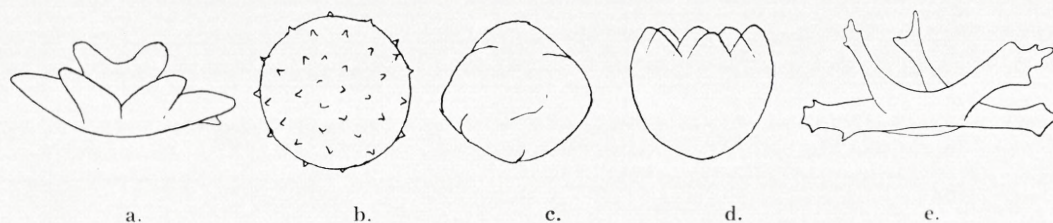
Fig. 29. Spicules from the posterior end of divers Auriculariæ, a. *Holothuria papillifera* Heding; b. *H. impatiens* (Forskål); c. *H. pardalis* Selenka; d. *H. difficilis* Semper; e. *H. (Microthele) nobilis* (Selenka). a. and e. × 700; b.—d. × 450.

At the age of about two weeks some of the larvæ were in beginning metamorphosis, the hydrocoel having formed lobes, the enterocoel being prolonged backwards, and the elastic balls having appeared (Pl. X. Fig. 3). It is a very interesting fact that the madreporite-skeleton has formed already at this stage. The larva is of the common type, not distinguishable by its shape from the other *Holothuria* larvæ known till now. It has a number of rather regularly distributed yellow pigment spots in the ciliated band, none in the body, except along the posterior end.

The various stages of metamorphosis were easily observable (Pl. X. Figs. 4—5), showing the breaking up of the ciliated band of the larva, the pieces uniting so as to form the rings of the pupa or "Doliolaria", as was described and figured in details by SEMON for *Synapta* (i. e. *Labidoplax*) *digitata* (Op. cit. 1888, Taf. I—II). I was able to ascertain definitely on these pupæ that the elastic balls are not always present in their full numbers, 5 pairs; not only those in the upper corners are often wanting, but some of the others may be present only on one side (Pl. X. Figs. 4—5).

Whereas a number of the larvæ metamorphosed when three weeks old, many of them continued life as fully formed, normal larvæ, not metamorphosing. Having already got a number of them metamorphosed, I did not take special care of these larvæ, and they were not transferred to fresh sea-water for a quite a long while. After three weeks more, still finding about 30 of them apparently quite normal and healthy

looking, I thought that perhaps lack of sufficient food might be the reason for their not having metamorphosed, and so I started again transferring them to fresh sea-water every day to see, whether they would now perhaps metamorphose — and so they did. After 6—7 days most of them had metamorphosed. This rather casual experiment throws important light on the ability of the larvæ to survive for a considerable time beyond their normal life-time and thus postpone metamorphosis when under unfavorable conditions (cf. above, pp. 9—10).

The young, newly metamorphosed Holothurians were put into a separate dish with small stones with algæ and a little sand on the bottom, thus under about normal conditions, in the hope that they would develop a little farther; and so they did, at least a few of them. At the age of 5—6 weeks some of them had the first tubefoot

a.   b.   c   d.   e.
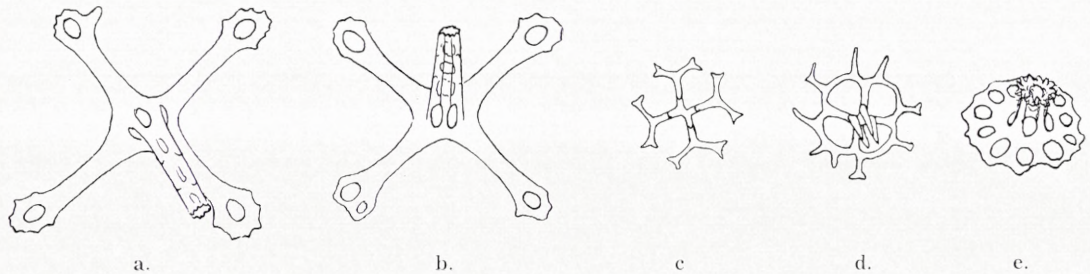
Fig. 30. Calcareous deposits from the skin of the young *Holothuria impatiens* (Forskål). a.–b. Slender form of tables; c.—d. development stages of the second type of tables (e.), from the posterior end of the body. × 300.

developed, and the tentacles were distinctly knobshaped (Pl. X. Fig. 6). Calcareous bodies, young tables, had begun to appear in the body wall and at the base of the tentacles, forming small prominences, like small feet; the larval calcareous ball from the posterior end of the larva remains undissolved in the posterior end of the body. The calcareous ring has been formed, but apparently as yet only the radials (their shape not to be made out distinctly). The elastic balls have disappeared.

When about to leave the station I searched the dish for eventually surviving specimens and succeeded in finding two, which were now 10 weeks old. They had grown quite considerably, the best one being about 2 mm long. There are still only 5 tentacles, but three tubefeet, close together, on the ventral side. The body wall is studded with spicules, viz. tables with a long, slender spire rising from a base with four long, slender arms, each with a small terminal widening with a single hole (abnormally sometimes two holes). In the posterior end of the body, where the larval ball is still distinct, are found a few tables of quite a different shape (fig. 30 e), in the main like those of the adult. No buttons formed as yet. The calcareous ring and the internal anatomy not to be observed through the dense coat of spicules.

The fact that the tables of the young *Holothuria impatiens* are so very different from those of the adult is, of course, of phylogenetic importance. The conclusion seems unavoidable that the ancestor of *H. impatiens* had tables of this primitive

type — but I think it preferable to put off a detailed discussion of this problem till the postembryonal development of more species of *Holothuria* (sensu lat.) has been studied.

14. **Holothuria pardalis** Selenka.
Pl. IX. Figs. 5—6.

A number of specimens of this beautiful species, which occurs — rather sparingly — on the reefs at Ghardaqa, particularly Abu Sadaf, were kept in the tanks of the station for quite a long time for eventual spawning. But no spawning took place, and the only hope of studying its development was then to try artificial fertilization, which was done on August the 26th — rather late in the afternoon. Although a good number of the eggs were ready for fertilization, showing no nucleus, it seemed at first that no fertilization had taken place. However, after about 20 hours there were a fair number of free-swimming gastrulæ, so that a small percentage of the eggs had actually been fertilized, the reason why it could not be ascertained at once being that the fertilization membrane lies very close to the egg-surface; and on account of the late hour when the fertilization was undertaken the cleavage did not begin till it was dark. But here, anyhow, was a case, where artificial fertilization of a Holothurian had succeeded.

At the age of two days the embryos were beginning to assume the Auricularia-shape, and on the third day a small ball had appeared in the posterior end of the body (Pl. IX. Fig. 5). At the age of two weeks the larva had reached its full shape, showing the signs of beginning metamorphosis, viz. the elongation of the enterocoel and hydrocoel vesicles, and the formation of the elastic balls. No lobes were visible as yet on the hydrocoel, but the madreporite spicule had already begun to form. The shape of the larva is quite as usual, as is also the colour (Pl. IX. Fig. 6), the only character by which this larva can be distinguished being the calcareous ball in the posterior end of the body, which is spherical, or somewhat angular, quite smooth, only with a couple of more or less irregular furrows (fig. 29, c).

As the larva only reached its full shape at the time when I had to leave the station, there was no possibility of having it reared through metamorphosis, the more so as only very few of the larvæ were then still in good condition.

15. **Holothuria papillifera** Heding (n. sp.)[1].
Pl. XI. Figs. 1—3.

Of this new species, so highly characteristic by its numerous long, soft, backward directed papillæ, only a few specimens were found on Abu Sadaf and Abu

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[1] According to information from Mr. S. G. HEDING, who has kindly undertaken to identify my Ghardaqa-Holothurians, this new species recalls by its calcareous deposits *H. vagabunda* Selenka, but differs strikingly from that species by its peculiar long, soft dorsal papillæ, and by lacking the Cuvierian organs. The colour is a uniform grayish-brown. The tables are c. 45 μ, with one cross-bar and c. 8 spines in the crown, disk usually well developed, with 10 large holes. Buttons very regular, 50 μ long, with 6 angular holes. In the longitudinal muscles 30—40 μ large oblong rings.

Fanadir. On the 19th of August two specimens, which I had in the tank, spawned — but both were males. On the 21st I got two more specimens, which spawned when put into the tank, and this time, fortunately, one of them was a female.

The eggs are 0.1 mm in diameter, of a very faint reddish colour. The fertilization membrane lies quite close to the egg-surface. About 12 hours old the embryos were in the blastula stage, but still lying within the membrane; also the gastrula stage begins within the membrane. At the age of about 22 hours the gastrulæ were free-swimming. Four days old the young Auriculariæ, which are unusually broad at the anterior end (Pl. XI. Fig. 1), have formed the spicule in the posterior end. At the age of two weeks the larvæ showed the first sign of the formation of the elastic balls, and at the time when I had to leave the station, the now nearly three weeks old larvæ were in beginning metamorphosis, the elastic balls having formed, and the enterocoel and hydrocoel vesicles being elongated, though lobes had not yet begun to appear on the hydrocoel.

The fully formed larva (Pl. XI. Fig. 3) is scarcely to be distinguished with certainty from the other *Holothuria* larvæ by its shape alone. Also its colour is as usual. But the larval spicule is highly characteristic (fig. 29 a; p. 53), a rather thick-lobed star, and distinguishes it at once from the other larvæ thus far known.

These larvæ were rather unusual in swimming so close to the surface that many of them were caught by the surface-film and thus killed. This was probably the main reason, why the few larvæ still alive when I left the station, disappeared without metamorphosing.

16. **Holothuria (Microthele) difficilis** Semper.

Pl. XI. Figs. 4—5.

Most of the specimens of this species, which is rather common on the reefs at Ghardaqa, were small and showed more or less evident signs of regeneration after autotomy. But in the beginning of August the sailors brought home a number of specimens, which were evidently adult (some 10 centimetres long, when fully extended). They were put into a separate dish under a faint current from the tap, and on the 10th of August I had the great pleasure of finding that they had spawned during the night. The embryos were free-swimming gastrulæ in the morning, so I have no observations on the earliest stages. Judging from the size of the gastrulæ the eggs must be of the usual size, c. 0.1 mm in diameter. Next day the embryos were young Auriculariæ, and two days old they had formed the calcareous spicule in the posterior end of the body.

At the age of 10 days the larvæ showed the first signs of metamorphosis, viz. the presence of elastic balls and the elongation of the enterocoel and hydrocoel vesicles. Two weeks old several of the larvæ had metamorphosed. After another two weeks the young Holothurians had developed the first tubefoot — while several of the larvæ still remained unmetamorphosed, but evidently normal. No doubt it would have been possible to induce these belated larvæ to metamorphose, as was

the case with the *Holothuria impatiens* larvæ; but there was no time to try this experiment.

The fully formed larva (Pl. XI. Fig. 5) is of the usual shape, not to be distinguished from the other larvæ except by its larval spicule, which shows a number of tight lobes (fig. 29, d; see p. 53). The madreporite spicule is beginning to appear in the fully formed larva.

In the most advanced of the young Holothurians tables were not yet fully formed, but still so far in their development as to show that they are not going to assume the same characteristic shape as that of the tables of the young *H. impatiens*.

As this species is referred to the subgenus (or genus) *Microthele* Brandt, I expected that it would differ to a fair extent from the larvæ of the *Holothuria* s. str. This, however, proved not to be the case.

17. **Holothuria (Microthele) nobilis** (Selenka).

Pl. XI. Fig. 6.

This large and very fine Holothurian is not rare on Abu Sadaf, where it is found lying on the sand, having covered itself with sand and algæ so that it is not very easily distinguished. A number of them were kept in the tank, where they spawned on July the 25th. The result of this spawning was, however, very poor, only few of the embryos reaching the gastrula-stage, and none of them beyond that stage.

Some other specimens were soon put into the tank, where they appeared to live quite well, though without food; they would usually come up to the edge of the water and stretch the fore-end out under the surface of the water, with the mouth turned upwards and the tentacles widely extended, affording quite a fine show. On the 15th of August, after they had been kept in the tank for more than two weeks, I found that they had spawned during the night, a great number of swimming gastrulæ being found in the tank. This time the embryos appeared normal and healthy. One day old they were beginning to assume the Auricularia shape, three days old they were young, fine Auriculariæ, but still without calcareous spicules. Not till the fourth day did the spicules appear — and proved to differ very conspicuously from those of *H. (Microthele) difficilis*, there being not a single spicule in the middle of the posterior end of the body, but one in each posterolateral corner (Pl. XI. Fig. 6). The spicules have the shape of irregular stars (fig. 29, e; see p. 53). The larva is a little broader than usual, but otherwise not peculiar.

In the course of the next few days the larvæ rapidly decreased in numbers and soon disappeared altogether, without having developed any further. They were on the whole very weak swimmers and evidently unusually delicate, so it will probably be a very difficult task to rear them beyond the first larval stage.

The fact that the larva of *H. nobilis* differs so very conspicuously from the larva of *H. difficilis* in the important character of the larval spicules, seems to indicate that

it is not justifiable to refer both these species to the same (sub)genus *Microthele*, a suggestion supported also by the fact that the two species differ so very considerably in their size and general appearance.

Crinoidea.

18. **Heterometra Savignyi** (Joh. Müller).

Pl. XII. Figs. 1—12.

During my stay at Ghardaqa in April—June last summer (1936) this very fine, large Comatulid, which is particularly common on grass bottom, at depths of 1—2 fathoms, never showed the slightest sign of ripeness. This summer (1937) I again found the same to be the case during July. But finally in the last week of August, at full moon, I found it to contain ripe sexual products. A good number of specimens were put together into a large dish, under a fairly strong jet of water from the tap, and on the 23rd I had the pleasure of seeing them spawning. The males first emitted the sperm, so that the water became quite milky, and immediately after the females spawned, the eggs, which were at once fertilized, sinking to the bottom. The following four days renewed spawning took place, always at about 3 oclock in the afternoon. Later on no spawning took place, although I had a number of fresh specimens put into the dish. It would have been of considerable interest to see, whether they would spawn again at the next full moon, in September, but this could not be done, because I had to leave the station before then. But, at least, it is certain that this Crinoid is not ripe till August.

The eggs are small, 0.15 mm in diameter, rather intransparent. The egg-membrane is spiny, as usual. The cleavage is perfectly regular (Pl. XII. Figs. 1—2); the gastrula invagination is distinct already about 6 hours after fertilization, while the embryo is still lying within the egg-membrane. At the age of c. 15 hours they are leaving the egg-membrane. It appears that the embryos have not so much difficulty in leaving the egg-membrane, as I found it to be the case in the other Crinoids, the development of which I have studied formerly.

Already at the age of $1^3/_4$ days many of the larvæ were attaching themselves, at the uppermost edge of the water in the light side of the dish, they showing a very pronounced positive phototropism. Here they formed a dense line, like a string of beads. The next morning, thus about $2^3/_4$ days old, they were young Pentacrinoids. Some few specimens had attached themselves to the underside of the surface-film, hanging head downwards; a few other specimens had attached themselves to the bottom of the dish, or the pieces of shells that I had put on the bottom of the dish.

This habit of the larvæ of attaching themselves mainly at the upper edge of the water was very advantageous for the further rearing of the Pentacrinoids. I could then place the dishes with the Pentacrinoids in situ directly in the tank under a faint jet of water from the tap; they were thus under constant renewal of the water, with the normal source of food, and not in danger of being killed by the unavoidable residue

from the tap-water. Even in their position high up on the sides of the dish such residue would attach itself to their stalks, which could, however, easily be removed by a gentle jet of water from a pipette. The Pentacrinoids thus lived very well, and after my departure Dr. CROSSLAND very kindly undertook the care of them.

My hope that the Pentacrinoids would under these fairly natural conditions grow normally was, however, not fully realised. They did grow somewhat, but rather slowly, probably much more slowly than they would have grown under normal conditions. The most advanced stage reached (specimens sent me by Dr. CROSSLAND by the end of September and thus one month old) was the formation of the radial plates (Pl. XII. Fig. 12); but there is still here no beginning of the formation of free arms.

It is a rather curious fact that the Pentacrinoids attached to the sides of the dish were not nearly as long-stalked as those which had attached themselves to the bottom of the dish. The number of joints in the stalk is a little larger (24) in the more long-stalked specimens than in the more short-stalked ones (c. 20), but the joints themselves are also slightly longer in the former (Pl. XII. Figs. 9—10). This may perhaps indicate that the normal attachment of the larvæ is on the bottom, so that they must stand in an upright position.

Whereas, as said above, many of the larvæ attached themselves already about two days old, a great number continued swimming for a longer period, a few of them attaching themselves by and by. These older larvæ had evidently lost their phototropism; they were no longer collecting at the upper edge in the light side, but swimming freely in the water, mainly near the bottom. Even after two weeks I found numerous larvæ, now swimming close to or lying on the bottom, only quite few of them having just attached themselves and formed Pentacrinoids. No doubt most of these larvæ would have perished without metamorphosing. But it is clear that this Crinoid larva, like the other three Comatulids (with free swimming larvæ), the development of which I have studied till now, has the property of putting off the metamorphosis for quite a while and continuing the free-swimming life, if it does not find conditions for attaching itself suitable, a fact of importance as a means of dispersal (cf. "Contributions" III. p. 63).

In regard to the skeleton the important fact is to be noticed that there are no Infrabasalia. The shape of the oral plates recalls that of the Antedonids, they being somewhat excavated in the anterior part, with outturned edges (Pl. XII. Figs. 11—12).

The cleavage is total and perfectly regular, and the further embryonal development is exactly as in *Tropiometra carinata*, as I have described it in my "Studies on the development of Crinoids" (1920), pp. 6—13, Pls. I—IV; I do not see any reason to go into details here, but may confine myself to giving a few figures, Pl. XII. 1—5, from which the perfect agreement with the development of *Tropiometra carinata* appears clearly.

Plate I.

All figures of *Prionocidaris baculosa* (Lamarck).

Fig. 1. Egg with fertilization membrane.
- 2—3. First cleavage-stages, 2- and 4-cells stage.
- 4. 16-cells stage.
- 5. Blastula, typical form.
- 6. Abnormal blastula, "half-twin".
- 7—8. One egged twin and triplet; blastula stages.
- 9. Young gastrula, 19 hours old.
- 10. Gastrula, 26 hours old, showing incipient formation of the enterocoel pouches and the first rudiments of the skeleton.
- 11. Young Echinopluteus, $2^{1}/_{4}$ days old.
- 12. Nearly fully formed Echinopluteus, 10 days old.

Figs. 1—11 $\times$ 150; fig. 12 $\times$ 112.

Pl. I.
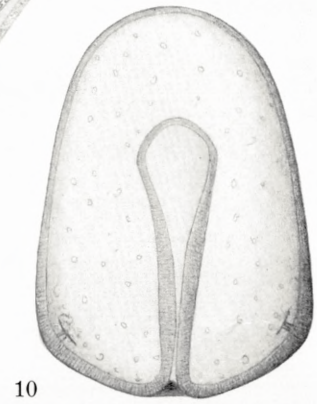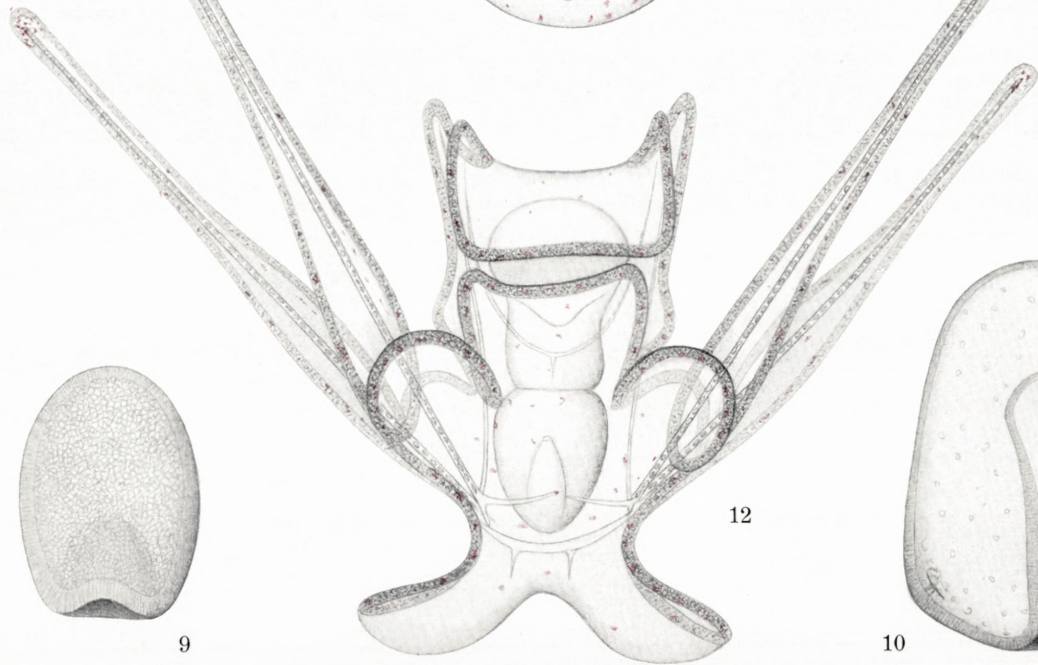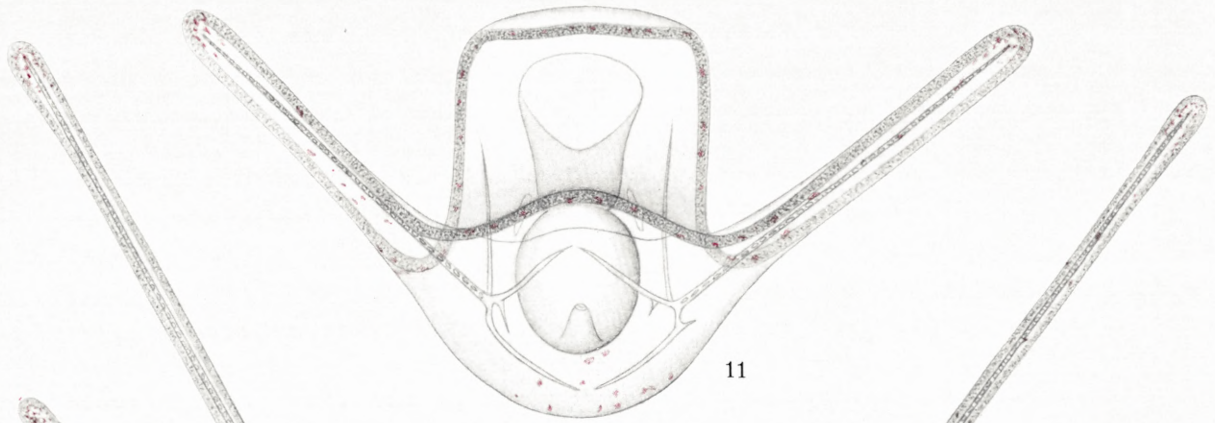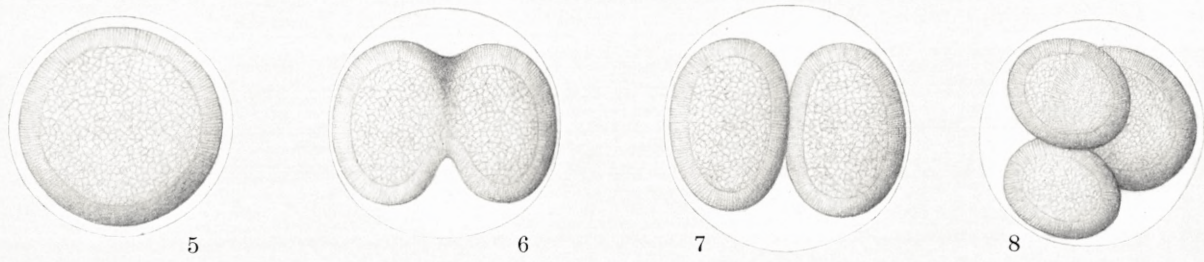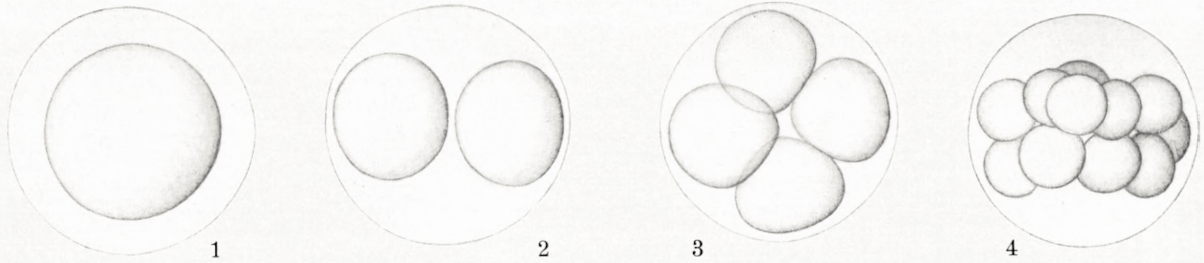
Plate II.

Prionocidaris baculosa (Lamarck).

Fig. 1. Fully formed Echinopluteus, from the oral side. × 60.
  - 2. Fully formed Echinopluteus in side view, with the postoral and posterodorsal arms thrown backwards. × 60.

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Plate III.

D. K. D. Vidensk. Selsk. Skrifter, naturv. og math. Afd., 9. Række, VII, 3.

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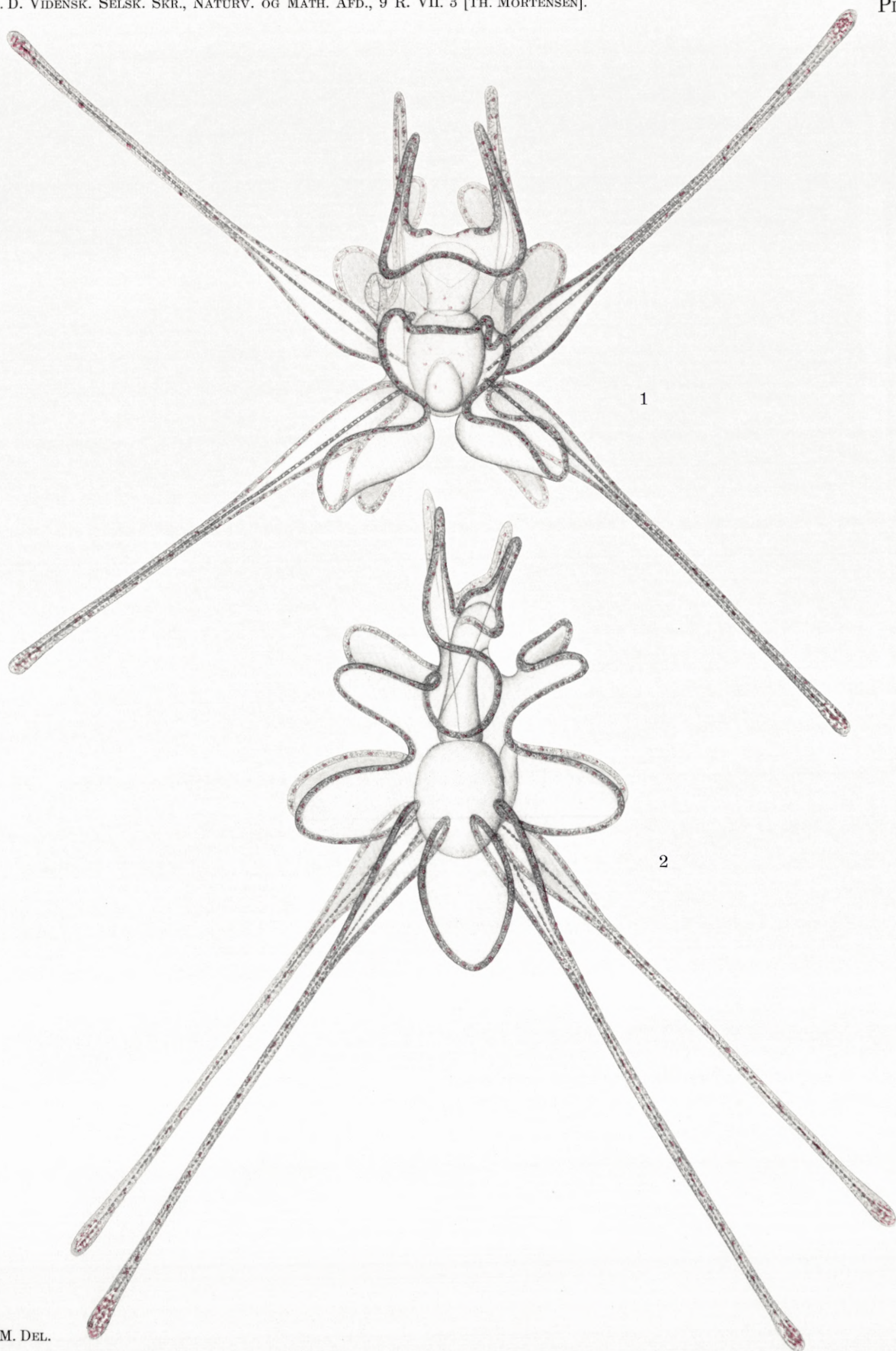
Prionocidaris baculosa (Lamarck).

Fig. 1. Fully formed Echinopluteus, seen from above. × 60.

- 2. Fully formed Echinopluteus, seen from below. The four long arms drawn a little too short (because they would too much exceed the frame of the plate), they should be as long as in fig. 1. × 60.

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Pl. III.
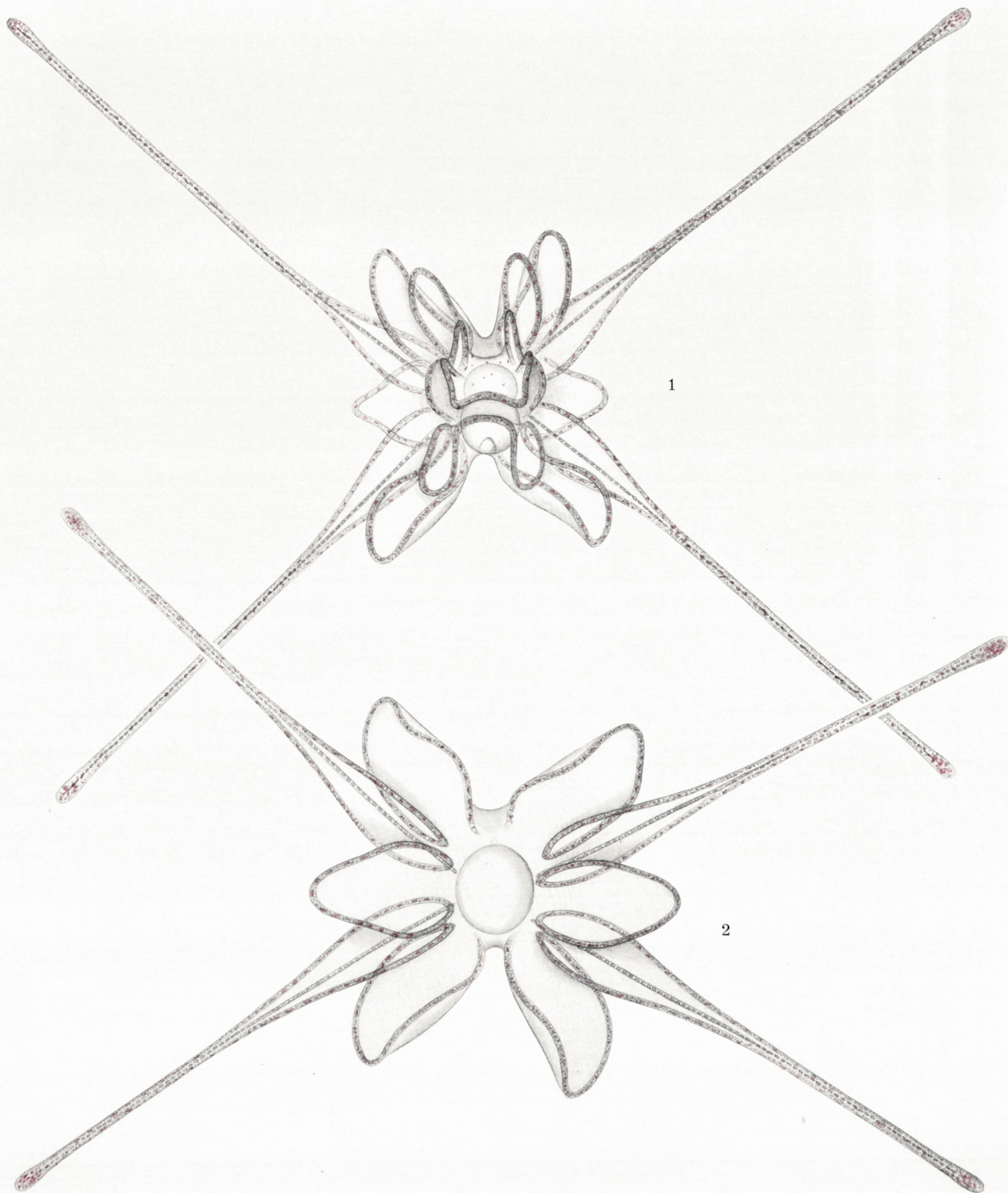
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Plate IV.

Fig. 1. Fully formed Echinopluteus of *Laganum depressum* L. Agassiz, 15 days old. Oral side. × 115.

- 2. Fully formed Echinopluteus of *Echinodiscus auritus* Leske. Oral side. × 115.

- 3—4. Larva of *Linckia multifora* (Lamarck) in the Brachiolaria stage. 24 days old. 3. Oral side, 4. side view. × 65.

Pl. IV.

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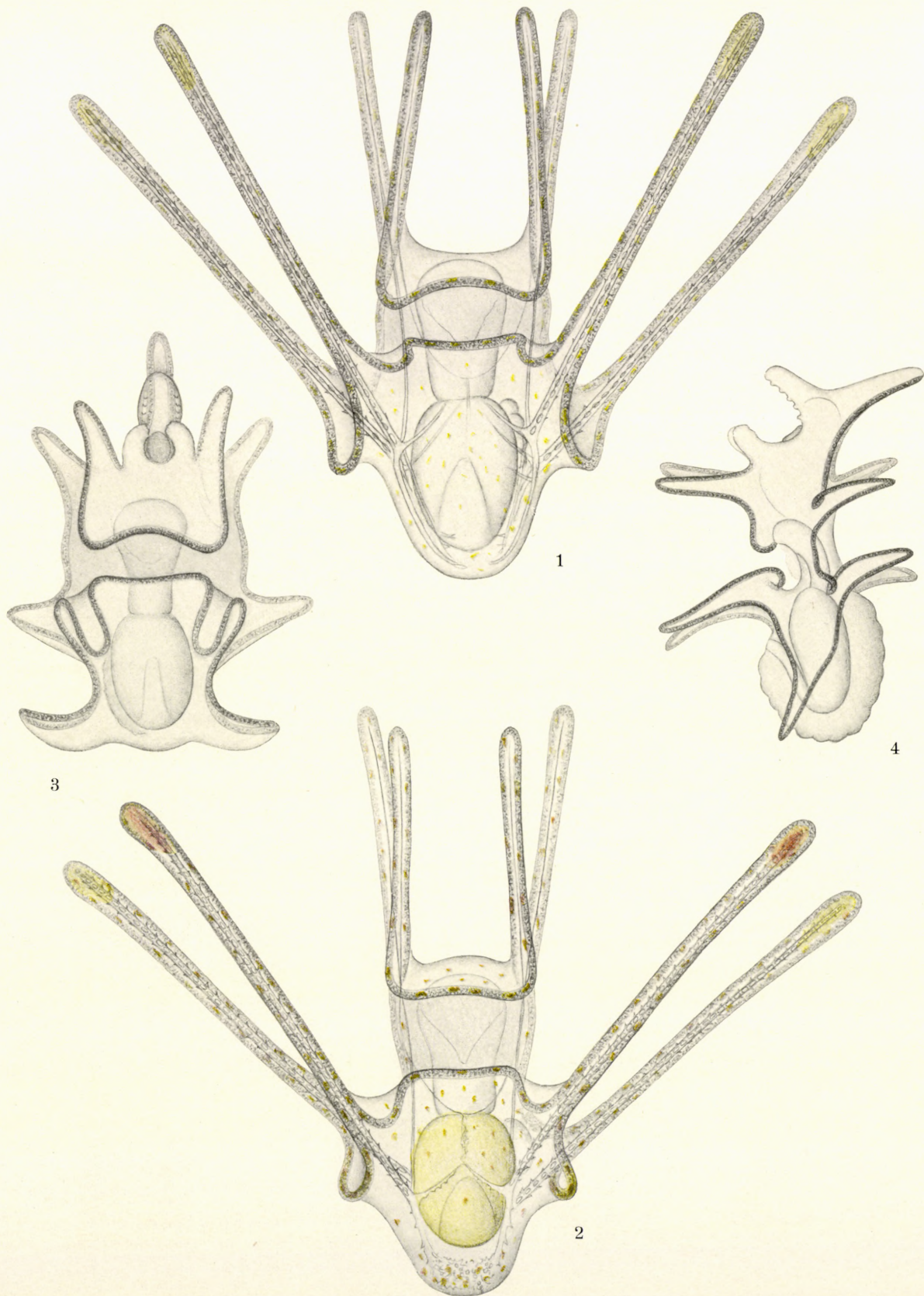
Plate V.

Fig. 1. Ophiopluteus of *Ophiothrix Savignyi* (Müll. & Troschel). 2 weeks old. × 115.
- 2. Young Bipinnaria of *Luidia Savignyi* (Audouin). Oral side. 5 days old. × 150.
- 3—4. Fully formed Bipinnaria of *Luidia Savignyi* (Audouin). Beginning metamorphosis. Oral side (3) and side view (4). 12 days old. × 60.
- 5. Metamorphosis stage of *Luidia Savignyi*. The larval body nearly resorbed. × 80.
- 6. Young Bipinnaria of *Pentaceraster mammillatus* (Audouin). 12 days old. Oral side. × 60.
- 7. Fully formed Bipinnaria of *Pentaceraster mammillatus* (Audouin). 3 weeks old. Oral side. × 50.

Pl. V.
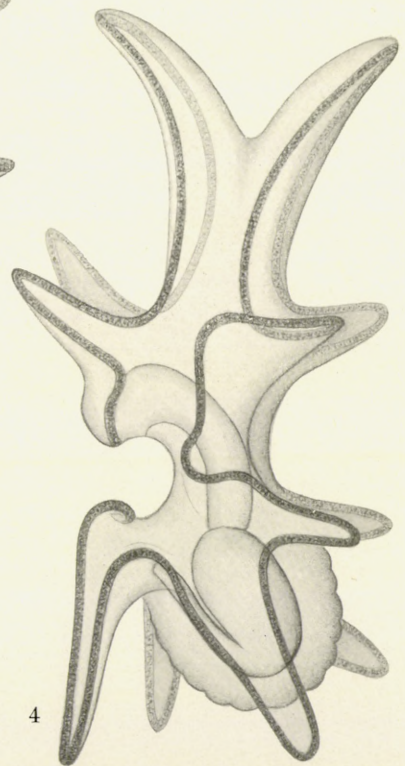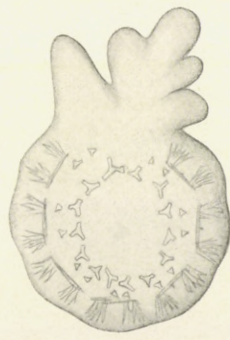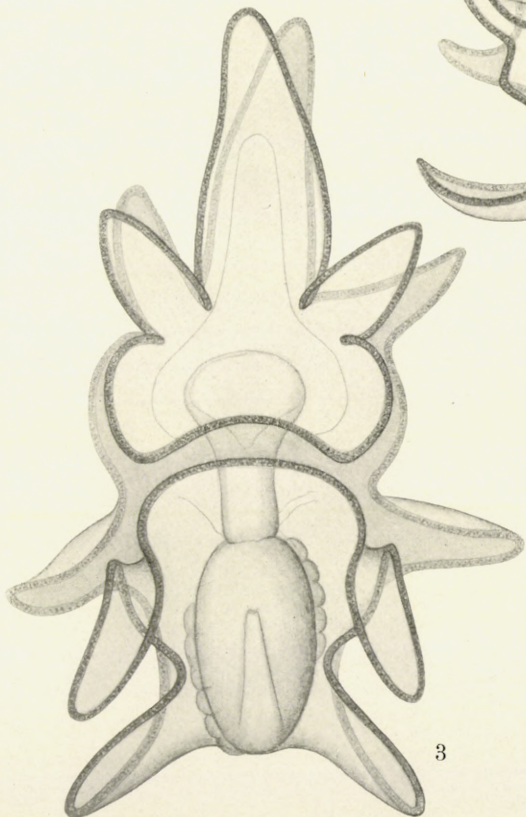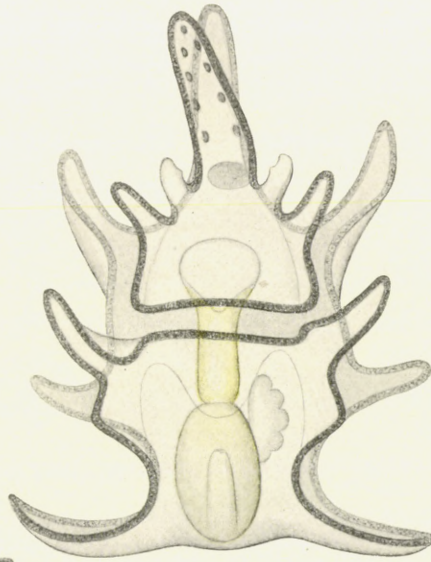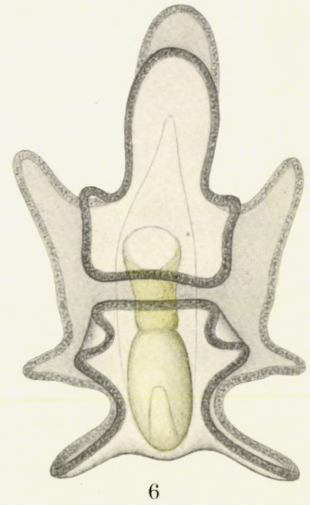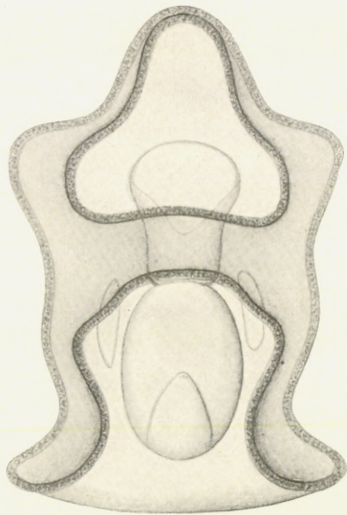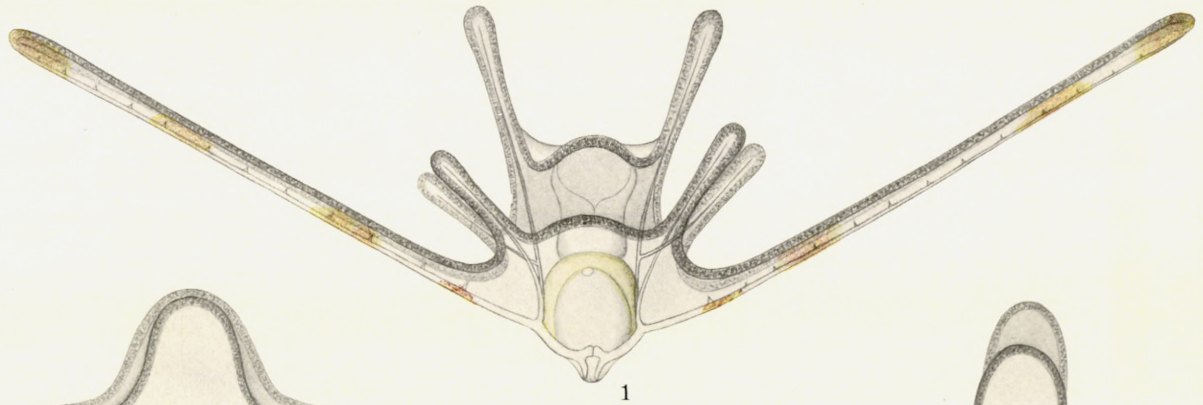
Plate VI.

Figs. 1—3. Embryos of *Fromia ghardaqana* Mrtsn. 1. Advanced Gastrula stage, $2^1/_4$ days old. 2. Young Brachiolaria stage, $3^3/_4$ days old, side view; beginning formation of dermal skeleton. 3. Brachiolaria stage, 8 days old; from the oral side. Secondary lobes on the paired Brachiolaria arms; behind these the large sucking disk on the anterior, unpaired Brachiolaria arm. The dermal skeleton somewhat more developed. All drawn from preserved specimens, cleared in Canada Balsam. $\times$ 65.

- 4. Embryo of *Fromia ghardaqana* Mrtsn., side view, drawn from life; natural colour. $\times$ 50.
- 5. Embryo of *Echinaster purpureus* (Gray), 6 days old; half side view. Natural colour. $\times$ 50.
- 6. Embryo of *Ophiolepis cincta* Müll. & Troschel. 4 days old. Natural colour. $\times$ 150.
- 7—9. Sections of embryos of *Ophiolepis cincta* Müll. & Troschel. 7. Incipient Gastrula stage, still within the egg-membrane, c. 12 hours old. 8. Gastrula stage, c. 18 hours old. 9. Sagittal section through an embryo $1^1/_2$ days old. $\times$ 300.

Pl. VI.

Th. M. Del.

E.H.P
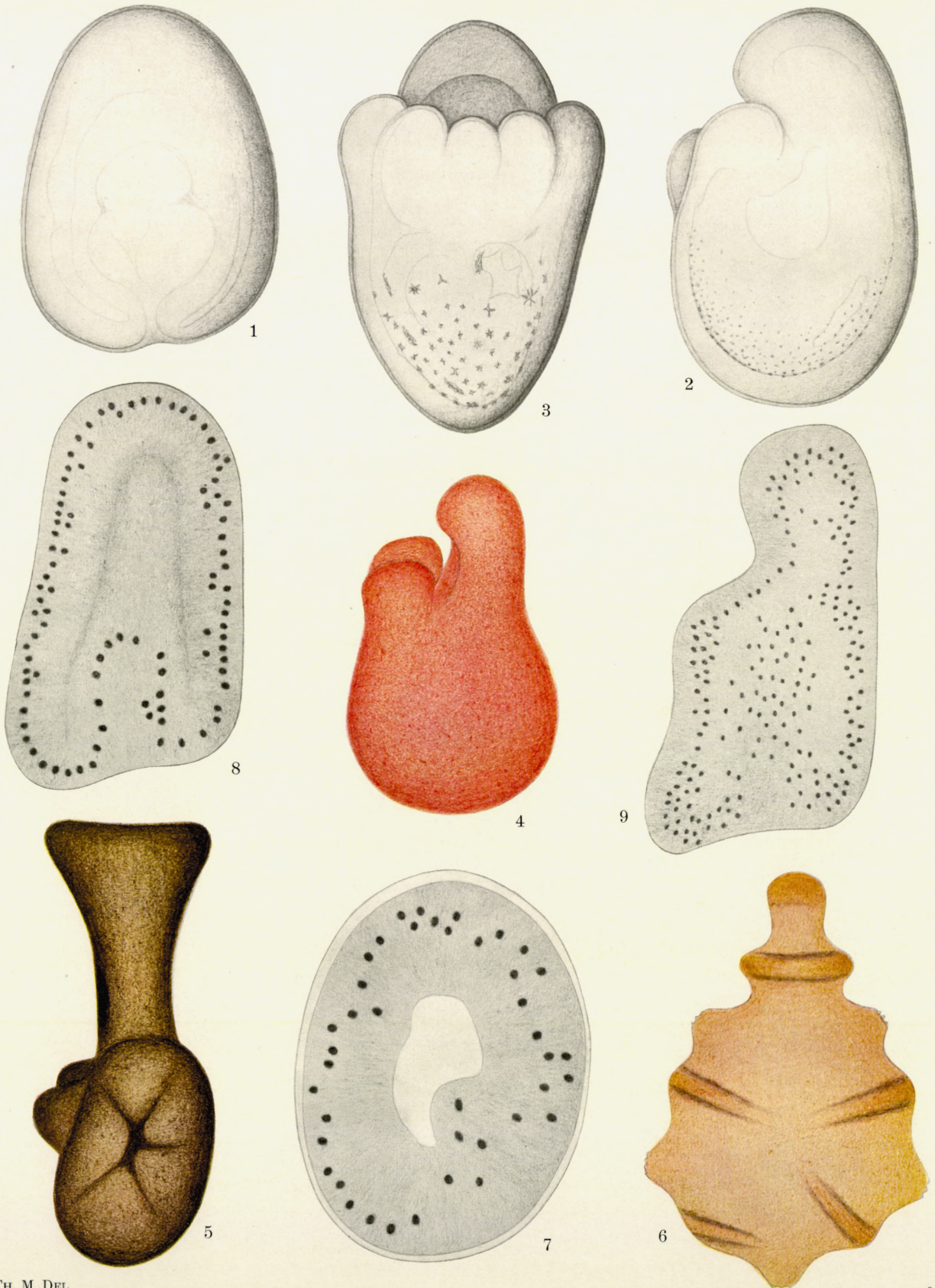
Plate VII.

All figures of *Fromia ghardaqana* Mrtsn.

Fig. 1. Section of embryo, 3 hours old. The nuclei scattered irregularly in the yolk.
- 2. Section of embryo, 5—6 hours old. The nuclei beginning to arrange themselves along the surface.
- 3. Section of embryo, 14—15 hours old. The nuclei are arranged in a single layer along the surface, and in irregular folds penetrating into the yolk.
- 4. Section of embryo, 28 hours old. Gastrula stage.
- 5. Section of embryo, 28 hours old. The embryo is abnormal, the nuclei having not reached the surface, a large proportion of the yolk thus being left outside the embryo.
- 6. Transverse section of embryo, $1^3/_4$ days old.
- 7. Longitudinal section of embryo, $1^3/_4$ days old.
- 8. Longitudinal section of embryo, $2^1/_4$ days old. The apical space is an artefact, due to preservation; naturally, the mesenchyme fills out completely the space between ectoderm and entoderm.
- 9. Median sagittal section of embryo, $3^3/_4$ days old. The invagination is the sucking disk.
- 10. Lateral sagittal section of embryo, $3^3/_4$ days old. Showing the hydropore.
- 11. Transverse section of embryo, 4 days old. Showing the hydropore.
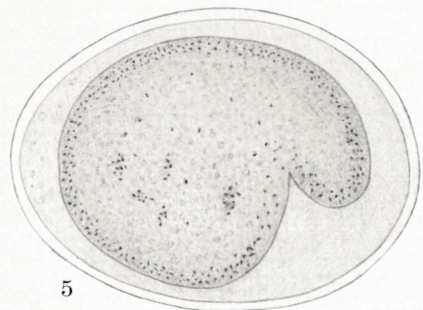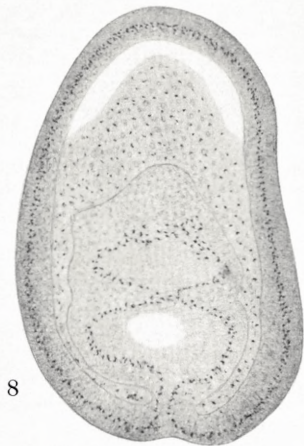- 12. Frontal longitudinal section of embryo, 4 days old.
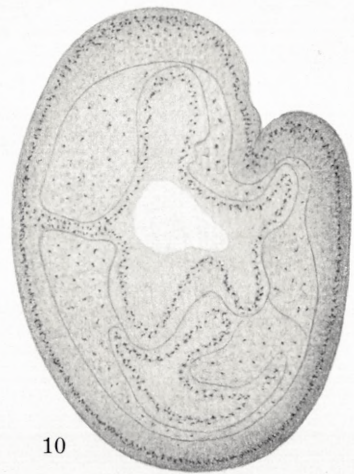
All figures $\times$ 65.

Pl. VII.

Th. M. Del.

E.H.P.
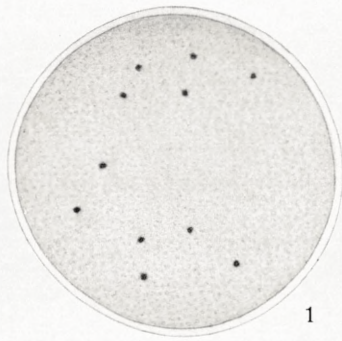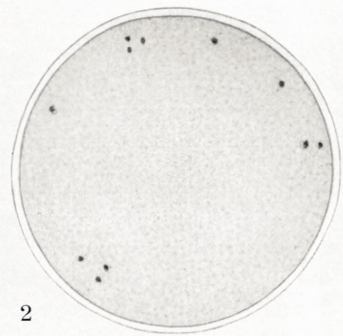
Plate VIII.

All figures of *Opheodesoma grisea* (Semper).

Fig. 1. Ripe egg.
- 2—6. Young cleavage stages; 2—16 cells-stages; 2 hours old.
- 7—8. Blastula stages, 4 hours old.
- 9—13. Gastrula stages at various ages: fig. 9, 8 hours old, fig. 10, 12 hours old, figs. 11—13, 15 hours old.
- 14—15. Embryos beginning to assume the Auricularia shape. Oral side (14) and side view (15).
- 16—18. Young Auricularias, from the oral side (16 and 18) and in side view (17). In fig. 18 the first wheel has appeared, and the larval nervous system is distinct.
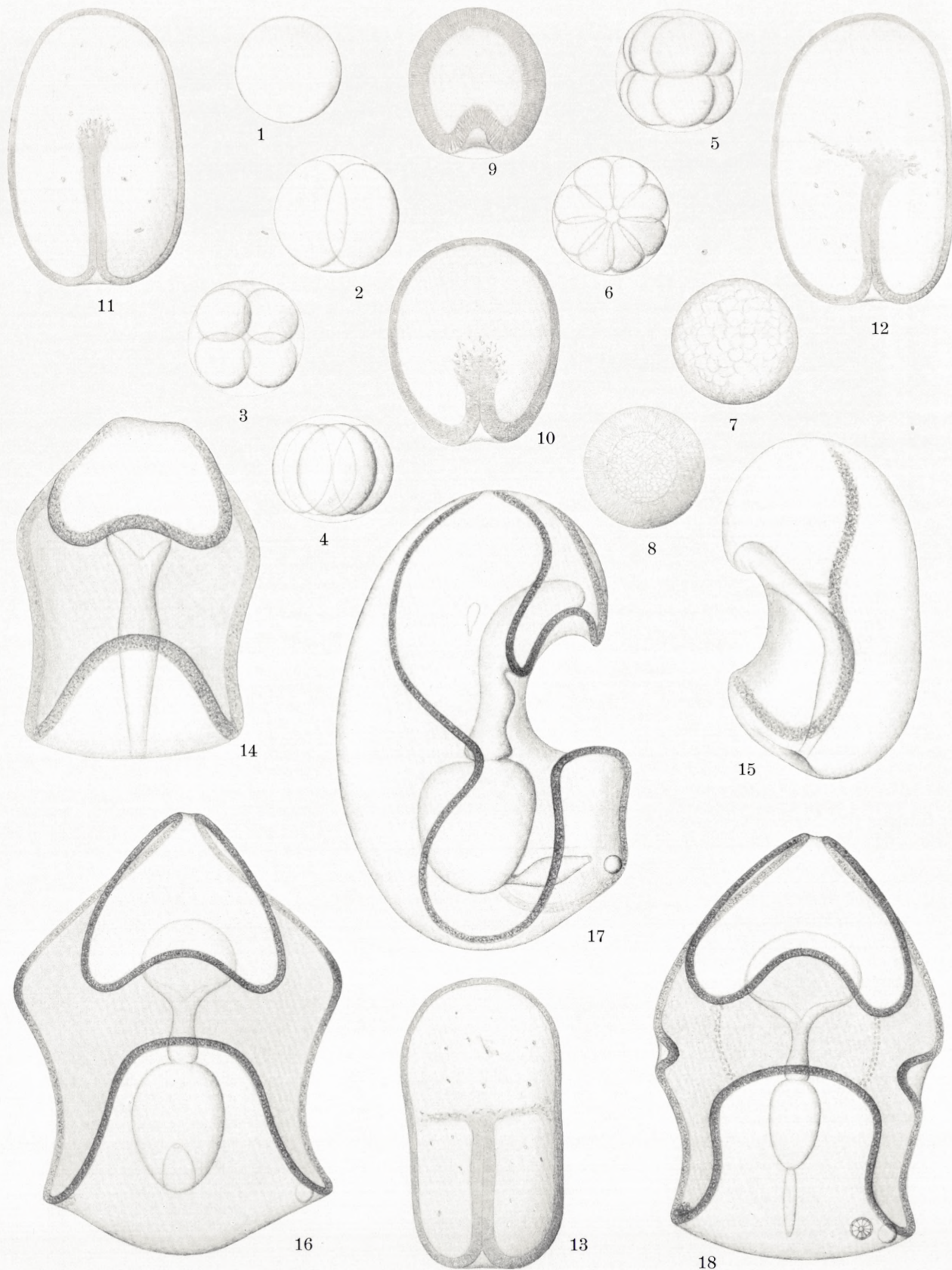
Figures 1—15 × 150. figs. 16—18 × 125.

Pl. VIII.

Plate IX.

Fig. 1. Fully formed Auricularia of *Synaptula vittata* (Forskål), oral side. 13 days old. × 85.
  - 2. Metamorphosis stage (Doliolaria) of *Synaptula vittata* (Forskål). 17 days old. × 130.
  - 3. Young *Synaptula vittata* (Forskål). 5 weeks old. × 160.
  - 4. Fully formed Auricularia of *Opheodesoma grisea* (Semper), oral side. 11 days old. × 100.
  - 5. Young Auricularia of *Holothuria pardalis* Selenka, oral side. 3 days old. × 100.
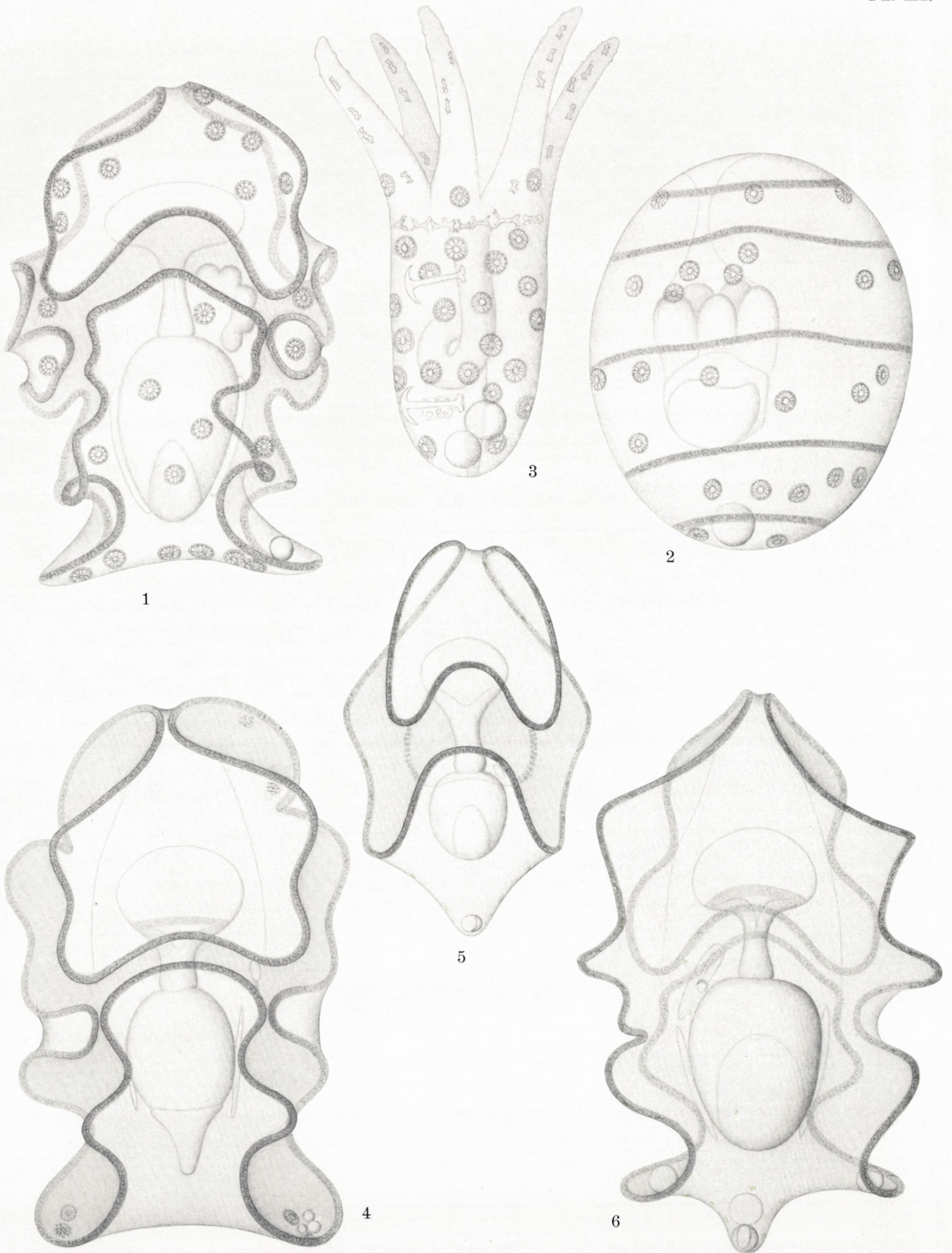 - 6. Fully formed Auricularia of *Holothuria pardalis* Selenka, dorsal side. 2 weeks old. × 100.

Plate X.

All figures of *Holothuria impatiens* (Forskål).

Fig. 1.   Young Auricularia, oral side. 8 days old. $\times$ 125.
-    2.   Young Auricularia, oral side. 9 days old, showing the unusual feature of having two calcareous bodies in the posterior end. $\times$ 125.
-    3.   Fully formed Auricularia, oral side. 14 days old. $\times$ 100.
-    4—5. Metamorphosis stages (Doliolaria). 16 days old. $\times$ 100.
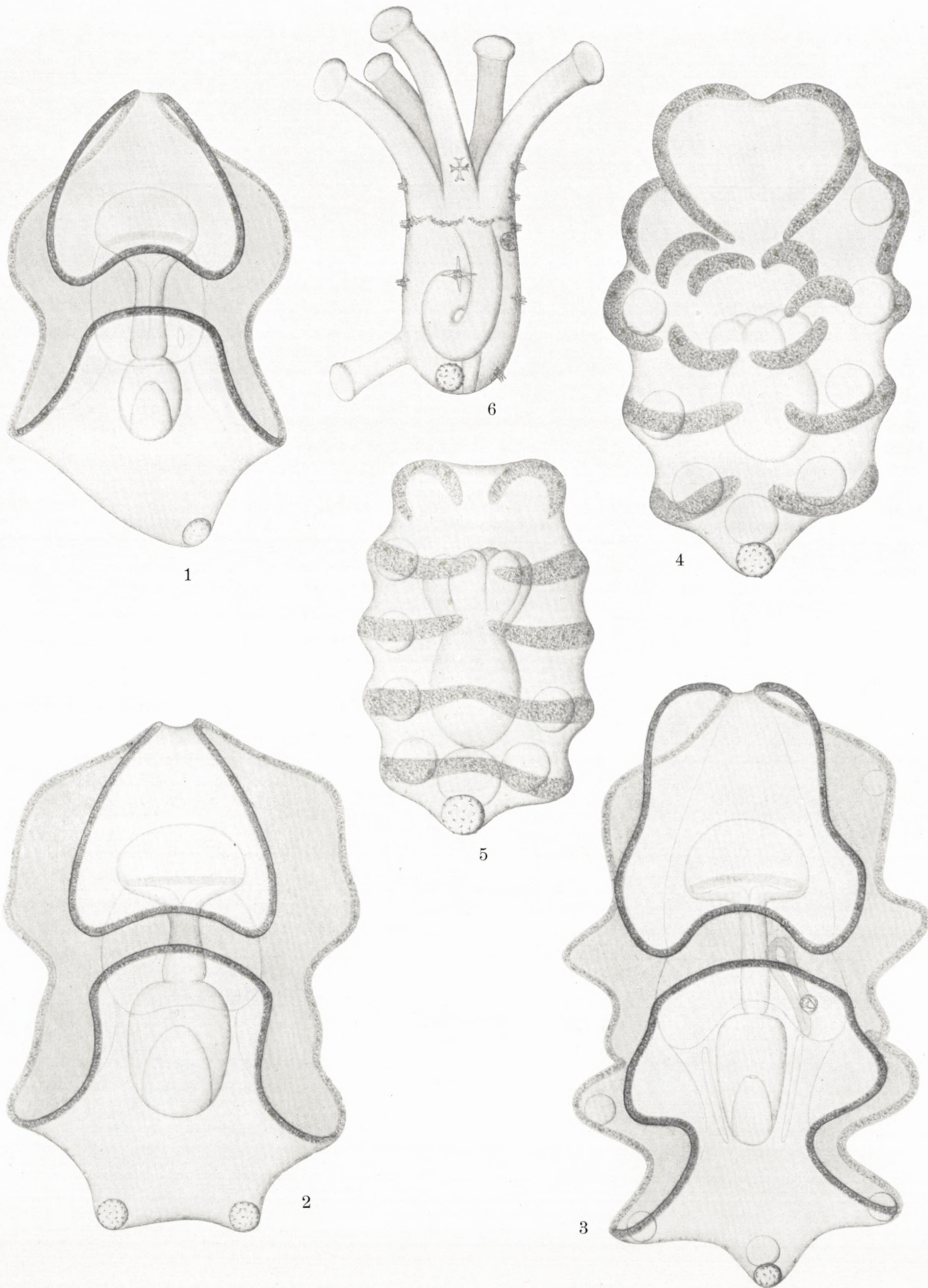-   6.   Young Holothurian, 6 weeks old. (Drawn on free hand.) $\times$ c. 80.

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Plate XI.

Fig. 1. Young Auricularia of *Holothuria papillifera* Heding. 4 days old. × 150.
- 2. Nearly fully formed Auricularia of *Holothuria papillifera* Heding. 2 weeks old. × 115.
- 3. Fully formed Auricularia of *Holothuria papillifera* Heding. 18 days old. × 100.
- 4. Young Auricularia of *Holothuria difficilis* Semper. 5 days old. × 125.
- 5. Fully formed Auricularia of *Holothuria difficilis* Semper. 16 days old. × 100.
- 6. Young Auricularia of *Holothuria (Microthele) nobilis* Selenka. 7 days old. × 150.
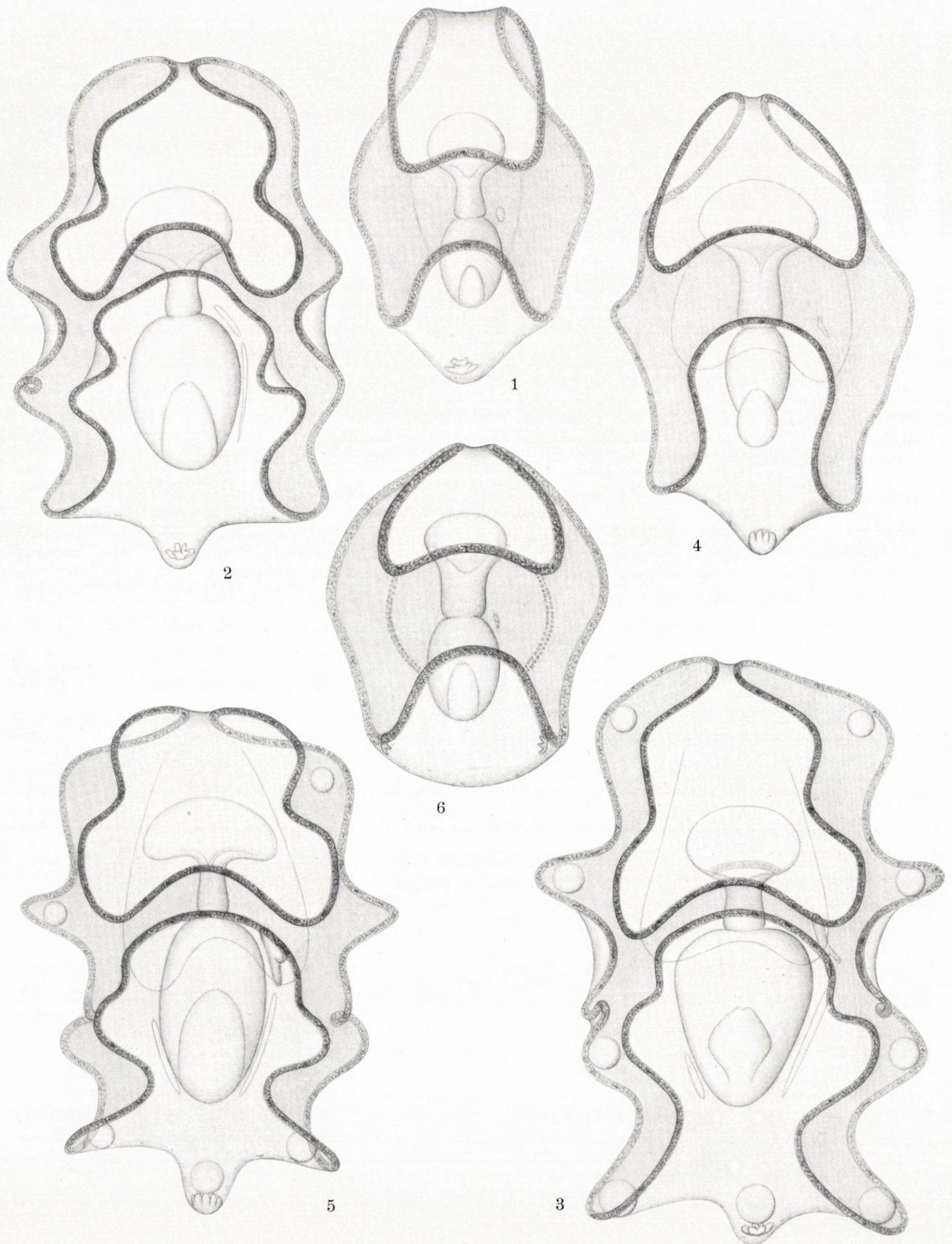
All from the oral side.

Pl. XI.

Th. M. Del.

E.H.P

Plate XII.

All figures of *Heterometra Savignyi* (Joh. Müller).

Fig. 1. First cleavage stage, 2 hours old. × 200.
 - 2. Section of embryo, 5 hours old. Blastula with incipient formation of mesenchyme. × 200.
 - 3. Section of embryo, 6 hours old. Gastrula. × 200.
 - 4. Section of embryo, 9 hours old. The archenteron separated from the ectoderm. The apical sucking disk beginning to form. The embryo still enclosed by the egg-membrane. × 200.
 - 5. Section of embryo 20 hours old. The archenteron has divided into two parts, the upper representing the entero-hydrocoel, the lower the entoderm. The embryo, which is now free-swimming, has begun to form the vibratile bands. The depression at the upper end is the sucking disk. × 200.
 - 6. Embryo, 25 hours old, showing the first rudiments of the skeleton. The notch on the left side is the incipient formation of the vestibulum. × 300.
 - 7. Embryo, 30 hours old. The skeleton in an advanced stage of development. × 300.
 - 8. Young Pentacrinoid. × 85.
 - 9. Pentacrinoid, later stage; from side of the dish. × 35.
 - 10. Pentacrinoid, later stage; from bottom of the dish. The stalk being too long for the plate, the basal part has been placed separately alongside the main part. × 35.
 - 11. Head of young Pentacrinoid. × 160.
 - 12. Head of more advanced Pentacrinoid. The radials have appeared. × 120.

Pl. XII.