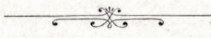


ON THE
POSTLARVAL DEVELOPMENT
OF SOME CIDARIDS

BY

TH. MORTENSEN

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 8. RÆKKE, XI. 5.



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI

1927

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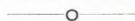
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During the Danish Expedition to the Kei Islands in 1922 I had the opportunity of staying, together with my friend Dr. H. Boschma, about one month (June) in Banda, making collections of the marine fauna there and studying the ecology of the sounds between these small islands. To a large extent we made use of a pearl-schooner which was stationed here between the two seasons allotted to the pearl-fishery at the Aru Islands, and thus unoccupied at the time of my stay at Banda. The schooner was fitted out with diving-apparatus and had a professional diver. The owner of the schooner, Sech Said Baädilla ben Abdullah, a rich Arab, very liberally complied with my desire to use the schooner and engage the diver. He turned out to be a great success; he was a very intelligent man and soon became most interested in our studies; as soon as he had understood what were our wishes, it was quite surprising what a lot of fine specimens, even of quite minute forms, he brought up from the sea-bottom. — Among the objects thus secured was a small Gorgonid, *Acanthogorgia* sp., growing on the bottom in great clusters, very much recalling our common heather. These clusters were the favourite haunts of numerous small animals, especially Crustaceans and worms. In order to secure also the more minute organisms living among these Gorgonians, the whole of such clusters was put into water with a little formaline, which makes the various animals swarm out and, when paralyzed by the formaline, sink to the bottom of the dish. Then the Gorgonians were well shaken in the same water, in order to get off from the clusters also such organisms as were unable to swim actively. The whole deposit thus resulting was then sifted off and preserved in alcohol (or formaline). The sorting out of this material at home, under the binocular microscope, gave splendid results — especially enormous numbers of small Crustaceans and worms, both Polychaetes and Nematods, also Molluscs and Echinoderms; among the latter were some very young Cidarids, which proved to be of such considerable interest that I have thought it right to make them the object of a special publication.

The youngest specimens measure only ca. 0.5 mm. diameter of test. All traces of the larval skeleton have, however, already disappeared at this stage; accordingly this material does not contribute much towards a solving of the problem whether the peculiar Echinoid larva *Echinopluteus transversus* is a Cidarid-larva (cf. the author's »Studies of the Development and Larval Forms of Echinoderms«, 1921,

p. 91—95); only the structure of the pedicellariæ in the young Cidarid has any bearing on this question — and that a negative bearing.

The general appearance of the youngest specimens¹) (figs. 1—2) is so unlike that of the adult form that it is hard enough to recognize the Cidarid in them. But the rather complete series of growth-stages makes it possible to ascertain that they really are Cidarids, and even to identify the genus and species with certainty.

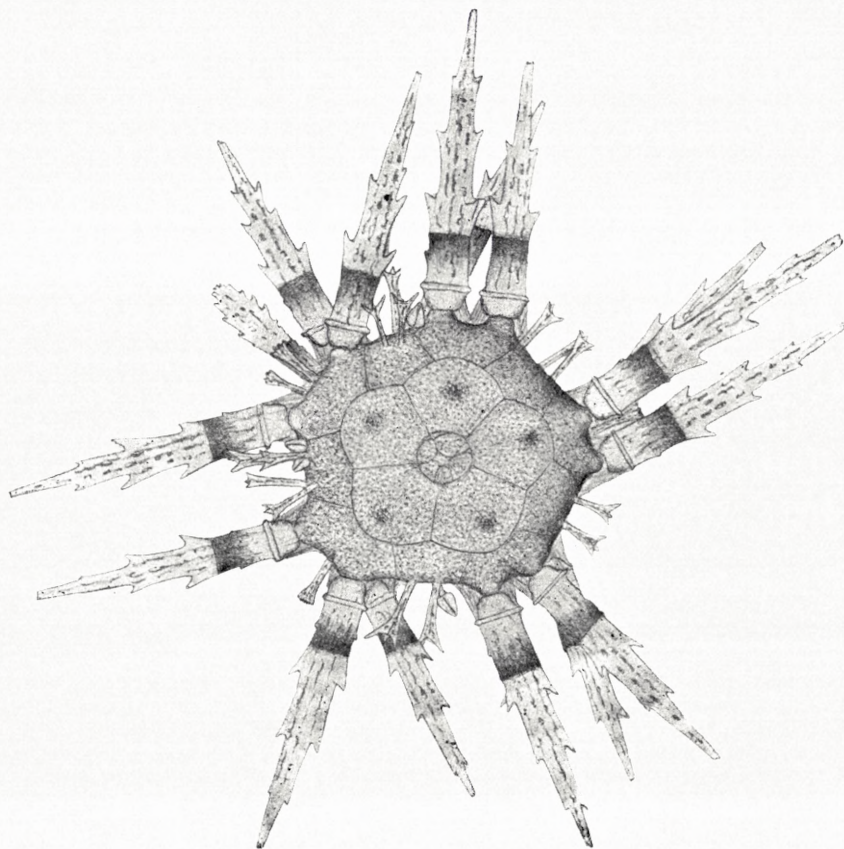


Fig. 1. Young *Eucidaris metularia*; aboral side. $\times 50$.

Only two littoral species of Cidarids were found at the Banda Islands, viz. *Prionocidaris baculosa* var. *annulifera* (Lamarck) and *Eucidaris metularia* (Lamarck). Even if it should ultimately prove that also other species occur there (e. g. *Plococidaris verticillata* (Lamarck)), there can be no doubt that the young specimens belong to *Eucidaris*

¹ Figs. 1—2 do not represent the youngest specimen in hand; this latter is, however, in a rather poor state of preservation, and does not figure well. It differs essentially from the stage figured only in the periproctal plates having just begun to appear (fig. 8. a), and in the primary spines being not yet fully formed, except for the one on the unpaired interambulaeal plate; there is, however, already the same number of primaries (and interambulaeal plates) as in the specimen figured.

metularia, the largest specimens of the series being, by their general appearance and especially by the characters of their primary spines, unmistakable *Eucid. metularia*.

The Cidarids being in several respects among the most primitive of all Echinoids, it will be of very considerable interest to get some information of the characters of the youngest post-larval stages and to trace their transformation to the adult forms. So far very little is known about this question. No Cidarid with free-living,

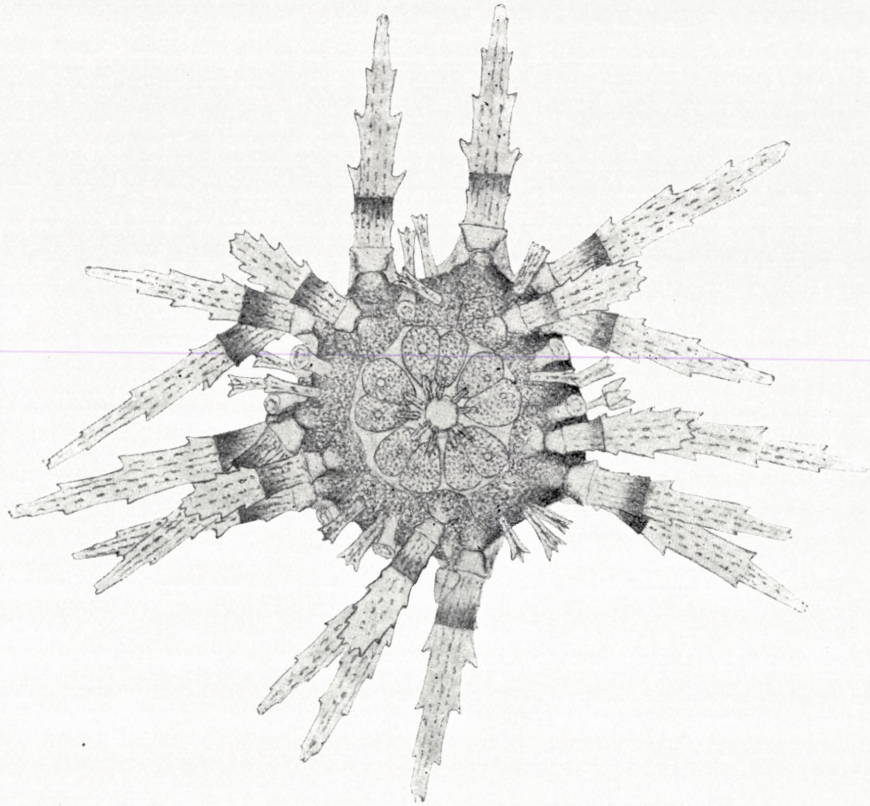


Fig. 2. Young *Eucidaris metularia*; oral side. $\times 50$.

pelagic larvæ has ever been studied with regard to its development, beyond the very first stages. The cleavage stages of *Phyllacanthus parvispinus* (Ten. Woods) were described in the author's work "Studies of the Development and Larval Forms of Echinoderms" (1921, p. 24. Pl. V. 3—4), where also the first larval stages of *Eucidaris Thouarsi* (Val.) are described. Figures of the early larval stages of *Eucidaris tribuloides* (Lamarck) are given by D. H. TENNENT, 1914, in his paper "The early Influence of the Spermatozoa upon the Characters of Echinoid Larvæ" (Papers from the Tortugas Laboratory of the Carnegie Inst. Washington Vol. V.). The only, more complete description of a Cidarid-larva is, however, still the one given by PROUHO in 1888 of *Dorocidaris papillata* A. Ag. (= *Cidaris cidaris* (Linn.)) in his "Recherches sur le Dorocidaris

papillata" (Arch. Zool. Expér. & Génér. V). He has reared this larva to the full Pluteus-shape. But the metamorphosis and the postlarval development of any Cidarid with a free-swimming larval stage still remains unknown.

About the postembryonal development of brood-protecting Cidarids we have a few observations, viz. of *Austrocidaris canaliculata* (A. Ag.) by A. AGASSIZ ("Challenger" Echinoidea, 1881, p. 45 Pl. II; Panamic Deep Sea Echini, 1904, p. 4. Pl. 13, 6), and by LOVÉN ("Echinologica", Bih. K. Svenska Vet. Akad. Handl. 18. 1892, p. 5—10, Pl. I—III); of *Rhynchocidaris triplopora* Mrtsn. and *Notocidaris gaussensis* Mrtsn. by the present author (Echinoidea d. Deutschen Südpolar-Exped. 1909, p. 10—11, Taf. XI etc., p. 21). References to the observations contained in the works quoted will

be given in their proper place in the following description.

It will be convenient to describe the corona and peristome under the same heading, while the apical system, the tube-feet and pedicellariæ are treated each in a special chapter.

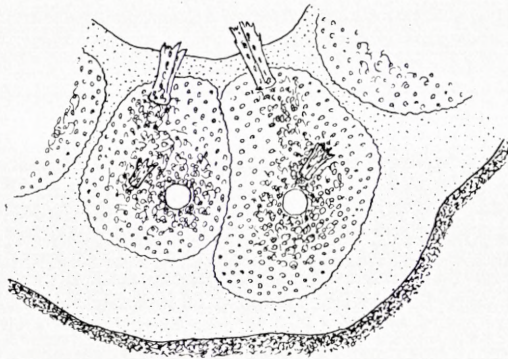


Fig. 3. Buccal plates of the young *Eucidaris metularia*. $\times 120$.

and 3 "paired" plates. On the peristome the buccal plates alone are present. These latter are of unequal size, (fig. 3), in conformity with the formula of LOVÉN, the plates I,a, II,a, III,b, IV,a and V,b being the larger. The mouth is opened, and the dental apparatus is already developed and in working condition in the specimen represented in figs. 1—2; in a slightly younger specimen the mouth appears to be still unopened, and the dental apparatus is not yet fully formed. In the following stages the ambulacral plates are gradually loosened from the corona and pass on to the peristome — the first pair at a size of ca. 1 mm. diameter of test, the next pair at a size of ca. 2 mm., the third pair at a size of ca. 3 mm. diameter of test (figs. 4—7).

The first pair, corresponding to the buccal plates of an *Echinus*, remain at the mouth-edge — where they may be observed in any adult Cidarid, distinguishable by their foot-pores being somewhat larger than those of the following plates, while they are about the smallest of all the ambulacral plates of the peristome.

I. Corona and peristome.

In the youngest specimens (figs. 1—2) the corona consists of 2—3 pairs of plates in each ambulacrum and 4 plates in each interambulacrum, viz. the primary unpaired

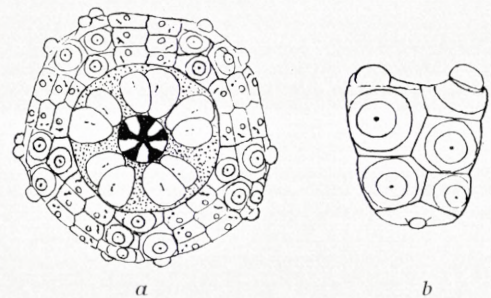


Fig. 4. a. Denuded test of young *Eucidaris metularia* of a stage corresponding to figs. 1—2. — b. An interambulacrum of the same specimen. $\times 50$.

As regards the development of the tubefeet it is important to notice that the buccal tubefeet are not the first to appear; in the youngest stage the first pair of tubefeet and one foot of the second pair are developed on the corona, while the buccal tubefeet are still indistinct; they develop at about the same time as the second-third pair of tubefeet on the corona. This is an interesting corroboration of the observation by

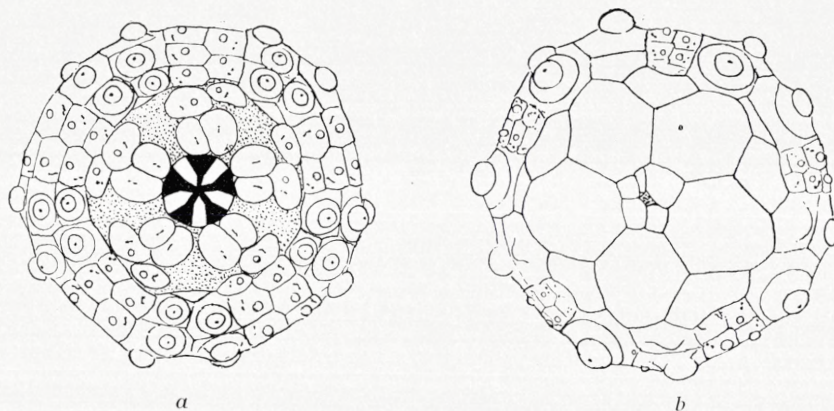


Fig. 5. Denuded test of young *Eucidaris metularia*, a little more than 1 mm. diameter. a. oral side. b. aboral side. $\times 30$.

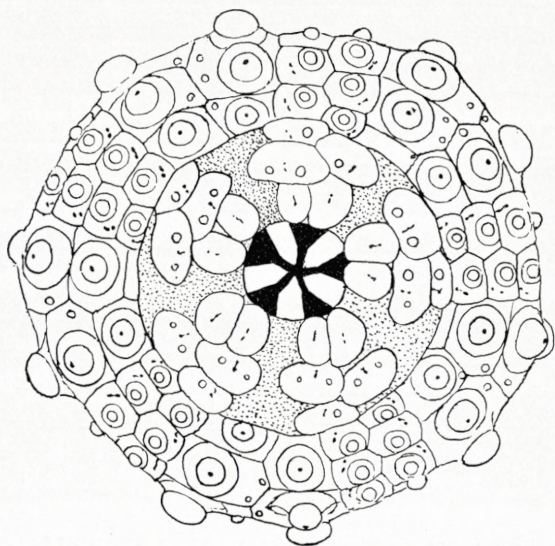


Fig. 6. Denuded test of young *Eucidaris metularia*, 2 mm. diameter. Oral side. $\times 30$.

Miss GORDON¹⁾ that in *Psammechinus miliaris* the buccal tubefeet do not appear until the first pair of coronal tubefeet have developed. The terminal tentacle is distinct, with a well developed sucking disk containing a ringshaped calcareous plate, in the youngest stage; in the stage figured it has already been reduced to a small wartlike prominence.

The primary unpaired plate of the interambulacra, so conspicuous in the youngest stage, soon begins to dissolve. In fig. 5, representing a specimen slightly more than 1 mm. in horizontal diameter of test, it has disappeared — together with its spine and tubercle — in two of the interradii, while in the three others there is still a small piece of it left. In the next stages some of the following, paired interambulacral plates have also been dissolved. In the specimen fig. 6 (2 mm. horizontal diameter of test) plates No. 2 and 3 have been quite dissolved, while plate No. 4 is about to dissolve, (the serial number of these plates may be recognized with certainty by their primary spine; see below, p. 378). At a size of

¹⁾ ISABELLA GORDON. The development of the calcareous test of *Echinus miliaris*. Phil. Trans. B. Vol. 214. 1926.

3.5 mm. diameter of test it seems to be the plates no. 5 and 6 which are about to dissolve (here the serial number of these plates is no longer to be ascertained beyond doubt). At the same time a corresponding number of new plates have been formed at the aboral end of the interambulacrum, so that there is always the same number of plates (4) in each series. In the specimen of 3.5 mm. the fifth plate is beginning to form. (In the adult specimens the number of interambulacral plates of the corona is 5—6 in a series).

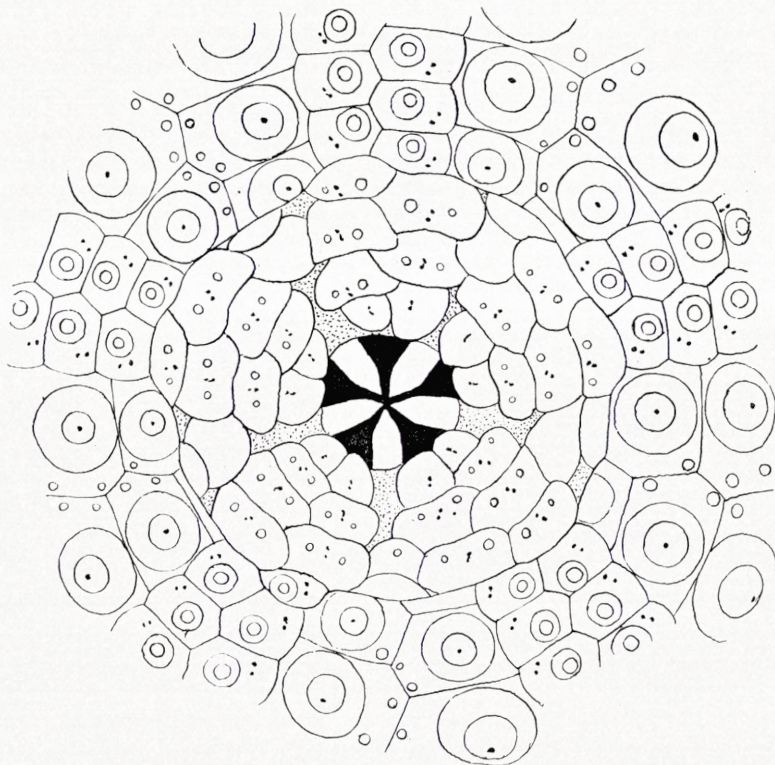


Fig. 7. Peristome and adjacent part of the test of young *Eucidaris metularia*, 3,5 mm. diameter. $\times 30$.

In the last mentioned stage (3.5 mm. diameter) two plates have also appeared on the peristome in the interradian spaces between the series of ambulacral plates (fig. 7).

The late appearance of these plates, after the disappearance of both the primary unpaired and the two-three first pairs of the interambulacral plates of the corona, is of importance for the question of the morphological value of these interradian plates of the

peristome in Cidarids, and gives the definite solution of this so far unsettled problem, the history of which we will briefly review. JOH. MÜLLER (Über den Bau d. Echinodermen 1854, p. 25) apparently regards them as true interambulacral plates, although he states that they "vermehrten sich am buccalen Ende der Reihen, wo sie am kleinsten (vielleicht auch am hinteren Ende der Reihen, wo die hinterste auch weniger breit ist)". LOVÉN (Études sur les Échinoidées, 1874, p. 47) does not express any opinion of their homology, only ventures on a suggestion as to their origin: "Il paraît qu'à la face intérieure des plaques qui constituent la limite temporaire de leur corona, il se fait une espèce d'écaillage, par suite duquel sont produites les plaquettes interradianales de la membrane buccale". A. LANG (Vergl. Anat. d. Wirbellosen Tiere. IV. 1894, p. 931) states that "sowohl die Platten der Ambula-

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cren als diejenigen der Interambulacren setzen sich in modificierter Weise über den Rand des Peristoms hinaus auf das Peristom selbst gegen den Mund fort", and HAMANN in "Bronn" (Seeigel, 1904, p. 1063) says: "die Platten der Ambulacren setzen sich bei den Cidariden in zwei Reihen auf das Peristom . . . fort, ebenso die Interambulacralplatten". This interpretation of the interradial plates on the peristome of Cidarids as a direct continuation of the interambulacra is adopted without any reservation in the larger modern textbooks (RAY LANKESTER'S "Treatise on Zoology", "The Cambridge Natural History" and DELAGE & HÉROUARD'S "Traité de Zoologie concrète").

The facts here brought forth give the definite proof that the interradial plates of the peristome in Cidarids have nothing to do with the interambulacral plates of the corona, but represent a new element, corresponding to the irregular plates occurring in varying number on the peristome of most regular Echinoids. This opinion was also expressed by JACKSON (Phylogeny of the Echini, 1912; p. 79), who designates these plates as "non-ambulacral", "because . . . they have no relation to the interambulacra of the corona". Their arrangement in Cidarids, generally in a single, rather regular column, also indicates that they are not a continuation of the double series of interambulacral plates of the corona. But the fact that they do not appear (in the present species) until both the primary unpaired and the 2—3 proximal pairs of the coronal interambulacral plates have been dissolved, is the conclusive proof that the interradial plates of the peristome have no relation to and are not homologous with the interambulacral plates of the corona — contrary to the ambulacral plates of the peristome which, with the sole exception of the first pair, the "buccal" plates proper, once formed part of the corona, but were loosened from the edge of the corona contemporaneously with the gradual absorption of the interambulacral peristomial border. The passage of the ambulacral plates on to the peristome is not due to an active wandering — or transplacing — of the said plates, but to the peristome widening so as to include the proximal part of the ambulacra.

In view of the opinion set forth by JACKSON (Op. cit.) that all Echinoids descend from the oldest known form, the ordovician *Bothriocidaris*, so unique on account of its single series of interambulacral plates, it would be of very great interest if a real *Bothriocidaris*-stage could be traced in the development of the Cidarids, which in several respects incontestably represent a primitive type of Echinoids. It can hardly be doubted that the existence of an unpaired primary interambulacral plate at the peristomial border throughout the whole of the Echinoid-class, (though resorbed in the course of development in most of the regular forms), is an inheritance from the *Bothriocidaroid* ancestor. But is there any indication of an original unpaired condition of the following interambulacrals? At a first glance there would seem to be no trace of such an original unpaired condition. On a closer inspection, however, it is seen that plate no. 4 is slightly larger than it ought to be, according to its place in the series; it is especially noteworthy that the tubercle of this plate

is somewhat nearer to the interambulacral midline than those of the other plates, the tubercles of the series, of which it makes a part, not forming a straight line as do the other series of tubercles in the interambulacrum (Fig. 4 *a, b*). This fact may well be regarded as pointing towards an originally more median place of the interambulacral plates. Very probably this feature will be found to be more pronounced at the first formation of the interambulacral plates in the young, metamorphosing sea-urchin, as it was found by Miss GORDON¹) to be the case in *Psammechinus miliaris* and *Echinocardium cordatum*. The suggestion set forth by Miss GORDON (Op. cit. p. 300) that the double series of plates arose from an original, single, linear series, the component parts of which have, owing to crowding, become somewhat displaced and arranged themselves in pairs, the first remaining single, is very likely, and seems the only natural explanation of the origin of the so-called "paired", in reality only alternating, condition of the interambulacral plates. — Nevertheless I cannot help feeling somewhat disappointed in not finding a clearer indication of the supposed Bothriocidarid ancestry in the younger stages of so primitive a type as *Cidaris*.

It is noteworthy that in *Notocidaris gaussensis*, *Rhynchocidaris*, and *Austrocidaris canaliculata* no trace of an original median position of plate 4 or any of the other plates after the first unpaired one has been observed.

II. The Apical System.

Nearly the whole aboral side of the young *Cidarid* is occupied by the 5 large genital plates, the more conspicuous on account of their red colour; the ocular plates, which are much smaller, are scarcely to be seen from above in the youngest stage, whereas later, with the growth of the corona, they become more and more aborally placed. It is a remarkable feature that the five genital plates do not from the beginning join in a regular pentagon, one of the plates being pushed somewhat outside (fig. 8 *a*). It appears that this is the madreporite; this cannot, however, be stated with certainty, on account of the remarkable fact that the madreporic pore is not discernible in the younger stages. This sounds very peculiar, as otherwise the madreporite is usually very distinctly discernible in young stages of Echinoderms; but nevertheless it is a fact that the madreporic pore is not discernible in this species until at a later stage, when there are already two pairs of ambulacral plates on the peristome (fig. 5). Whether this is due to the pore being so small as not to be discernible from the usual holes, or meshes, of the calcareous network of the plates, or whether perhaps the pore is obliterated in the younger stages, only future research can decide.

As to the very important question of the existence of a single primary large anal plate, covering the whole periproct — as is the case in the young *Psamme-*

¹) ISABELLA GORDON: The development of the calcareous test of *Echinocardium cordatum*. Phil. Trans. B. Vol. 215. 1926.

chinus or *Strongylocentrotus*, and as was supposed by LOVÉN and AGASSIZ to be the typical condition in all young Echinoids, including also the Cidarids — it is very easy to ascertain that such a plate does not exist. In the youngest stage (fig. 8 *a*) only one plate is just beginning to form, but immediately after several more plates appear, so that the periproct is from the first covered by 5 plates, of

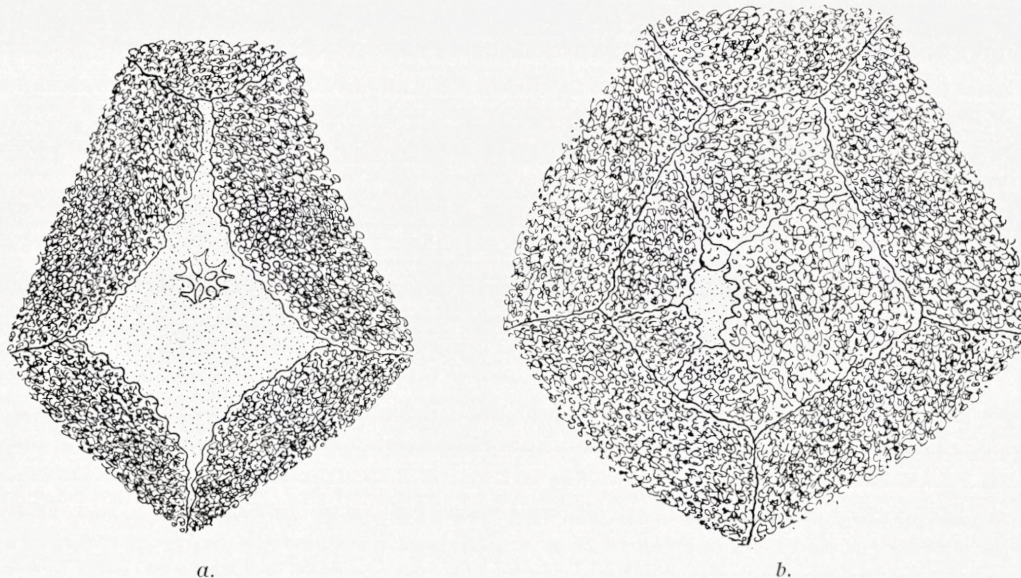


Fig. 8. Periproct and adjoining part of the five genital plates of young *Eucidaris metularia*. *a*. From the youngest stage, slightly younger than the specimen represented in Figs. 1—2. *b*. From a specimen corresponding to fig. 5. $\times 95$.

unequal size and not placed regularly in the corners between the five genital plates (figs. 1, 5 *b*, 8 *b*).

This is in perfect agreement with my previous observations on other young Cidarids, as set forth in my "Echinological Notes III. The central (suranal) plate of the Echinoidea" (Vid. Medd. Dansk Naturhist. Foren. Bd. 63. 1911, p. 31—35), and corroborates the conclusion there reached (p. 56) that the single, large anal plate found in some Echinoids is not a primitive but a highly specialized feature, and does not support the supposed homology between the apical system of Echinoids and the Crinoid calyx.

III. Spines and Pedicellariæ.

What makes the young Cidarids look so strikingly different from the adult is above all the spines, both primary and secondary (Figs. 9—13), and the very interesting problem, therefore, presents itself: how are these spines transformed into the shape of the spines of the adult?

The primary spines. In the youngest stage all the primaries viz. the one of the unpaired interambulacral plate and the three following ones, are provided with a single yellowish-green band, rather sharply limited distally, at the distal end of the collar, gradually disappearing downwards; these spines are otherwise quite colourless, transparent. The spine of the first, unpaired plate (Fig. 9 *a*) is flat, the

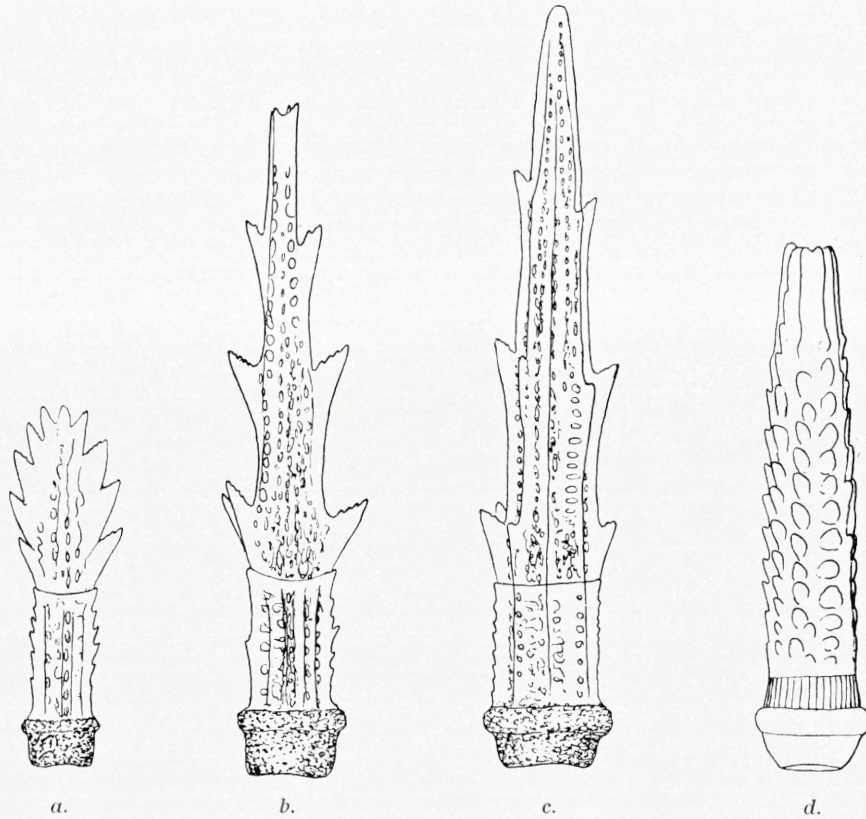


Fig. 9. Primary spines of young *Eucidaris metularia*. *a*. From the first, unpaired plate; *b*. from plates 2—4; *c*. from plates 5—6; *d*. from plates 7—8. *a*—*b*. $\times 125$; *c*. $\times 95$. *d*. $\times 30$.

outer part, the “shaft”, which is only as long as the collar, is somewhat widened, with coarsely serrate edges. The other primaries are not flattened or widened; they taper gradually, and carry two or three sets of coarse thorns, mainly laterally placed. At the base there is a distinctly limited collar, more finely serrate than the shaft. The thorns are finely serrate along their anterior edge (Fig. 9 *b*). The following two primaries (Fig. 9 *c*), viz. nos. 5—6, are of a similar structure, only somewhat coarser, though transparent like the first ones, but of a beautiful uniform pink colour, which makes them look conspicuously different from the uncoloured first ones, with the greenish-yellowish band. The next pair of spines (Fig. 9 *d*) are much coarser, untransparent, reddish with some series of white, obtuse thorns.

As seen from the transverse sections (Figs. 10. a—b), the two first forms of primaries have no special outer-layer, ostracum, as is otherwise found in the

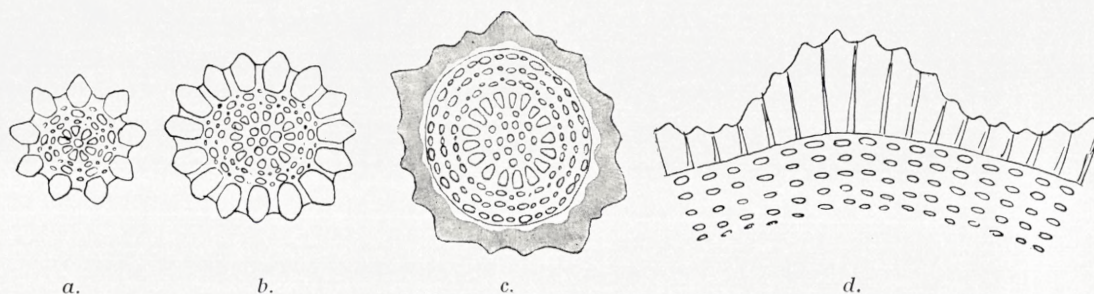


Fig. 10. Transverse sections of primary spines of young *Eucidaris metularia*. *a.* From a spine of plates 2—4 (cf. fig. 9. *b.*); *b.* from a spine of plates 5—6 (fig. 9. *c.*); *c.* from a spine of plates 7—8 (fig. 9. *d.*); *d.* from a spine of the nearly adult type of a specimen 3.5 mm diameter. *a—c.* $\times 120$. *d.* $\times 95$.

primary spines of Cidarids when fully formed (the collar is of the same structure as the shaft). In the third form (Fig. 10 *c*) an ostracum has developed on the shaft (the ostracum is always lacking on the collar), but different in structure from that of the adult spines, forming a uniform layer, in which a very fine radiating striation may be observed, but none of the canals leading to the exterior seen in the ostracum of the adult (Fig. 11). Fig. 10 *d* represents part of a transverse section of one of the later formed spines of a young specimen of 3.5 mm diameter. The ostracum has the same structure as in the adult spines, but without the coarse "hairs" that through their anastomosing branches form a sort of secondary cover in the adult spines of *Eucidaris metularia* and the majority of Cidarids. As a matter of fact these spines of the younger specimens show the same structure of the outer layer as is found in the adult *Histocidaris*. As, in my opinion, *Histocidaris* represents the most primitive type of recent Cidarids, it may perhaps be justifiable to see in the structure of these spines of the younger specimens a reminiscence of an ancestral type. That this is the case also with the youngest spines seems to me beyond doubt; but this, of course, is only a suggestion as we do not know the structure of the spines of the ancestors.

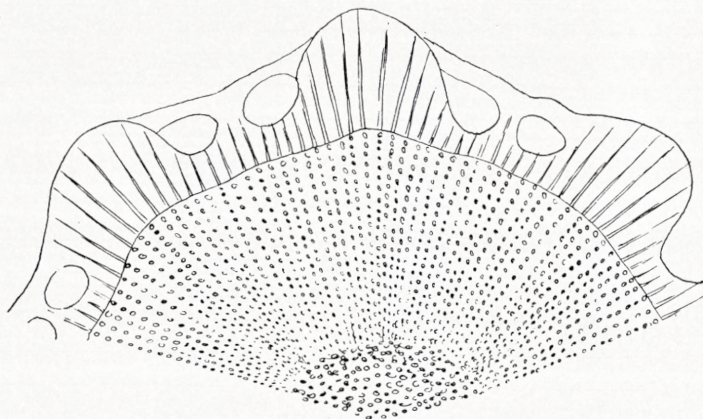


Fig. 11. Part of transverse section of a primary spine of the adult type; *Eucidaris metularia*. $\times 50$.

The different structure and colour of the successive primary spines make it easy to identify them with certainty in the different specimens and thus to follow their fate. It is thus seen that the spines once formed, are not transformed at all; the spines from plates 2—3 will never be able to assume the shape of the later spines, with the ostracum layer. If all the spines of the adult are of the adult type, with the ostracum layer, this is due to the fact that the first formed spines are lost. As the interambulacral plates at the peristomial edge are gradually resorbed, their spines are dropped (— probably not also resorbed. But this I cannot prove definitely; in order to prove this it would be necessary to follow the development and growth of a single specimen). Therefore, in an adult specimen of *Euclidaris metularia* the primary spine nearest to the peristomial edge is morphologically by no means the first but about the 6th—7th, all those adorally to it having been dropped (or resorbed) together with the plates to which they belonged.

The secondary spines of the young specimens are likewise very different in shape and structure from those of the adult Cidarid. The most extraordinary are those found on the ocular plates in the youngest specimens (Fig. 12); they are formed of three vertical ridges, at the end widening into a high, fenestrated keel, produced into some small teeth. This form, which recalls the embryonal spines of the Echinidæ (cf. "Die Echinoiden d. Deutsch. Südpolar-Exped. p. 68, Taf. XVII, 17, 27; Studies of the Development and Larval Forms of Echinoderms, 1921, p. 74), is found only on the ocular plates in the youngest stages. The other secondary spines of the young specimens are somewhat more complicated, though still very different from the secondary spines of the adult, being cylindrical, with the point widened, crown-shaped. As is the case with the primary spines these spines, when once formed, are not transformed into the more complicated structure of those found in the following stages; they remain in the shape once assumed. But as new coronal plates are formed at the upper border of the corona, the secondary spines appearing on these plates become more and more complicated, until the adult shape is reached (Figs. 13 a—f). The original, more simple spines pass down with the plates, to which they are attached, towards the peristome to be dropped (or resorbed)



Fig. 12.
Spine from ocular
plate of youngest
specimens of *Eu-*
clidaris metularia.
(Figs. 1—2).
× 120.

there, as the plates are resorbed (the interambulacral), or to pass on to the peristome (the ambulacral plates), where these embryonal spines may be observed until a much later stage, when — probably — they are lost and replaced by new ones of the adult shape of the peristomial spines. The fine, original spines of the ocular plates are soon lost and replaced by the more advanced type.

The pedicellariæ. As seen from figs. 14 a—b the pedicellariæ of the youngest stages are already distinctly of the type of Cidarid globiferous pedicellariæ; evidently they rather represent a more generalized form of the globiferous type — not to be referred with certainty to the large or small form of globiferous pedicellariæ of the adult. The same structure was observed in the pedicellariæ of the young *Rhynchocidaris*

triplopora (Ech. d. deutschen Südpolar-Exp. p. 11, Taf. XV, 9) and likewise in the young Cidarid described in the Echinoderms of New Zealand and the Auckland-

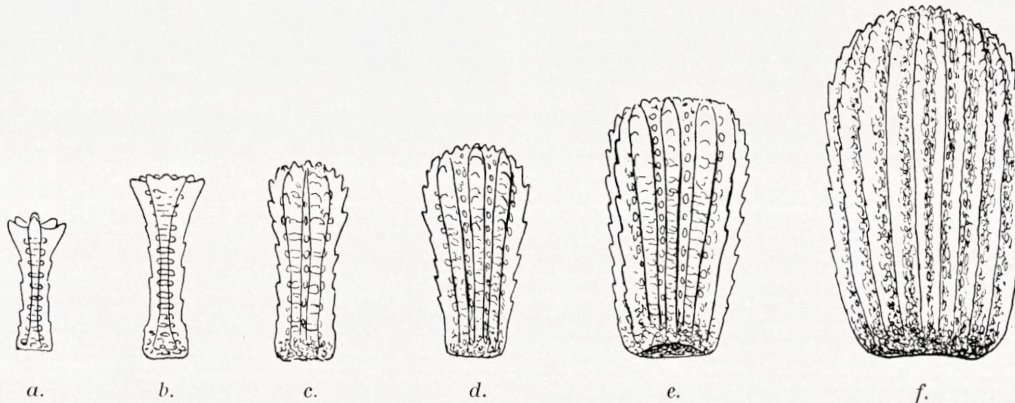


Fig. 13. Secondary spines of young *Eucidaris metularia*; to illustrate the more and more complicated structure of the spines, corresponding to the age of the animal. *a.* From the youngest specimen (figs. 1—2); *f.* from specimen 3.5 mm diameter. All $\times 120$.

Campbell Islands. I. Echinoidea. (Vid. Medd. Bd. 73. 1921, p. 152 Pl. VII, 3 — not Pl. VIII, as is stated, by a misprint, on p. 152).

The fact that already the first formed pedicellariæ are distinctly of the Cidaroid type is of considerable interest, and has an important bearing on the question whether the remarkable Echinoid larva *Echinopluteus transversus* Mrtsn. might possibly belong to a Cidarid (cf. the author's "Studies of the Development and Larval Forms of Echinoderms, 1921, p. 91—95). As shown there (fig. 37, p. 92) the pedicellariæ of the developing sea-urchin are distinctly of the ophiocephalous type of Echinids. This fact decidedly speaks against referring this larva to a Cidarid, as it is very unlikely that the pedicellariæ of the young Cidarid should already have changed from an ophiocephalous pedicellaria in the metamorphosing larva into a globiferous pedicellaria of true Cidaroid type in the newly metamorphosed sea-urchin — the change being again due to replacing by new forms, the transformation of a fully formed pedicellaria from one type into another being as impossible as the transformation of one type of spine into another.

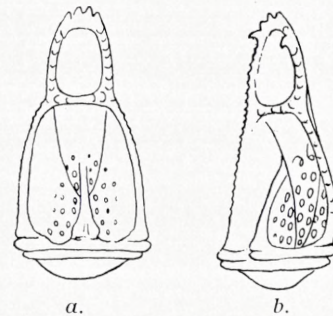


Fig. 14. Valves of pedicellariæ of *Eucidaris metularia*, youngest stage. *a.* From the inside; *b.* side view. $\times 325$.

The existence of such peculiar embryonal primary spines in Cidarids has previously been noticed, namely in *Rhynchocidaris triplopora* Mrtsn., the development of which viviparous species was described in the author's report on "Die Echinoiden der Deutschen Südpolar-Expedition 1901—03" (Deutsche Südpolar-Exped. XI. Zoolo-

gie III. 1909, p. 10—11). A primary spine is described and figured there (p. 11, Taf. XIII, 20. XVI. 13) but not correctly understood, it being stated “dass sie noch nicht fertig gebildet sind, indem die Aussenlage noch nicht vorhanden ist”. At the then state of knowledge the true character of these spines could not be imagined. In the light of the facts brought forward through the study of the young *Eucidaris metularia*, there can, however, be no doubt that these spines of *Rhynchocidaris triplopora* correspond to those of interambulacral plates 2—3 of *E. metularia*, and that they should not be transformed into the adult type of spines but be dropped (or resorbed) contemporaneously with the resorption of the plates to which they belong. The secondary spines of *Rhynchocidaris* do not present any peculiarities like those of *Eucid. metularia*. They are late in appearing, their development having scarcely begun in the stage represented in Taf. XIII, 4, 6 of the “Ech. d. Deutschen Südpolar-Exped.”, where already the two first pairs of ambulacral plates and the four first interambulacral plates have been formed, with their primary spines, these latter being, however, still in an unfinished stage. In the stage Taf. XIII, 7, 9 the secondary spines have been formed; they differ from those of the adult form only in being more slender.

In *Notocidaris gaussensis* Mrtsn. the secondary spines are likewise late in appearing and seem from the first to assume very nearly the same shape as in the adult, not the elegant shape of the embryonic spines of *Eucid. metularia*¹). The same evidently holds good of *Austrocidaris canaliculata* (cf. LOVÉN “Echinologica”, p. 6, Pl. I). The first primary spines of these two Cidarids apparently never assume a shape similar to those of *E. metularia* and *Rhynchocidaris*, as evidently holds good also of *Aporocidaris Milleri* (see below). It may well be suggested that this is a secondary character, probably due to the large size of the eggs and their rich contents of yolk. That this is, however, not a character common to all brood-protecting Cidarids is clear from the fact that in *Rhynchocidaris triplopora* and *Goniocidaris umbraculum* the first primary spines have not the same shape and structure as the adult spines. Possibly the reason for this difference in the character of the first primary spines may lie in the different size and yolk-contents of the eggs — but of this we have no definite knowledge.

It may be pointed out here that the young Cidarid described by the author in the “Echinoderms of New Zealand and the Auckland-Campbell Islands I. Echinoidea” (Vid. Medd. Bd. 73. 1921. p. 152) is evidently in a stage corresponding to that of the young *Eucid. metularia*, the primary spines being distinctly of embryonal type.

Among a number of *Goniocidaris mikado* Döderlein from the Sagami Sea, Japan, I found a young specimen, 2 mm in diameter, which may be said almost with certainty to belong to this species. It agrees in its main features with the young *Euci-*

¹) According to renewed examination of the embryos; in the original description (Echinoiden d. deutsch. Südpolar-Expedition, p. 21) this is not stated definitely.

daris metularia, as described above. There are 4 pairs of interambulacral plates, but the first, unpaired plate has as yet hardly begun being resorbed. Four pairs of tube-feet are developed, besides the buccal tube-feet; none of the ambulacral tube-feet have as yet passed on to the peristome, in accordance with the fact that the primary unpaired interambulacral plate is still intact. The terminal tentacle is quite rudimentary. The primary and secondary spines are in all essentials like those of the young *Eucidaris metularia*, only the thorns are not serrate along their distal edge; the spines are all colourless. In this species it would therefore not be possible to ascertain the exact serial number of the spines and plates about to disappear at the peristomial edge (beyond the first, of course).

IV. Description of an Embryo of *Goniocidaris umbraculum* (Hutton).

In the "New Zealand Journal of Science and Technology" VIII 1926, p. 192 I published a small note "Goniocidaris umbraculum, a brood-protecting species",

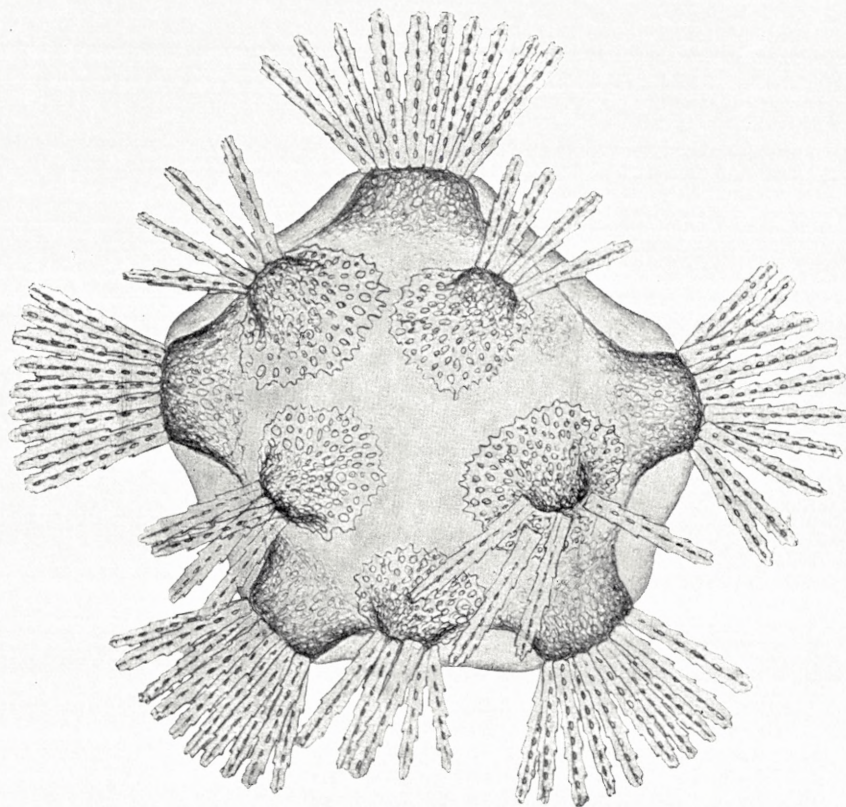


Fig. 15. Embryo of *Goniocidaris umbraculum*. $\times 65$.

in which is recorded the observation that this species carries its eggs and young on the peristome, covered by the primary oral spines. Unfortunately the material of developing embryos available was very scarce, four samples in all, and all in the same stage of development. But this young Cidarid is quite extraordinary and, in fact, unlike anything else known in Echinoid embryology. It is, therefore, well worth a description, even though it represents only a single stage.

As seen from fig. 15 two alternating sets of five plates have been formed, each plate carrying a group of spines. On the other side of the embryo a third set of five plates, corresponding in position to those of the upper circle, has appeared, but these plates are still quite small and do not carry spines. The interpretation of these three sets of plates is somewhat doubtful. Supposing — as might well seem reasonable — that the largest plates represent the five primary interambulacral plates, the upper circle would represent the ocular plates, and the plates about to develop on the opposite side would then necessarily represent either one of each

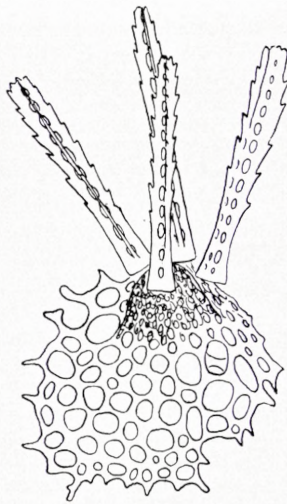


Fig. 16. Ocular plate (?) with its spines, of an embryo of *Goniocidaris umbraculum*. $\times 125$.

pair of buccal plates or the first true ambulacral plate. As there is no distinct trace of the terminal feeler or of anything else of the ambulacral system, there is no definite proof that this interpretation is the correct one, but it may well seem the most probable.

The main interest concerning this embryo attaches to the feature, quite unique, not only in Cidarids, but in all of the Echinoids, as far as hitherto known, that each plate carries, instead of a single spine, a bundle of slender, embryonic spines, all attached to the same tubercle, each bundle thus evidently representing the single spine corresponding to each tubercle in other Echinoids. While the — supposed — ocular plates carry only 3—5 spines each, there is a bundle of ca. 10 spines attached to the very conspicuous tubercle of the primary interambulacral plates. The spines are very slender, flattened, of very evident embryonic structure (Fig. 16).

It would be of quite unusual interest to get an opportunity of studying the complete development of this species, and, as it is very common in places in the New Zealand Seas (cf. MAXWELL YOUNG: Occurrence of the Echinoderm *Goniocidaris umbraculum* Hutton. *New Zealand Journ. of Science and Technology*. VII, 1924 p. 189) it may well be hoped that the necessary material will be available some day. For the present, the stage described above especially serves to emphasize the extraordinary difference which may exist in the development of otherwise nearly related forms — a warning against generalizing the results achieved from the study of a single species as applying to the whole of the class to which this species belongs — as is not so rarely done.

V. A young Stage of *Aporocidaris Milleri* (A. Ag.).

Among the Echinoids from the "Albatross" Philippine Expedition which have been entrusted to me for study were also some few very young Cidarids from the "Albatross" stations 3360 and 3415, i.e. from the Panamic Deep Sea Expedition 1891 — not from the Philippines. With the kind permission of the Authorities of the U. S. National Museum I am including the little information that can be derived from this material in the present paper, as a representative of a third type of young Cidarids.

On the said stations of the "Albatross" only one species of Cidarids was secured, viz. *Aporocidaris Milleri*. There is thus a priori every probability that the young specimens belong to this species, and this is raised to certainty by two additional facts. The young specimens are very thick and clumsy, as different from the elegant young *Eucidaris metularia* as could well be imagined; it is very evident that they have developed from large eggs, rich in yolk substance, and one would surmise that they belonged to some brood-protecting species. *Aporocidaris Milleri* was not known to be a brood-protecting species, but as a matter of fact it is; during a visit to the U. S. National Museum in September 1926 I found there one specimen with a young one on the peristome, and another with a yellowish mass on the peristome which could hardly be anything but disintegrated eggs.

The other fact of importance is this that the pedicellariæ are of the same type as those of the adult; before I had examined these structures I was rather inclined to think that these young Cidarids belonged to some species of *Histocidaris*, but the pedicellariæ give definite proof that they are no *Histocidaris*, and the three facts: the occurrence of only *Aporocidaris Milleri* in the locality where the young were found, the brood-protection of the species, and the character of the pedicellariæ, make it practically certain that we have here the young of *Aporocidaris Milleri*.

The general aspect of this young Cidarid (Fig. 17) is very much like that known from another brood-protecting Cidarid, *Austrocidaris canaliculata* (cf. Lovén, Echinologica, Pl. I). As in the latter species the test of the young is invested with a

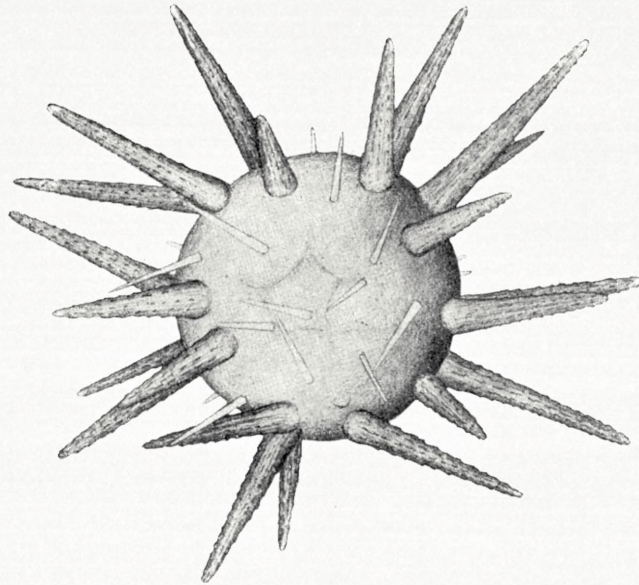


Fig. 17. Young *Aporocidaris Milleri*; aboral side. $\times 19$.

thick skin which conceals all the calcareous plates and the sutures between them. Even when dried none of these details become distinct. This explains the curious statement by AGASSIZ ("Challenger" Ech. p. 45) that in *Austro-*



Fig. 18. Buccal plate of young *Aporocidaris Milleri*. $\times 125$.

cidaris canaliculata in a corresponding stage "we find as yet no separation of ambulacral or interambulacral plates"..... "the test is not subdivided into zones by plates; it is as yet composed only of more or less close reticulation and irregularly shaped plates". As shown by LOVÉN ("Echinologica", Pl. II) the test of the young *A. canaliculata* is composed of the usual regular plates, and the same, of course, is seen to be the case in *Aporocidaris Milleri*, when the test has been cleared up and the necessary preparation made for making the structural details distinct.

The specimens are all of nearly the same size, about 2 mm in diameter. The mouth is not yet open, the dental apparatus being in an embryonal condition. The primary spines differ to some extent in length, but otherwise the specimens do not



Fig. 20. Spines of young *Aporocidaris Milleri*. a. primary, b. secondary. a. $\times 50$. b. $\times 65$.

differ much as regards their stage of development. Three pairs of tubefeet have been developed, and the fourth is about to appear. The terminal sucker is large. The buccal tubefeet are distinctly smaller than the ambulacral tubefeet and evidently do not appear until about contemporaneously with the third pair of ambulacral feet.

It is interesting to note a conspicuous difference in the relation of the tubefeet to the ambulacral plates and to the buccal

plates. While the ambulacral plates lie from the first at the aboral side of the suckers and gradually grow round the latter, in the buccal plates a hole is formed by resorption in the middle of the plate, through which the sucker grows out (Fig. 18). These



Fig. 19. Periproct and adjoining part of the genital plates of young *Aporocidaris Milleri*. Two periproctal plates have appeared contemporaneously. $\times 125$.

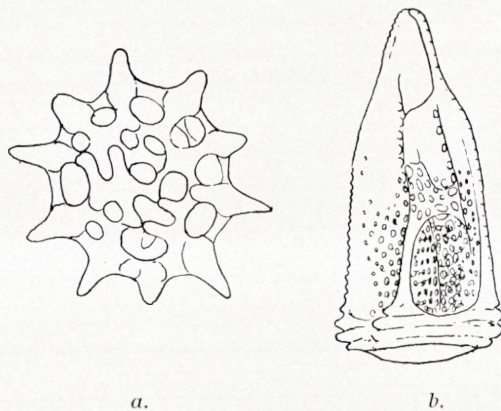


Fig. 21. Transverse section of primary spine of young *Aporocidaris Milleri* (a). Valve of pedicellaria of same (b). a. $\times 230$. b. $\times 215$.

facts are in correspondence with the observations on the development of the ambulacral plates of *Psammechinus miliaris* by Miss GORDON (Op. cit. p. 289).

There are two interambulacral plates in each series, besides the primary unpaired plate at the peristomial border, which has as yet not begun being resorbed. There is a scarcely discernible trace of the plate No. 4 being slightly larger and nearer the interambulacral median line.

In the apical system the anal plates are, as usual, from the first not represented by a single primordial plate. Fig. 19 shows that here two plates have appeared contemporaneously.

The spines are very markedly different from those of *Eucidaris metularia* (and *Goniocidaris umbraculum*), and can scarcely be said to be of a special embryonal type. The primaries are all alike, only the two first ones are slightly curved (Fig. 20 *a*); they are simply spiny and of a very unfinished type, without a special outer layer, as seen in transverse sections (Fig. 21 *a*). They are still covered by skin, and there is thus far no hindrance to their developing directly into the adult type of spine. The secondary spines (Fig. 20 *b*) are very slender, but otherwise not peculiar.

The pedicellariæ (Fig. 21 *b*) are of typical Cidarid structure and recall the large globiferous form of the adult.

This young Cidarid is very like the young specimens of *Austrocidaris canaliculata* and *Notocidaris gaussensis*. One might well expect all the brood-protecting species, with their large, yolky eggs, to agree in the general features of their post-embryonal development. This, however, is not the case. *Rhynchocidaris triplopura* is somewhat different, but especially *Goniocidaris umbraculum* differs extraordinarily from the other species in its development. It is, therefore, very desirable to study as many species, as possible, also of the brood-protecting species, with regard to their development. Only in this way may we expect to learn which characters are of general and which are only of specific value.

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