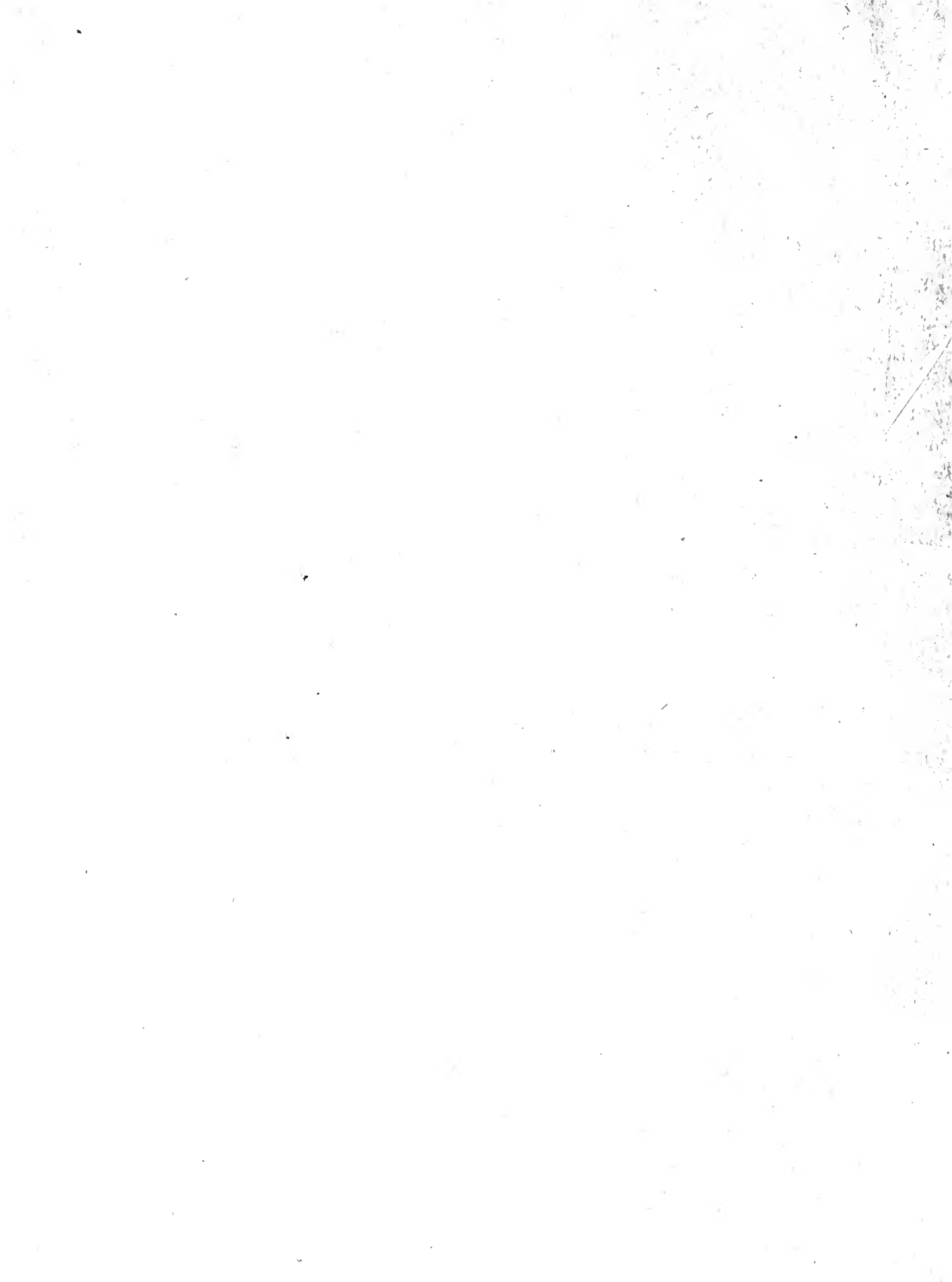






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STUDIES  
OF THE  
DEVELOPMENT AND LARVAL FORMS  
OF  
ECHINODERMS

BY  
**Dr. TH. MORTENSEN**

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WITH 33 PLATES AND 102 FIGURES IN THE TEXT

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## INTRODUCTION

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EVER since Joh. Müller about seventy years ago published his celebrated studies on the Echinoderm larvæ, showing such unexpected richness of forms to exist among them and making known in the main features their wonderful metamorphosis, these larvæ have been among the favourite objects of zoological research. The study of the larval forms themselves, the differentiation of the original simple larval type into the many highly specialized or even quite extreme forms (e. g. *Auricularia nudibranchiata* or *Echinopluteus transversus*), tracing the morphological transformation of the different parts of the larval body (so masterly done already by Joh. Müller) or of the supporting skeleton makes in itself quite a fascinating subject. The metamorphosis of the bilateral, free-swimming larva into the radial, more or less sedentary, adult — a metamorphosis no less striking than that of a caterpillar into a butterfly (indeed, the Echinoderm metamorphosis has been characterized as the most remarkable ontogenetic change in the animal kingdom) — presents a number of interesting problems. Then the Echinoderm larvæ have proved to be exceptionally good objects for experimental embryological studies, for experimental hybridization and for heredity studies. No wonder that an extensive literature has arisen on forms presenting so many points of interest.

The significance of the pelagic larvæ for the study of geographical distribution was pointed out in the author's work „Die Echinodermenlarven der Plankton-Expedition“ (1898. p. 108), and this was in the author's mind when, speaking of the relation between the East African and the West Indian Echinoid fauna<sup>1)</sup>, the desirability of studying the development of the forms common to both regions, as, upon the whole, that of tropical Echinoderms in general, was emphasized, this being almost a terra incognita, „an ample field of most promising research“.

<sup>1)</sup> Th. Mortensen. On some West Indian Echinoids. Bull. U. S. Nat. Museum. 74. 1910. p. 25.

The author of the present work has for a long time realized that the study of the larvæ would have an important bearing also on the classification of the adult forms, and it was, indeed, mainly from this point of view that the investigations recorded in this work were undertaken.

While it is obvious enough that the pelagic larvæ must be of considerable importance for the geographical distribution, the question whether they have also a bearing on classification is, however, not so easily settled. It is, of course, undeniable that their organization and shape is stamped by the adaptation to the pelagic life; but are the larval characters purely secondary adaptations, which cannot possibly afford any clue to the natural affinities of the adult forms? The author has gradually become more and more convinced that this is not the case, but that they do really have a classificatory value. Already in the Part I of the "Ingolf" Echinoidea (1903, p. 111) the possibility of finding in the larval forms facts that might be of value for classification was hinted at, the great difference known to exist e. g. between the larva of *Sphærechinus granularis* and those of the *Echinus*-species being mentioned as indicating "at all events, that very interesting things may be found here."

The facts hitherto made known regarding the larval forms of Echinoderms would seem upon the whole to support the idea that there is a distinct interrelation between the larvæ and the adults, that the classification of the larvæ corresponds to that of their adult parental forms. Thus e. g. the Spatangoid larvæ have the peculiar character in common that there is a long unpaired process from the hindpart of their body, and not a single exception is known to this rule. The larvæ of *Echinus*, *Psammechinus* and *Paracentrotus* all agree in having in their first stage the body considerably elongated beyond the stomach and supported by an elongated, clubshaped body rod, while in the later stage this rod becomes absorbed, so that the body is shortened, being in the same time provided with vibratile epaulettes, while no posterior transverse rod is developed. It would thus seem that here we have a distinct larval type peculiar to the family Echinidæ. The Clypeastroid larvæ hitherto described (*Echinocyamus pusillus*, *Echinarachnius parma* and *Mellita testudinata*) all agree in the general character of the larval shape and the structure of the larval skeleton (the body skeleton forming a basket structure), so that it has the appearance that there is a Clypeastroid larval type as distinct as the Spatangoid type. Among the Asteroids it seems evident that there is a distinct larval type, the so-called *Brachiolaria*, peculiar to the family Asteridæ, characterized mainly by its round Brachiolarian processes, while the type of *Bipinnaria asterigera* (the first Echinoderm larva described) appears to be characteristic of the family Luidiidæ.

While no definite conclusions can be drawn from the few larvæ of Holothurians hitherto known, and likewise the Crinoids are out of question in this connection having no true pelagic larvæ, the Ophiuroid larvæ have an important bearing on the problem. Larvæ belonging to the genera *Ophiothrix*, *Ophiopholis*, *Ophiactis* and *Amphiura* are known but only one of each genus. They do not afford so very characteristic differences as one should expect, since they belong to three different families, and those of *Ophiopholis* and *Ophiactis* are more different than should be expected after the apparently near relation of these two genera. Then within the genus *Ophiura* we know with certainty the larvæ of the two species *Oph. albida* and *texturata*, and these are so different that one would rather think they must belong to different families. The larvæ which are with a considerable degree of probability referred to *Oph. affinis* and *Homalophiura gelida* (Kochler) again are very different from each other as well as from the two named above. — These facts are thus decidedly opposed to the conclusions to be drawn from our previous knowledge of the Echinoid and Asteroid larvæ. Considering, however, that our knowledge of the natural affinities of the vast number of Ophiurids is still rather unsatisfactory, even in spite of the more recent attempt at a natural classification of this group by Matsumoto, it seems to me that the facts known of the Echinoid and Asteroid larvæ outweigh those of the Ophiuroid larvæ, and lead to the conclusion that these larvæ, on the contrary, tend to prove that there is something wrong with our classification of the Ophiuroids.

In spite of these *Ophiura*-larvæ it seemed then a legitimate conclusion that the Echinoderm larvæ are really of considerable classificatory value, the larvæ of nearly related forms agreeing in their main characters; the opposite conclusion would then be equally legitimate, that when the larvæ of two forms, apparently nearly related, prove to be essentially different, those forms are not in reality nearly related. The study of the larval forms will then afford a very important test for the value of our classification of the adult forms.

It is evident that the knowledge of a very much larger number of Echinoderm larvæ than the comparatively few known till now is required for placing the idea of the classificatory value of these larvæ on a more firm base. Nearly all the researches hitherto made on the development and the larval forms of Echinoderms were carried out on species occurring in the European and North American Seas, only a few forms from the tropical seas of America having more recently been made the object of study (Tennent). But, moreover, it is mainly a few selected types which have, over and over again, been studied, so that even of the com-



paratively few North European Echinoderms a great percentage still remain unknown as regards their development, our knowledge having for a great part not reached beyond Joh. Müller. To a no smaller extent this holds good also for the North American types.

It is a strange fact that in the numerous works on hybridization of Echinoderms it is generally only the first larval stage which is taken into consideration. Beyond this stage the investigators rarely go. Thus e. g. *Sphærechinus granularis*, which is used over and over again for hybridization experiments, has not yet been reared to its full larval shape; in fact, it is only by inductive evidence that we may now with a fair degree of certainty refer one of the larvæ described by Joh. Müller to that species. Similarly the larvæ of *Strongylocentrotus franciscanus* and *purpuratus* used so very much for hybridization studies by American investigators are as yet known only in their first stage. As MacBride<sup>1)</sup> justly says: "to judge from much of what has been written on this subject, no one would ever suspect that the larva of an Echinoid had more than four arms." A highly praiseworthy exception from the rule forms the work by Shearer, Morgan and Fuchs "On the experimental hybridization of Echinoids"<sup>2)</sup>, these investigators having studied not only both the young and the final stage of the normal as well as the hybrid larvæ, but also reared the hybrids beyond metamorphosis and even nearly to the full size of the sea-urchin. Hybrids of the same forms (*viz.* *Echinus esculentus*, *acutus* and *Psamm-echinus miliaris*) were likewise reared through metamorphosis by Debaisieux<sup>3)</sup>. Also Tennent<sup>4)</sup> has reared some of the larvæ used for his experiments to their full shape. But, as stated, the general rule is that only the first larval stage is used in the hybridization and heredity studies, the experimentators having apparently no idea of what the normal larvæ look like in their full shape.

I do not mean to deny, of course, that the young larvæ do very often afford striking characters already in the first stage, so that something may be concluded from the mixing up of these characters in the young hybrid larvæ as to the inheritance and dominance of the maternal or paternal characters. But it seems selfevident that much more valuable results would be gained from these hybridization studies if carried through at least to the final larval form. The ideal must be, evidently, to rear not only the hybrid larvæ to their full size, but to get

<sup>1)</sup> Studies in Heredity. I. The effects of crossing the Sea-urchins *Echinus esculentus* and *Echinocardium cordatum*. Proc. R. Soc. B. Vol. 84. 1911. p. 398.

<sup>2)</sup> Philos. Transact. Ser. B. Vol. 204. 1914.

<sup>3)</sup> Quart. Journ. Micr. Science. N. S. Vol. 58. 1913.

<sup>4)</sup> David H. Tennent. Echinoderm Hybridization. Publ. No. 132. Carnegie Inst. Washington. 1910.

them through metamorphosis, and then further to rear the metamorphosed hybrids to maturity and then again study their offspring. That this can be done is beyond doubt; the way has been shown by Shearer, Morgan and Fuchs<sup>1</sup>). So far, however, nobody has done this. But, in any case, it should be the minimum claim that the investigators should really know the normal shape of the larval species they use for their hybridization studies. — It is, of course, more explicable that the students of experimental embryology generally confine their studies to the youngest larval stage, the larvæ often not being able to survive after the varied chemical or mechanical treatment. Still, the fact that MacBride<sup>2</sup>) has succeeded in rearing unto metamorphosis larvæ treated so as to have developed a double hydrocoel or no hydrocoel at all shows that probably in many cases a good deal more might be done than is generally the case.

Having for a long time felt this unsatisfactory character of most of the hybridization and heredity studies hitherto carried out on Echinoderms, one of the objects of my studies was this, to aid in bringing about a more satisfactory base for the hybridization work in making known the normal larval forms of as many Echinoderms as possible. — That I have confined myself to the study of the normal larvæ, not entering on hybridization experiments, does not mean that I take no interest in hybridization studies — on the contrary, I should think such studies, carried out after the ideal sketched above, most fascinating — but there was simply no time to extend the researches so far. On the other hand, the fact that I did not use artificial parthenogenesis either, although that might have been very advantageous in several cases, where material for fertilization was scarce, is in accordance with my wish to study the normal larvæ, there being, as yet, not sufficient guarantee that artificially parthenogenetic larvæ show the normal characters of the larvæ to the full extent.

As already stated it is only a few species out of the comparatively poor Echinoderm fauna of Europe and North America which have hitherto been studied as regards their larval forms. A few of the West Indian forms have been studied; but the vast majority of the numerous species occurring there are still unknown as regards their development. And then the immense number of Echinoderms peculiar to the Indo-Pacific region, including many forms of the greatest morphological and systematic import-

<sup>1</sup>) These authors (Op. cit. p. 256) also point out the unsatisfactory character of the usual method, to take only the skeletal structures of the first larval stage into consideration in the hybridization studies.

<sup>2</sup>) E. W. MacBride, The artificial production of Echinoderm larvæ with two water-vascular systems, and also of larvæ devoid of a water-vascular system. Proc. R. Soc. B. Vol. 90. 1918.

ance, were till now absolutely unknown as regards their development. Thus e. g. of the Echinoidea the great and important families Diadematidæ, Temnopleuridæ and Echinometridæ are, with the exception of one or two forms of each, confined to the Indopacific (and, moreover, the few forms which do occur in European and American Seas have not been made the object of embryological study till now). Only the family Arbaciidæ is confined to the European and American seas and the family Echinidæ for the main part so. For the rest the European-American Echinoid-fauna forms only a small outskirts of the Indo-Pacific fauna, and, accordingly, even if we knew the development of all the European-American forms, such knowledge would be fragmentary and altogether insufficient for forming a decisive judgment of the classificatory value of the larvæ.

For a long time it has been my ardent desire to tackle this subject, taking up the study of the Echinoderm larvæ methodically from the point of view expressed here. As an introduction a visit was made at the marine Laboratory at Plymouth in the summer of 1913, especially in order to become acquainted with the excellent methods of rearing marine larvæ worked out there through the efforts of the director, Dr. E. J. Allen and his fellow workers. A preliminary report on the researches made there, resulting in the rearing of several forms the larvæ of which were till then unknown, was given in the paper "Notes on the development of some British Echinoderms".<sup>1)</sup> But the main thing was, of course, to undertake such investigations in the Pacific regions. This was at length made possible for me through liberal grants from the Carlsberg Fund and from the Government (the "Kommunitet" Fund), enabling me to spend more than two years there in different localities. As the Expedition had several other objects besides the study of the Echinoderm larvæ the plan of the voyage could not be laid exclusively with regard to the latter purpose, but it need scarcely be stated that every opportunity was seized for making the most out of this special subject.

The first place visited was the Philippines, where Zamboanga, on the Southern end of Mindanao, and Jolo were the main spots chosen for working places. No embryological researches were carried out here — this being mainly due to lack of experience, not of undertaking artificial fertilization, but of what may be done even where all laboratory facilities are wanting, as they were here — an experience which there was rich opportunity of gathering by the continued work during the voyage.

In Japan, the next place visited, the Biological Station at Misaki, at the Sagami Bay, offered splendid opportunities for carrying out embryological work, and the author's efforts in this direction were very success-

<sup>1)</sup> Journ. Mar. Biol. Assoc. N. S. X. 1913.

ful, the development of no less than 16 different forms of Echinoderms being studied more or less completely during the stay there from the end of April to the beginning of July 1911. A preliminary report on the researches carried out there was published in the "Annotationes Zool. Japonenses" Vol. VIII. 1914 ("On the development of some Japanese Echinoderms").

By the time I had to leave Misaki there were several good cultures of larvæ, which I was very sorry to leave behind and I resolved to try to carry some of them along with me to the next place to be visited, namely Sydney, N. S. Wales. This was carried out partly successfully and an important experience thus gained which was made useful at later occasions.

During the first stay in Australia, from the middle of August to the middle of October, there was no opportunity of making embryological studies, no species being found to have ripe products by that time.<sup>4)</sup> In New Zealand a few species were reared successfully under very unfavourable circumstances onboard the little steamer "Hinemoa". On an excursion by land to Napier N. Z. numerous specimens of *Arachnoides placenta* were found in a small lagoon; as they appeared to be ripe, fertilization was tried, although I had only a pocket lens with me and was thus unable to test the result. The supposed culture I then took along with me in a jar to the interior of the country, carrying also a jar with pure seawater for eventually transferring the young embryos. These were found swimming at the surface the next day, and being then transferred to the other jar they went on developing normally, and the culture was kept successfully during a fortnight without any change of the water. — Fertilization of the interesting *Echinobrissus recens* was made in Wellington on the day before the departure; the culture was brought successfully to Sydney. On the return hereto opportunity was found of rearing the embryos of *Heliocidaris erythrogramma*. A preliminary report on the remarkable shortened development of this Echinoid was published in the Proceedings of the Linnean Society of N. S. Wales (Vol. XL. 1915).

On Hawaii, the next place visited, fertilization was made of quite a number of species, among which such interesting forms as *Colobocentrotus* and *Heterocentrotus*. Conditions were, however, not very favourable for rearing the larvæ beyond the younger stages. At the place where the work was carried out (near the little town Hilo), the water (which had to be taken from the shore, no boat being available) not being as pure as desirable and perhaps also less salt than desirable (on account of submarine springs, which abound in several localities along the coast of the island

<sup>4)</sup> There may have been some species with ripe sexual products by the middle of August, but I had no time for making such studies just then.

of Hawaii); the unfortunate circumstance that there was no possibility of making drawings of the living specimens also has lessened the value of the researches carried out here.

Better opportunities were found on the following places visited, the Biological Station at Nanaimo, Vancouver, B. C. and at La Jolla, California, where, of course, the usual laboratory facilities were available. Several interesting forms were studied here, more or less completely. Also at the next place, the Island of Taboga in the Bay of Panama, a rich fauna was available for study, and fertilization of quite a number of species was undertaken; the results were, however, not so good as desirable here, the larvæ generally dying off before the full shape had been acquired. This was doubtless due to the water being not pure enough there near the great Canal and all the traffic.

While staying here at Taboga I had the great pleasure of being invited to partake in the Carnegie Expedition to Tobago, B. W. I, (near Trinidad). In the temporary laboratory established here close to the coral reef at Buccoo Bay excellent results were obtained, the development of ten different species being studied more or less completely during the stay of only four weeks. — On leaving this place I undertook again to carry some of the cultures along with me, namely of *Tropiometra carinata* and *Echinometra lucunter*, the first in the Pentacrinoid stage, the second just metamorphosed. While the first of these was too much chilled during one cold night near New York, the latter stood the transport and, after having been kept for some weeks in the New York Aquarium was again taken onboard the steamer to Europe and taken to Copenhagen. Some few of the specimens were still alive and in fairly good condition on the arrival to Copenhagen and thus had stood the transport from the Westindies to Denmark under conditions not altogether favourable.

The successful experiments made with such transports of larval cultures, as upon the whole the several successful rearings of larvæ under very adverse conditions give an indication of their often surprising hardiness and open the view to far reaching experiments.

It is well known to everybody, who has undertaken to rear Echinoderm larvæ, how this task has been facilitated to a very high degree through the work of Allen and Nelson<sup>1)</sup>, the pure cultures of the Diatom *Nitzschia closterium*, forma *tenuissima* obtained by them being in many cases very successfully used as food for the Echinoderm larvæ. When starting on my voyage I had a small sample of such culture sent to me from Plymouth. Unfortunately, however, it was all dead, before I could arrange for rais-

<sup>1)</sup> C. J. Allen and E. W. Nelson. On the artificial culture of marine Plankton organisms. Quart. Journ. Micr. Science. Vol. 55. 1910.

ing new cultures from it. Several times it was tried to start new cultures in the way indicated by Allen and Nelson, and thus far successfully. Still, I never succeeded in getting the same species of *Nitzschia* or any other organism, which was so well fit for serving as food for the larvæ, and the full use of such food cultures was not obtained. In the last working place, Tobago, B. W. I., this way of rearing the larvæ was then given up, and instead the larvæ were given fresh sea-water every day — a considerably more troublesome way of rearing the larvæ, but otherwise perfectly successful.

I may point out here that, while the *Nitzschia*-food has proved excellent for Echinoid-, Asteroid- and Holothurioid larvæ, it appears to be not well accepted by the Ophiuroid larvæ. In the stomach of these larvæ is very often found the skeletons of different Silicoflagellates. If cultures could be raised of these forms, they would doubtless prove to be excellent for rearing the Ophiurid larvæ, which would be of considerable importance. Possibly other Flagellates would also prove successful.

The main object of my work being, as stated, the comparative study of the larval forms it is only a matter of course that not much attention was paid to the embryological processes — cleavage, enterocoel formation etc., as well as the process of metamorphosis or the postembryonal development. Not that I think the study of these processes of minor importance; on the contrary, I feel convinced that such studies carried out on different forms will give most important correctives to the results reached from the comparatively few forms hitherto studied in these regards, such as was the case with the Crinoids studied by the author. But there was simply no time to do all that work; having to do all the work myself: collecting, preserving, making biological observations, rearing cultures etc., I had simply to confine myself to studying the stages especially important for my purpose; only in cases where unusual features were observed more attention was paid to the embryological processes, as e. g. in *Peronella Lesueurii*.

As a consequence of my having altogether too much work to do I could not always get the necessary time for making drawings of the living larvæ, which was also in several cases impossible on account of the conditions under which the cultures were reared. In such cases the different stages of the larvæ were carefully preserved for future study at home, partly in alcohol, partly mounted in Canada balsam. Now this resulted in some very serious drawbacks. It is, upon the whole, a very difficult thing to preserve such larval forms as the Echinoid- and Ophiuroid larvæ quite satisfactorily; the arms generally shrink considerably, though not in length, of course, the skeletal rods preventing a shortening. The two figures of the larva of

*Mespilia globulus*, Pl. VII Figs. 1 and 2, one being drawn from a living specimen, the other from an especially carefully preserved specimen, give a striking example of this. (The Asteroid and Holothurioid larvæ, which have no supporting skeleton, are much easier to preserve in good shape). — But then, worst of all, in many cases the skeleton was found to have been dissolved. The slightest trace of acidity will result in destroying such fine calcareous structures; although I used always the purest alcohol obtainable for the preservation of these larvæ, the result proved fatal in only too many cases. Traces of the skeleton are still recognizable in many cases and the dissolution has generally proceeded so slowly that the organic matrix of the calcareous substance may still show the shape of the skeleton almost undisturbed; but for the purpose of studying the morphology of the skeleton and its specific characters in the different larval forms it is of no use. Even the preservation in Canada balsam does not give safe guarantee against the dissolution of the skeleton; in some of these larvæ also their skeleton has disappeared more or less completely. The matter is not simply explained by stating that the alcohol or the balsam must have been acid. It may happen that while some specimens have had the skeleton dissolved, others preserved in the same fluid and lying side by side with them in the same jar have the skeleton well preserved; in the same way, of larvæ imbedded in Canada balsam from one and the same tube and at the same time some may have the skeleton preserved, while in others it is completely dissolved. — Whatever now the explanation may be, this dissolution of the larval skeleton has in several cases considerably deteriorated the value of my researches — especially much of the work done on Hawaii was spoiled thereby.

Besides the morphology of the larvæ attention has also been paid to the question about their distribution over the ocean. Already during the author's voyage to Siam in 1899—1900 opportunities were taken to collect plankton samples on the passage across the Indian Ocean, and again on the passage out to the East across the Indian Ocean plankton was collected daily, by means of the wash-deck pump, the water from it being sifted through a usual plankton net. Although somewhat deteriorated by rust such plankton samples could be very well utilized and gave very valuable information about the occurrence of Echinoderm larvæ in the open sea.

In the years 1910—1913 plankton samples were collected for me on board the Danish cruiser "Ingolf" on its cruises to the West Indies by the young naturalists H. Blegvad, P. Kramp and H. Fogh. In this way six series of samples were collected across the Atlantic, which have resulted in important information of the distribution of Echinoderm larvæ over this ocean — as also in the finding of several interesting larval types. In



the summer of 1920 Mr. G. L. Granelund at my request undertook to collect a series of plankton samples (by means of the wash-deck pump) on a trip to Buenos Aires. The result was remarkably poor, only two of the samples containing any Echinoderm larvæ at all; still some information was gained hereby also. Further, Mr. H. Faye, St. Cruz, West Indies, undertook to collect some plankton samples for me in the harbour of Christianssted, which contained several interesting Echinoderm larvæ. To all these gentlemen I beg to tender my best thanks for this assistance.

Plankton samples were generally taken at the different places in the Pacific where longer stay was made: not few important and interesting forms of larvæ have been secured in that way, especially of the Ophiuroid-larvæ which are generally found quite well preserved in such plankton samples: descriptions of such forms are included in the following report. On the author's expedition to Siam in 1899-1900 there were also collected several Echinoderm larvæ, which are likewise included in the present report. - It may, however, be emphasized that by no means all the larvæ thus collected have been described here. Only such as were found to present special and noteworthy features or that could be identified with forms hitherto described and thus affording zoogeographical information have been included.

It is a very agreeable duty to me to express my indebtedness and sincere thanks to all those authorities and colleagues who have rendered me assistance on my voyage or otherwise in connection with this work. First of all my thanks are due to the Carlsberg Fund which by its liberal grant made it possible for me to realize my plan of the Expedition to the Pacific, and from which grants were also received for publishing this report. A special grant was also given me from the Danish Government for enabling me to complete the reports on the material from my voyage. -- Adopting a chronological arrangement I then beg to address my sincere thanks to the director of the Biological Station at Misaki, Japan, Professor I. Ijima, Tokio, and Dr. Fujita, then Assistant at the said Biological Station; to Professor W. A. Haswell and Dr. S. Johnston, at the University of Sydney; Professor H. B. Kirk, Wellington; Professor W. A. Bryan, Honolulu, and Mr. D. Thaanum, Hilo, Hawaii; Dr. Ch. MacLean Fraser, Director of the Biological Station, Nanaimo, Vancouver B. C.; Professor Wm. Ritter, Director of the Biological Station of the Scripps Institution, La Jolla, California; Professor James Zetek, Panama, and Professor A. G. Mayor, Director of the Department of Marine Biology of the Carnegie Institution, Washington D. C. A special thank I owe to the New Zealand Government for inviting

me to join the "Hinemoa" on its trip round the North Island of New Zealand, and to the Director of the Carnegie Institute for allowing me to include in this report the results obtained during the Expedition to Tobago B. W. I. — For the hospitality offered me from the Philippine, the Japanese and the Australian Government I shall have to thank at another occasion, having to confine myself at present to what has a connection with the present work.

It may be practical, and useful, to give here a short summary of what has been accomplished hitherto in the study of the larval forms of the different species of Echinoderms, either by direct rearing of the larvæ or by identifying the pelagic larvæ found in the plankton, tracing their origin through combinations of known facts.

From this summary are omitted all larvæ not traced with any reasonable degree of certainty to their parental forms. Further viviparous forms or such as protect their young, the embryos not having a free or pelagic stage, are not mentioned. Likewise such cases, where only the postembryonal stages are described (e. g. several species of Comatulids), are omitted from this summary. Observations relating only to the fertilization, cleavage and gastrulation, but not carried so far as to the beginning larval form are generally not considered either; further generally no mention is made of the great number of papers relating to experimental studies on the larvæ—treatment with various chemical agents, hybridization etc.—, except in cases where also pure bred larvæ are reared.

The enumeration of the species mentioned follows the systematic arrangement, not the chronological order of the observations. The arrangement is that adopted in the special part of this work, beginning with the Echinoidea.

### I. Echinoidea.

*Cidaris cidaris* (L.) (Syn. *Dorocidaris papillata*); reared until nearly the full larval shape by Pronho, 1888.

*Arbacia lixula* (L.) (Syn. *Arbacia pustulosa* Gray; *Echinocidaris æquituberculata* (Blv.)); reared by W. Busch, A. Krohn, 1853, 1854, to first larval stage; the fully formed, pelagic larva identified by Joh. Müller, 1853; reared through metamorphosis by Giesbrecht, 1909 (in v. Ubisch, 1913).

*Arbacia punctulata* Gray; reared to full larval shape by Fewkes, 1880; to full larval shape by Brooks, 1882, through metamorphosis by Garman & Colton, 1882.

*Psammechinus miliaris* (Müll.) (Syn. *Echinus*, *Parechinus miliaris*); pelagic

larva identified by the present author, 1898; reared to full larval shape and through metamorphosis by MacBride, 1898, 1903; by Théel, 1892 (published 1902; no description of larva); by Shearer, Morgan and Fuchs, 1909 (1913).

*Psammochinus microtuberculatus* (Bly.) (Syn. *Echinus pulchellus* Ag.); reared to first larval stage by Joh. Müller, 1852; Selenka, 1879 (wrongly named *Echinus miliaris*); Seeliger, 1896; reared through metamorphosis by Giesbrecht, 1909 (in v. Ubisch, 1913; no description given of the fully formed larva).

*Echinus esculentus* L.; reared to full larval shape and through metamorphosis by MacBride, 1898, 1903; Shearer, Morgan and Fuchs, 1913.

*Echinus acutus* Lamk.; reared to full larval shape and through metamorphosis by Shearer, Morgan and Fuchs, 1913.

*Stereochinus Neumayeri* (Meissner); pelagic larva identified by the present author, 1913.

*Paracentrotus lividus* (Lamk.) (Syn. *Strongylocentrotus lividus*); reared to young larva by A. Derbès, 1817; Krohn, 1819; to beginning metamorphosis by Joh. Müller, 1852; Metschnikoff, 1869.

*Strongylocentrotus drobachiensis* (O. F. Müll.); young pluteus reared by A. Agassiz, 1861 (other pelagic larvæ wrongly described as the later stages of this larva by the same author).

*Strongylocentrotus franciscanus* Ag.; young larva reared by Loeb, 1909; Hagedoorn, 1909.

*Strongylocentrotus purpuratus* Stimps.; young larva reared by Hagedoorn, 1909.

*Lylechinus variegatus* (Lamk.) (Syn. *Toxopneustes variegatus*); reared to beginning metamorphosis by Tennent, 1910.

*Tripneustes esculentus* (Leske) (Syn. *Hipponoë esculenta*); young larva reared by Tennent, 1910.

*Sphaerechinus granularis* (Lamk.) (Syn. *Echinus brevispinosus* Risso); young larva reared by Krohn, 1853; fully formed, pelagic larva identified by Joh. Müller, 1855.

*Echinocyamus pusillus* (O. Fr. Müller); reared through metamorphosis by Théel, 1892.

*Mellita testudinata* (Klein); reared through metamorphosis by Caswell Grave, 1902, but no description given of the larva; reared by Tennent, 1910.

*Echinarachnius parma* (Lamk.); pelagic larva identified by A. Agassiz, 1861; reared through metamorphosis by Fewkes, 1886.

*Peronella Lesueurii* (Val.); reared through metamorphosis by the present

- author, 1914 (designated as *Laganum decagonale*); by Tennent, designated as *Laganum* sp. (in Grace Medes, 1915).
- Spatangus purpureus* O. Fr. Müll.; young larva reared by Krohn, 1853; reared to full larval shape by the present author, 1913.
- Echinocardium cordatum* (Pennant); pelagic larva identified by the present author, 1898; reared through metamorphosis by MacBride, 1913.
- Moira atropos* (Lamk.); reared through metamorphosis by Grave, 1902, but no description given of the larva; young larva reared by Tennent, 1910.
- Brissopsis lyrifera* (Forbes); pelagic larva identified by the present author, 1920.

## II. Ophiuroidea.

- Ophiolthrix fragilis* (O. Fr. Müll.); pelagic larva identified by Joh. Müller, 1852; young larva reared by Apostolidès, 1881; Metschnikoff, 1885 (no description); Ziegler, 1896; reared through metamorphosis by MacBride, 1898; young larva reared by Carlgren, 1900 (no description).
- Ophiacantha antarctica* Koehler; pelagic larva identified (not beyond doubt) by the present author, 1913.
- Ophiocoma echinata* Ag.; reared to full larval shape by Grave, 1898, but no description or figures given.
- Ophiocomina nigra* (Abildg.) (Syn. *Ophiocoma nigra*); pelagic larva identified by Graham Kerr, 1911; young larva reared by the present author, 1913.
- Ophionereis Schayeri* (Müll. & Troschel); reared by H. B. Kirk, 1916; (identification not beyond doubt).
- Ophiopholis aculeata* (Linn.); young larva reared, pelagic larva identified by Fewkes, 1886.
- Ophiactis Balli* (Thomps.); young larva reared by the present author, 1913.
- Amphiura filiformis* (O. Fr. Müll.); young larva reared, pelagic larva identified by the present author, 1920.
- Ophiura albida* Forbes.; pelagic larva (the *Pluteus paradoxus* of Joh. Müller) identified by V. Hensen, 1886.
- Ophiura texturata* Lamk. (Syn. *Ophioglypha ciliaris*, *lacertosa*); pelagic larva identified by the present author, 1898.
- Ophiura affinis* Ltk.; pelagic larva identified by the present author, 1920.
- Homalophiura gelida* (Koehler) (Syn. *Ophioglypha gelida*); pelagic larva identified (not beyond doubt) by the present author, 1913.
- Ophioderma brevispina* (Say); reared through metamorphosis by Caswell Grave, 1900.

## III. Asteroidea.

- Astropecten aranciaca* (Linn.): pelagic larva (the "Bipinnaria von Triest" of Joh. Müller) identified by Graeffe, 1880, (although without sufficient evidence); reared by Metschnikoff, 1885, and by Driesch, 1897 (according to Ludwig: *Seesterne d. Mittelmeeres*, p. 16; note); no figures of reared larvæ published.
- Astropecten pentacanthus* (Delle Chiaje); reared by Metschnikoff, 1885; no figures of larva published, but stated to be exactly like that of *A. aranciaca*, only smaller.
- Luidia Sarsi* Düb. & Kor.: pelagic larva (the *Bipinnaria asterigera* Sars) identified by Ludwig, 1895.
- Luidia ciliaris* (Phil.): pelagic larva identified 1898, young larva reared by the present author, 1913, by Gemmill, 1915.
- Cheiraster gurlachei* Ludwig; pelagic larva identified, not beyond doubt, by MacBride, 1920.
- Porania pulvillus* (O. Fr. Müller): reared to beginning metamorphosis by Gemmill, 1915.
- Solaster endeca* (Linn.): reared through metamorphosis by Gemmill, 1912.
- Solaster papposus* (Linn.): reared through metamorphosis by Gemmill (not yet published).
- Echinaster sepositus* (Gray): larva identified by Joh. Müller, 1852; reared by L. R. Löhner, 1913; reared through metamorphosis by H. Nachtsheim, 1911.
- Stichaster roseus* (O. F. Müller): young larva reared by Gemmill, 1916; pelagic larva identified by the present author, 1920.
- Asterias rubens* Linn.: reared to full larval shape, but no description or figures of larva published, Greeff, 1876; young larva reared by Semon, 1891; Chadwick, 1911; pelagic larva identified by the present author, 1898; reared through metamorphosis by Gemmill, 1916.
- Asterias glacialis* Linn.: reared a little beyond the gastrula by Busch, 1851; young larva reared by Russo, 1892, the present author, 1913, Gemmill, 1916; parthenogenetic larva reared to full larval shape, DeLage, 1901.
- Asterias Forbesi* (Desor) (Syn. *Asterias berylinus* A. Agass.). Young larva reared by A. Agassiz, 1877.
- Asterias vulgaris* Verrill. (Syn. *Ast. pallidus* A. Agass.): pelagic larva identified by A. Agassiz, 1877; reared through metamorphosis by S. Goto, 1896.



## IV. Holothurioidea.

- Labidoplax digitata* (Montagu) (Syn. *Synapta digitata*); pelagic larva identified by Baur, 1864; metamorphosis described from pelagic material, Semon, 1888.
- Leptosynapta inhærens* (O. Fr. Müller) (Syn. *Synapta inhærens*); reared through metamorphosis, Wyv. Thomson, 1862. (It remains uncertain, whether it has a pelagic larva, the younger stages not having been noticed in the aquarium, where the rearing took place).
- Holothuria tubulosa* (Gmelin); reared to young Auricularia. Selenka, 1876.
- Holothuria nigra* Peach; reared to young Auricularia, the present author, 1913.
- Holothuria floridana* Pourtalès; reared through metamorphosis, Edwards, 1888 (1909).
- Psolus phantapus* Strussenf.; larva identified, the present author, 1898; reared through metamorphosis, Runnstrom (not yet published).
- "*Psolinus brevis*" Forbes. (undecided, which species is really meant, but probably a *Cucumaria*); reared through metamorphosis, Kowalevsky, 1867.
- Cucumaria Planci* v. Marenz. (Syn. *Cuc. doliolum*); reared through metamorphosis, Selenka, 1876; Ludwig, 1891.
- Cucumaria frondosa* (Gunnerus); young stages reared (partly abnormal), Des Arts, 1910; reared through metamorphosis, Runnstrom (not yet published).
- Cucumaria echinata* v. Marenzeller; reared through metamorphosis, Ohshima, 1918.
- Cucumaria Normani* Pace; reared through metamorphosis, H. G. Newth, 1916.
- Cucumaria saxicola* Pace; reared through metamorphosis, Newth, 1916.

## V. Crinoidea.

- Antedon bifida* (Pennant); development described, Wyv. Thomson, 1863.
- Antedon mediterranea* (Lamk.); development described, Barrois, 1886, 1888; Bury, 1888.
- Antedon adriatica* A. H. Clark; development described, Seeliger, 1892.
- Antedon petasus* (Düb. & Koren); reared to beginning metamorphosis, W. Busch, 1851<sup>1)</sup>; the present author, 1920.

<sup>1)</sup> The Crinoid from which Busch, 1851, reared the larva to beginning metamorphosis was probably this species; the statement that the eggs were dropped "wie einen Staubregen" by the ripe female decidedly points to this species, the other *Antedon*-species keeping their eggs on the pinnules until the larva is ready to swim.

*Isometra vivipara* Mortensen; development described, the present author, 1920.

*Compsometra serrata* (A. H. Clark); part of the development described, the present author, 1920.

*Tropiometra carinata* (Lamarck); reared through metamorphosis, the present author (1916), 1920.

*Notocrius virilis* Mortensen; larva described, the present author, 1920.

In the present memoir are given, besides additional observations on the development of the following species: *Strongylocentrotus franciscanus*, *Lytechinus variegatus*, *Tripneustes esculentus* and *Peronella Lesueurii*, observations on the development and the larval form of the following species, which were hitherto entirely unknown as regards their development:

*Phyllacanthus parvispinus* Woods; cleavage and gastrulation only.

*Eucidaris Thouarsi* (Val.); reared to beginning pluteus.

*Arbacia stellata* (Blv.); pelagic larva identified.

*Diadema antillarum* Phil.; reared to first larval stage.

*Astropyga pulvinata* (Lamk.); reared to first larval stage; pelagic larva identified.

*Tripneustes gratilla* (Linn.); reared to first larval stage.

*Lytechinus anamesus* H. L. Clark; reared to full larval shape.

*Lytechinus pictus* (Verrill); reared to first larval stage; fully formed pelagic larva identified.

*Lytechinus panamensis* Mrtsn.; reared to first larval stage.

*Lytechinus verruculatus* (Ltk.); reared to first larval stage.

*Toxopneustes pileolus* (Lamk.); reared to first larval stage.

*Toxopneustes roseus* (A. Ag.); reared to first larval stage; pelagic larva of more advanced stage identified (not beyond doubt).

*Pseudocentrotus depressus*; reared to first larval stage.

*Strongylocentrotus pulcherrimus* (A. Ag.); reared to nearly full larval shape.

*Temnopleurus torenumaticus* (Klein); reared to nearly full larval shape.

*Temnotrema sculpta* A. Ag.; reared to nearly full larval shape.

*Mespilia globulus* (Linn.); reared to full larval shape.

*Evechinus chloroticus* (Val.); reared to full larval shape.

*Heliocidaris tuberculatus* (Lamk.); reared to full larval shape.

*Heliocidaris erythrogramma* (Val.); reared through metamorphosis.

*Echinometra lucunter* (Linn.); reared through metamorphosis.

*Echinometra oblonga* (Blv.); reared to nearly full larval shape.

*Echinometra Mathwei* (Blv.); reared to first larval stage.

*Echinometra van Brunti* A. Ag.; reared to first larval stage.

*Colobocentrotus atratus* (Linn.); reared to nearly full larval shape.



*Heterocentrotus mamillatus* (Klein); reared to first larval stage  
*Arachnoides placenta* (Linn.); reared to full larval shape.  
*Echinurachus mirabilis* Agass.; reared only to the gastrula stage.  
*Dendraster excentricus* (Esch.); reared to full larval shape.  
*Astriclypeus muuni* Verrill; reared through metamorphosis.  
*Eucope micropora* Agass.; reared to full larval shape.  
*Mellita 6-perforata* (Leske); reared through metamorphosis.  
*Clypeaster japonicus* Döderl.; reared to nearly full larval shape.  
*Lagarium diplopora* H. L. Clark; reared to first larval stage.  
*Echinobrissus (Oligopodia) recens* (M. Edw.); reared to full larval shape.  
*Brissus Agassizi* Döderl.; reared to first larval stage.  
*Brissus obesus* Verrill; reared to first larval stage.  
*Meoma grandis* Gray; reared to first larval stage.  
*Echinocardium australe* Gray; reared to nearly full larval stage.

*Astropecten scoparius* M. & Tr.; reared to metamorphosis.  
*Astropecten polyacanthus* M. & Tr.; reared to young Bipinnaria.  
*Asterina pectinifera* (M. & Tr.); reared to full larval shape.  
*Asterina regularis* Verr.; reared to young Bipinnaria.  
*Gymnasteria carinifera* (Lamk.); reared to young Bipinnaria.  
*Ophidiaster Guildingii* Gray; reared to beginning larva.  
*Asterias calamaria* Gray; reared to beginning larva.  
*Pisaster ochraceus* (Brandt); reared to young Bipinnaria.  
*Euasterias Troscheli* (Stimpson); reared to young Bipinnaria.  
*Orthasterias leptolena* Verrill; reared to young Bipinnaria.  
*Pycnopodia helianthoides* (Brandt); reared to beginning larva.

*Ophiothrix angulata* Say (Var.); reared to young Pluteus.  
*Ophionereis squamulosa* Koehler; reared through metamorphosis.  
*Ophionotus hexactis* (E. A. Smith); larva described<sup>1)</sup>.

*Stichopus californicus* (Stimps.); reared to full larval shape.  
*Stichopus Kefersteinii* Sel.; reared to young Auricularia.

While thus hitherto the development has been studied, more or less completely, or the pelagic larvæ identified, with more or less certainty, of in all 70 Echinoderms, excluding the viviparous forms (several of them being reared or the larvæ identified by the present author), there are given in the present work descriptions of the larval development, more

<sup>1)</sup> In spite of being viviparous this species has a very well formed larva; there is then reason to name this species also in this list.

or less completely, of no less than 55 different forms of Echinoderms, the development of which was totally unknown till now. The present contribution accordingly represents a very considerable addition to our knowledge of the development and the larval forms of Echinoderms and — combined with our previous knowledge — forms a reasonable foundation for a discussion of the problem that was the main object of these researches: the interrelation between the larvæ and the adults in regard to a natural classification. Also the comparative study of pelagic larvæ of unknown parentage, especially of the Ophiurid larvæ, yields valuable support for the conclusions to be drawn. Of course, very much more needs to be done. The investigations here recorded may only be regarded as an introduction. Still, enough is done already to give us a glimpse of the end; it is evident that the way here entered upon is the right way, which will lead to the desired results. I hope to be able in the future to carry these researches further towards a definite solution of the problem.

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## SPECIAL PART

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THE first Echinoderm larvæ described were designated, more or less consistently, by binominal names — *Bipinnaria asterigera* Sars, *Pluteus paradoxus* Joh. Müller, *Pluteus bimaculatus* Joh. Müller. — It is true, they were partly not recognized as Echinoderm larvæ; but this does not alter the fact that these larvæ got binominal names. In the author's work on the Echinoderm larvæ of the Plankton Expedition this principle was carried through consistently for all Echinoderm larvæ known till then, in view of the necessity of having the different larval forms designated in such a way that we may understand without too much trouble what we are speaking of. This request is met in a satisfactory way by the binominal nomenclature, but not by such designations as "Auricularia mit Kugeln", "Bipinnaria aus Helsingör" or the like, used so often in the elder literature (Joh. Müller, Metschnikoff). For larvæ of known origin no special larval name was created, which was, of course, unnecessary. This way of naming the larvæ has been generally adopted by the few authors who have since then described Echinoderm larvæ of unknown parentage (MacBride, Gemmill).

In the present work the same method is also adopted, but modified to some extent. On account of the great number of new larval forms of unknown origin described here, especially of Ophiurids, it was felt as a difficulty that there would result a great number of "specific" names, from which nothing could be seen as to their mutual interrelation. The object with describing especially the many different Ophiopluteus species being mainly to show that also among the Ophiurid larvæ there are several well characterized groups, corresponding to what is found among the other Echinoderm larvæ, notably among the Echinoid larvæ, it was found preferable to give only each type a binominal name, and then to designate the different species under that type as species **a**, **b**, **c** etc. A consequence of this is then further that it is incorrect to designate such new larval type as "nova species"; it is then designated as "nova

forma". We have thus e. g. *Ophiopluteus undulatus* nov. forma, species **a**, species **b**, etc. This method will, I think, meet all reasonable claims to a system of larval nomenclature, which will remain a necessity so long as we do not know the origin of all the larvæ we meet with in the plankton.

For the description of the larvæ it was felt a necessity to have a consistent nomenclature of the parts of the larval body, and such was worked out in the author's said work in the Plankton Expedition, which nomenclature has also been generally adopted by the recent workers, excepting most of those dealing with the larvæ only from an experimental point of view. In the said work it was maintained to be less appropriate to designate the larval prominences as "arms", which could not, in any case, be used in the descriptions of Auriculariæ and several forms of Bipinnariæ, and it was accordingly advocated that they should be termed "processes". This has not been generally adopted. I agree it is not a necessity either and, since it is really somewhat troublesome with all those "processes" in the descriptions — the more so as it cannot be avoided speaking of "processes" also in the skeletal parts — I have given it up and am designating the long prominences of the larval body as arms, while the short, less differentiated prominences of the larval body in forms like Auricularia may be termed processes or lobes. This is easier and confusion is not likely to occur for that reason.

In the following descriptive part the Echinoids are placed first, then the Ophiuroids, Asteroids and Holothurians. This is due to the fact that the Echinoids have yielded the best results, then the Ophiuroids etc. No other meaning is connected with this arrangement. That no observations on Crinoids are included in the present work is due to the fact that my studies on the development of Crinoids have been published in a separate work<sup>1</sup>).

## I. Echinoidea.

Of all Echinoderms the sea-urchins are the most favourable objects for artificial fertilization; indeed, there is hardly any other group in the whole animal kingdom which equals them in this regard. If specimens with well ripe genital products are available, one may nearly always be sure to obtain fertilization and to secure good cultures. Even in such cases, where the eggs are large and yolk-laden I have never had any difficulty in obtaining fertilization in the usual way, while in the case

<sup>1</sup>) Studies in the development of Crinoids. Papers from the department of Marine Biology of the Carnegie Institution, Washington. Vol. XVI, 1920.

of Asteroids and Holothurians it seems hardly possible to obtain artificial fertilization of those forms which have large eggs, rich in yolk. Still, I have met with two surprising exceptions to this general rule. One of the objects of my visit to New Zealand was to rear the larva of *Pseudechinus albocinctus* (Hutton); the systematic position of this form is very uncertain, and I expected by means of rearing its larva to be able to settle the question of its true affinities. Perfectly ripe specimens were available, but in spite of several attempts carried out in the usual way fertilization was never obtained. The small transparent eggs were surrounded by the actively swimming spermatozoa, but none of these succeeded in entering the eggs. Later on I have had the same experience with an Echinoid of our own seas, namely *Brissopsis lyrifera*. It is possible that in this case the spermatozoa did enter the eggs, as a fertilization membrane apparently began to form; but it never came to the beginning of the cleavage. — The reason for the failure in obtaining fertilization in these two cases is hard to see. Possibly both species are very sensitive to changes of temperature, so that the failure may be due to the temperature in the laboratory being somewhat higher than in their natural surroundings. I have, however, had no opportunity of testing this suggestion by direct experiments. Anyhow, these two exceptional cases, so disappointing from the view of the present researches, are very noteworthy and may give occasion to interesting experiments.

Although the total number of Echinoids here studied is fairly considerable, the author is disappointed in being unable to give satisfactory information about the larval forms within some important families, especially the Cidarids and Diadematids. This is mainly due to the fact that the breeding season of these forms did not coincide with the time of my visit in the different places; even under the uniform conditions of the tropical seas they do not breed continuously, and accordingly a stay of two-three months will not give the opportunity of studying the development of all the species occurring in such place.

### **Eucidaris Thouarsi** (Val.)

Pl. V Figs. 1—2.

Of this species only the very youngest larval stages were reared, but these already afford more than usual interest, so that it seems justifiable to include a record of them here.

Ripe specimens were found in considerable numbers at Taboga, in the Bay of Panama, in October 1915, while in November and December only very few specimens had ripe sexual products; the breeding season thus practically had ended before November. Although artificial fertiliza-

tion was undertaken repeatedly, none of the cultures proved very successful, evidently on account of the water being not of sufficiently good quality. The youngest stages were excellent, but as soon as the formation of the Pluteus was about to begin, the larvæ became abnormal and died.

The eggs are very small — I regret to have omitted to notice the exact size — and very transparent. The developing embryos are most beautiful objects, the cells are large and very clear, and the cell limits are very distinct. 6 hours after fertilization they were swimming blastulae; about 20 hours after fertilization the gastrula stage was reached.

The young larva is a very curious object, rather unlike other young Echinoderm larvæ. It has the shape of a biconvex lens, with a perfectly circular band, and recalls, in fact, a Trochophora by its shape (Pl. V Fig. 1), while it is, of course, quite different from a Trochophora in its anatomical structure. The digestive organs are very small, the mouth opening being on the upper, the anal opening on the lower side.

This stage was reached in three different cultures, and there is no reason to doubt that this is the normal shape of the young larva. It was only after this stage was reached that the cultures went wrong. Only in one case I succeeded in getting them a little farther in their development. In Pl. V Fig. 2 is figured a young Pluteus which is, to all appearance, normal. It is no less peculiar than the younger stage. The postoral arms are quite horizontal. (In the specimen drawn, — the only good specimen available — the left arm is slightly upwards directed. It has been corrected in the figure to suit the right arm, which is quite horizontal and has all the appearance of having preserved its natural form and direction, while the other has more the appearance of being slightly distorted. However, since the skeleton is dissolved, it is impossible to ascertain definitely which is the correct form of the arms — and I have omitted to notice anything about it from the living specimens.) Other processes are not yet indicated; there is only an elevation indicating the oral and anal lobe. This larva is 6 days old. The skeleton was beginning to form at the age of three days. Unfortunately the skeleton has been dissolved in all the preserved specimens, and I have omitted to make drawings of the living specimens. It was only noticed that the postoral rods are fenestrated.

In spite of the incompleteness of this record of the development of *Eucidaris Thouarsi* it is sufficient to show that it differs most conspicuously from *Cidaris cidaris* (*Dorocidaris papillata*), the only Cidarid the development of which was studied hitherto<sup>1</sup>). The young larva of this

<sup>1</sup>) H. Prouho. Recherches sur le *Dorocidaris papillata* et quelques autres Échinides de la Méditerranée, 1888. Arch. Zool. expér. génér. 2. Sér. V. Pl. XXIII—XXV.

Dr. Racovitza has kindly sent me a pair of specimens determined by Prouho as *Doro-*

latter species has not the peculiar shape of a biconvex lens, and the post-oral arms are not horizontal, and, upon the whole, it appears that the larvæ of these two forms must be very unlike. The horizontally directed postoral arms of *Eucidaris Thouarsi*, which must doubtless be much longer in the fully formed larvæ, recall the remarkable *Echinopluteus transversus*; were it not for the ophicephalous pedicellariæ of the latter, I would think them to belong together. — The few facts brought forward here can only make one the more anxious to get an opportunity of working out the complete development of *Eucidaris*. That, at least, *E. melularia* has a similar larval form is very probable. Its eggs are quite similar to those of *E. Thouarsi*, as I was able to ascertain during my stay at Hilo, Hawaii. Fertilization of this species could, however, not be undertaken, as I never succeeded in getting a ripe male and female at the same time.

While the larva of *Cidaris cidaris* is the only Cidarid-larva hitherto reared to what must be at least very nearly its full shape, it is quite possible that also the larva of another Cidarid, viz. *Stylocidaris affinis* (Phil.) is known. As I have explained in my paper on "Die Echiniden des Mittelmeeres"<sup>1)</sup> there is some reason to think that the larva figured by Joh. Müller in his 7th Memoir on the larvæ and metamorphosis of Echinoderms, Taf. I Fig. 1—2, belongs to this Cidarid, not to *Sphærechinus*, as was hitherto supposed.

### **Phyllacanthus parvispinus** Ten. Woods.

Pl. V. Figs. 3—4.

During a short stay at Port Jackson in the beginning of March 1915 I found a few specimens of this species containing ripe genital products and I succeeded in getting a small culture. The eggs are few in number, rather large, ca. 0.5 mm, of a greenish colour, and they float at the surface. The fertilization membrane is very thick, gelatinous, not sharply limited on the outside. The first division was seen to take place about 3 hours after fertilization. As the fertilization was undertaken in the evening the process of the cleavage could not be followed in details, only a very poor light being available. It appeared, however, that the

*cidaris papillata*, so that I have been able to confirm that it is really this species, which was studied by Prouho, not the more common mediterranean form, *Stylocidaris affinis*, which was at the time Prouho wrote his paper not recognized as separate from *Cidaris cidaris*.

<sup>1)</sup> Th. Mortensen. Die Echiniden des Mittelmeeres. Eine revidierte Übersicht der im Mittelmeere lebenden Echiniden mit Bemerkungen über neue oder wenig bekannte Formen. Mitt. a. d. Zool. Stat. Neapel. 21. 1913. p. 20.

There is, however, also a possibility that this larva may belong to *Genocidaris maculata* A. Ag., the larva of this common mediterranean species being also unknown.



cleavage was total and regular, in spite of the large size of the egg. The next day the embryos had a very peculiar appearance, being folded in such a way as to recall the convolutions of a brain. Sections through embryos of this stage show that this is due to a strong folding of the blastula (Pl. V Fig. 4), much as it occurs in *Astropecten*<sup>1)</sup>, *Luidia*<sup>2)</sup>, *Solaster*<sup>3)</sup>, *Henricia*<sup>4)</sup> and probably many other Asteroids, and as it is described here also for *Perouella Lesueurii*. The cells are full of vacuoles, which may probably be filled with some kind of nutritive fluid. But there is no reason to enter on a discussion thereof on this occasion. — Also in the following stage numerous vacuoles are seen, only much smaller.

At the age of 28 hours they were found to be swimming gastrulæ, very slowly moving, quite opaque and with a very wide mouth. Pl. V Fig. 4 represents a section through one of these gastrulæ; it is very thickwalled, the nuclei lying in a thick layer. The invagination appears bipartite, which will probably mean that the formation of the coelomic pouch has begun. The blastocoel cavity is nearly filled by mesoderm cells. It appears that the invagination is set with long cilia — but the preservation is not sufficiently good for ascertaining this definitely.

None of the embryos got beyond this stage, and it was impossible to get a new culture. But the facts here recorded are sufficient to show that this species is very different as regards its development from the other Cidarids thus far studied. Most probably its development will prove to be direct, without a Pluteus-larva, or, in any case, the larva must be greatly modified, on account of the character of the egg. The full record of its development must be expected to be of quite unusual interest.

### **Diadema antillarum Phil.**

Pl. V Fig. 5.

After having sought in vain for ripe specimens of *Diadema* in both Japan, at Hawaii and Panama<sup>5)</sup> I was very pleased in finding, at the end of March 1916, at Tobago B. W. I. ripe specimens of *Diadema antillarum*, from which an excellent culture of larvæ was obtained.

<sup>1)</sup> E. Metschnikoff. Vergleichend embryologische Studien. Zeitschr. f. wiss. Zool. Bd. XLII. 1885. p. 660.

<sup>2)</sup> Th. Mortensen. On the development of some British Echinoderms. Journ. Mar. Biol. Assoc. U. Kingdom. X. 1913. p. 7.

<sup>3)</sup> J. F. Gemmill. The development of the starfish *Solaster endeca*. Trans. Zool. Soc. London. XX. 1912.

<sup>4)</sup> A. T. Masterman. The early development of *Cribrella oculata* (Forbes) with remarks on Echinoderm development. Trans. R. Soc. Edinburgh. XL. 1902.

<sup>5)</sup> A few small specimens of *Diadema mexicanum* were found to contain ripe sexual products in January and February 1916 at Taboga, Panama. Fertilization was undertaken twice, but the embryos did not develop beyond the gastrula stage.

The eggs are very small, only ca. 0.07 mm, and very clear. The cleavage is of the usual, regular type, affording no special features. Swimming blastulæ were observed after about 16 hours: they are very clear and transparent, with beautiful, polygonal cells, the limits being very distinct. At the age of two days the skeleton begins to form, and the Pluteus-shape is assumed, but the arms are still very short. The three days old larvæ are typical young Plutei (Pl. V, Fig. 5) with long postoral arms:



Fig. 1. Skeleton of the larva of *Diadema antillarum*; from the ventral side. <sup>200</sup>/<sub>1</sub>.

In all the figures of Echinoid larvæ the same letters are used to designate the same parts. al. anterolateral rod; b. body rod; po. postoral rod; r. recurrent rod; vtr. ventral transverse rod.

rod. The body rods are slightly curved; at the end they are widened into a disk; also the connecting rods and the ventral transverse rods are thus widened at the end, where they meet. Sometimes the disk may be more or less irregular, so that they meet like a pair of clasping hands. The whole skeleton is very little thorny, sometimes perfectly smooth. The postoral rods are fenestrated.

<sup>1</sup>) I have previously designated this type of structure of the body skeleton as a "frame"; the designation "basket" used by Tennent seems to me more appropriate, and I therefore adopt it.

there is a fairly prominent red pigment spot in the end of these arms, and a few red pigment cells scattered on the body. The suboral cavity is very large, reaching below the level of the ventral transverse rods.

The skeleton (Figs. 1—2). The body skeleton forms a basket<sup>1</sup>)-structure, very oblique; the recurrent rods are rather abruptly bent at the point, where the connecting rod proceeds, the lower part running from here very obliquely towards the point of union with the body

In this stage the larvæ remained for some days without apparent changes, when by an accident the whole culture was destroyed. In vain I attempted to get ripe specimens

for making a new culture. More than a hundred specimens were opened, but all of them were perfectly empty. There was thus no possibility of getting the later developmental stages, which would have been of very considerable interest, nobody having as yet studied the fully formed larva or the metamorphosis of any Diadematid —

excepting the larva described by Joh. Müller (VII. Abh. p. 9, Taf. V. 1—4), which is probably, but not beyond doubt, the larva of *Centrostephanus longispinus*.

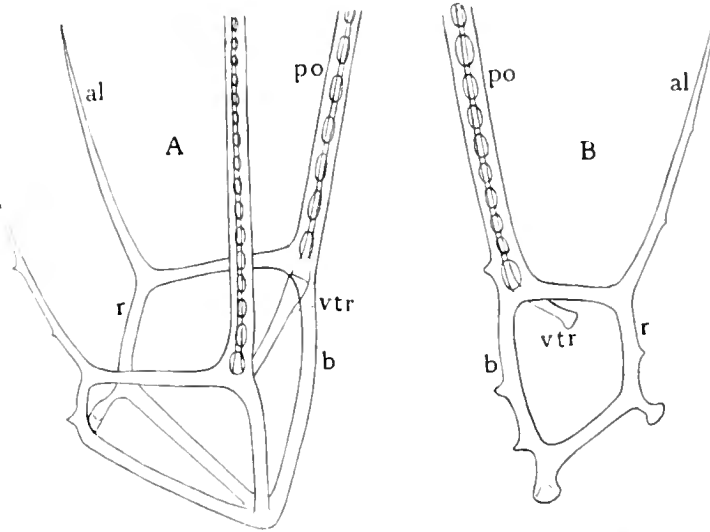


Fig. 2. Skeleton of the larva of *Diadema antillarum*; side view. A. showing the whole basket structure,  $\frac{300}{1}$ ; B. half part of the skeleton.  $\frac{290}{1}$ . Letters as in fig. 1.

### *Astropyga pulvinata* (Lamek.).

Pl. V. Figs. 6 and 7 (?).

At the beginning of December 1915 I succeeded in finding (at Taboga, Panama) some specimens of this fine Diadematid containing ripe genital products. Fertilization was undertaken and a very good culture obtained. The larvæ developed quite normally till the first Pluteus-stage was reached, but then they became unhealthy and died at the age of 6—7 days. Another culture made some days later went on exactly in the same way. Thus also of this Diadematid only the first stage was obtained. As might be expected, it is in the main features similar to that of *Diadema*.

The eggs are small (exact measurements were not made) and transparent. The cleavage is of the usual regular modus, presenting no especially noteworthy features; the process of gastrulation may perhaps prove unusual, but on account of absence on a dredging trip I could not follow it satisfactorily so I shall not enter on the subject. At the age of ca. 21 hours the embryos had begun to assume the Pluteus-shape. They are at this stage rotating at a great speed, always to the right<sup>1)</sup>, so fast, indeed,

<sup>1)</sup> In my paper "On the development of some British Echinoderms" (Journ. Mar. Biol. Assoc. X. 1913. p. 6) I have stated that the young embryos of *Asterias glacialis* and other



that it is almost impossible to discern their shape. Gradually this rotation ceases completely. Two days old they have the shape of young *Plutei*, with a red pigment spot at the end of the postoral arms and scattered pigment cells in the body. The suboral cavity apparently is not so large as in *Diadema*.<sup>1)</sup> (Pl. V, Fig. 6).

The skeleton (Figs. 3—4). The body-skeleton forms a basket structure as in *Diadema*, but differs from the latter in being generally conspicuously thorny. Sometimes the lower part may be fenestrated, which means,

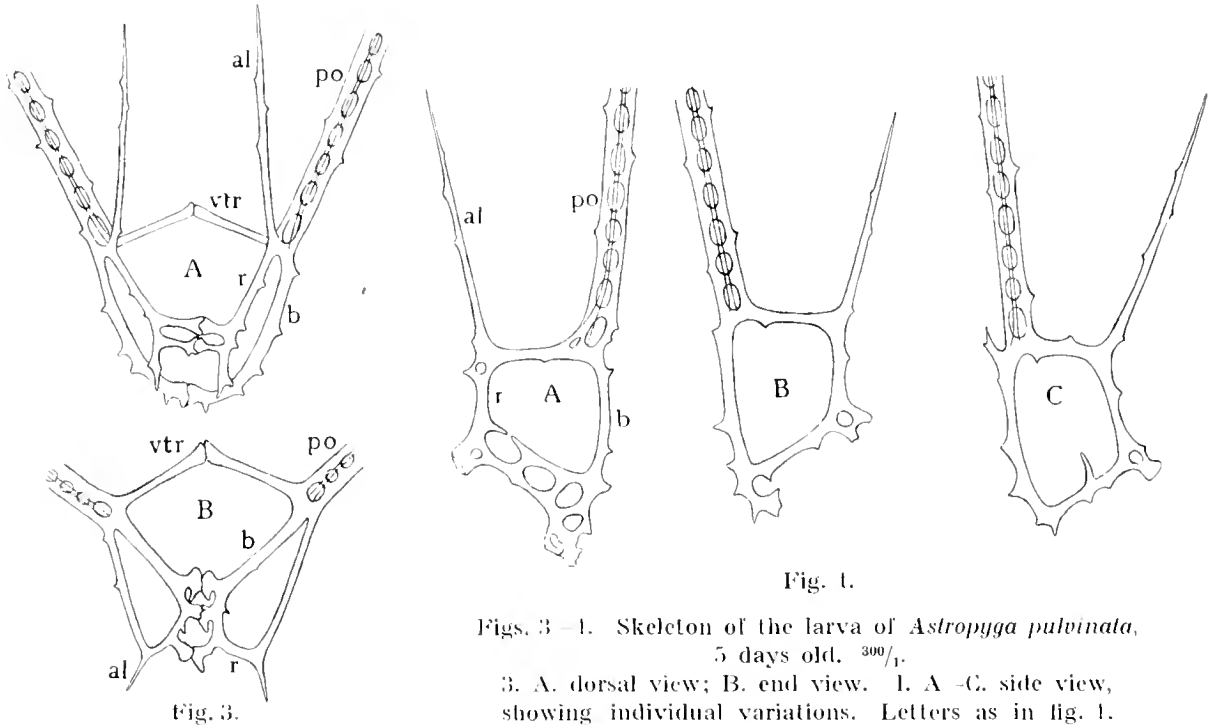


Fig. 3.  
Fig. 4.  
Figs. 3—4. Skeleton of the larva of *Astropyga pulvinata*, 5 days old. <sup>300</sup>/<sub>1</sub>.  
3. A. dorsal view; B. end view. 4. A—C. side view, showing individual variations. Letters as in fig. 1.

evidently, only an unusual development of the thorns. The transverse rods connecting the recurrent rods (—not the same as the dorsal transverse rod of the later stage, which is a process from the base of the postero-

Echinoderms reared by me "in swimming rotate around their longitudinal axis, always turning to the left". Gemmill (On the development and certain points in the adult structure of the Starfish *Asterias rubens*. Philos. Transact. B. 205. 1914. p. 238) finds this statement difficult to understand, since he has found the rotation to be dextral. I am myself at a loss to explain this statement. In my notes from the stay in Plymouth I have repeatedly stated expressly that the rotation is always to the right. The error is not even due to a lapsus memoriae; I have been too impressed with the observation of this constant dextral rotation. In fact, I have no excuse to offer for this erroneous statement. I may take the opportunity here to say that I have not seen any of the numerous Echinoderms, which I have reared, to make an exception to this rule of dextral rotation; only now and then a single embryo may be seen to turn to the left. But I have observed that only very rarely.

<sup>1)</sup> On the figure of this larva, which was drawn from life, the suboral cavity was not indicated. The line representing the lower limit of this cavity was added to the figure after preserved specimens; possibly it is larger in the living specimens and really of the same extent as in *Diadema*.

dorsal rod —) may be double (Fig. 3 A). The postoral rods are fenestrated, thorny.

In a plankton sample from off the island of Taboga from the end of November 1915 three specimens of an Echinopluteus were found, which may with no small degree of probability be referred to *Astropyga pulvinata*. (Pl. V, Fig. 7). The larva shows so considerable resemblance to that figured by Joh. Müller in his VII. Memoir on the Echinoderm larvæ (Taf. V) that it seems beyond doubt they must be nearly related to one another. Joh. Müller referred his larva to *Centrostephanus longispinus*. There is still no definite proof that he was right herein, but there is nothing either to disprove the correctness of this reference. The present larva should then also be referred to a Diadematid. *Diadema mexicanum* being out of question as not having its breeding season at this time of the year, *Astropyga pulvinata*, the only other Diadematid known to occur here, should then be the species to which this larva belongs. (A new *Astropyga* found by the author at Las Perlas — not yet described — hardly comes into consideration). It should, however, be pointed out that the postoral and posterodorsal rods are entirely smooth in these larvæ, while in the reared young larvæ of *Astropyga* the postoral rods were found to be distinctly thorny. This fact is thus not in favour of the supposition that these larvæ belong to *Astropyga*. Since, however, they must in all probability belong to a form which has a near relative in the Mediterranean, there is hardly any other Echinoid which could come into regard — be it not *Euclidaris Thouarsi*, which I would not think very probable, judging from the shape of the young larva reared.

The extensive development of the vibratile lobes, the very long postoral and posterodorsal arms (— they are broken, so that their full length cannot be ascertained, but they are very long —), and otherwise the whole shape of the larva is very much like that of the Mediterranean larva, *Echinopluteus Mülleri*, as I have named it. The posterior transverse rod has a long median process to each side.

### ***Arbacia stellata* (Blv.)<sup>1)</sup>**

Pl. VII, Fig. 3.

Although a considerable number of young specimens of this species was secured at Taboga, Panama, only a single adult specimen was observed.

<sup>1)</sup> H. L. Clark in his paper "Echinoderms from Lower California, with Descriptions of new Species" (Bull. Amer. Mus. Nat. Hist. XXXII, 1913, p. 220) rejects the name *Arbacia stellata* (Blv.), because of the name *Echinus stellatus* being used by Gmelin (Linn. Syst. Naturæ. Bd. XIII, 1788, p. 3171), "even though we do not know at present what species Gmelin had in mind": instead of the long used name *A. stellata* (Blv.) he then names it *Arbacia incisa* (A. Ag.) reviving the name given to this species by Agassiz in 1863. I do not see the necessity of making this change, and therefore keep the old name.

and it was thus impossible to rear the larva. Nevertheless I can give some description of this larva. In some plankton samples from Taboga from November and December 1915 I find three specimens of an Arbaciid-larva. Since *Arb. stellata* is the only species of the Arbaciidæ known to occur in the Gulf of Panama<sup>1)</sup>, and since young specimens of this

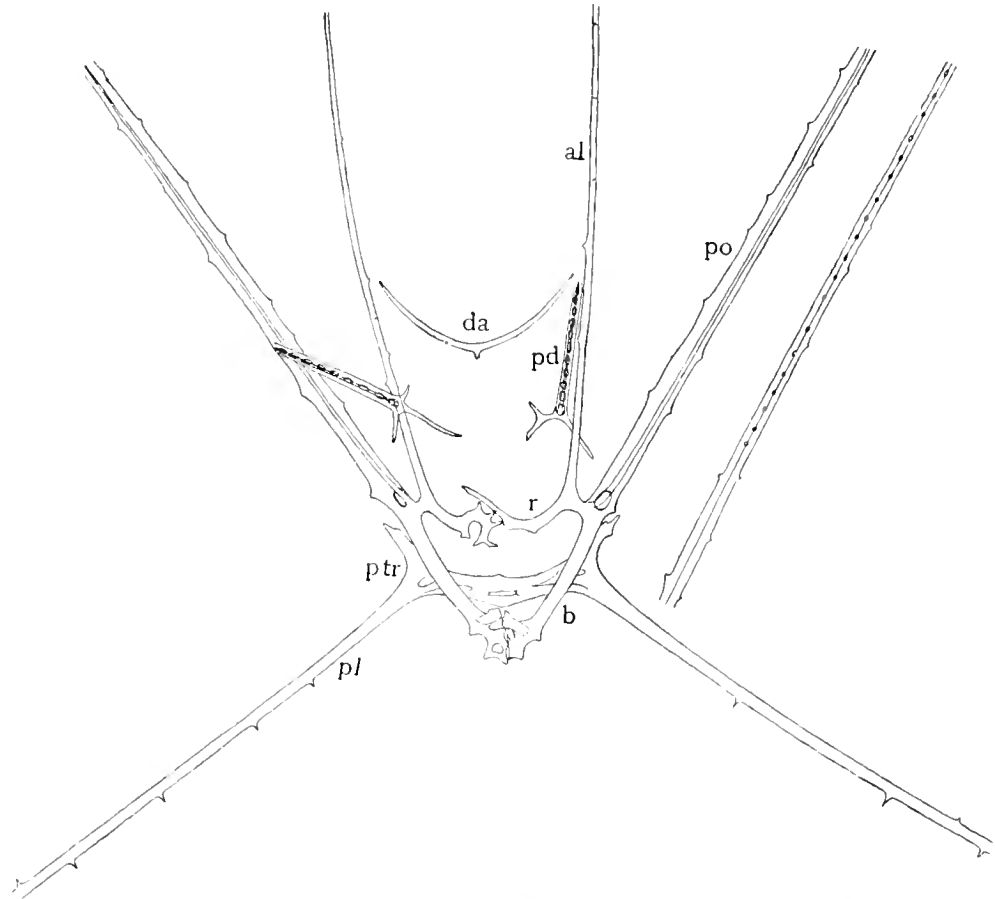


Fig. 5. Skeleton of larva of *Arbacia stellata*. <sup>250</sup>/<sub>1</sub>. To the right side is represented separately part of the outer end of the postoral rod.

al. anterolateral rod; b. body rod; da. dorsal arch; pd. posterodorsal; pl. posterolateral; po. postoral; ptr. posterior transverse; r. recurrent rod.

species were fairly common in the said locality, there can be no doubt that this larva does really belong to *A. stellata*.

None of the three specimens are quite fully developed, but the specimen figured is in a sufficiently advanced stage to give the proof of the important fact that the larva of this species conforms closely with the two other *Arbacia*-larvæ hitherto known, viz. of *A. livula* and *punctulata*. The

<sup>1)</sup> It may perhaps hardly be possible to distinguish with certainty the young specimens of *A. stellata* from those of *A. spatuligera*; since, however, the latter species is not found to the North of Guayaquil, there can be no question of the identity of these young specimens from Taboga with *A. stellata*.

preservation being not as good as desirable, it is impossible to ascertain whether there are large pigment spots at the point of the long arms, as is the case in the larvæ of *A. livula* and *punctulata*. The vibratile lobes are not yet developed, but there is no reason to doubt that they will be found here as in the other *Arbacia*-larvæ.

The skeleton (Fig. 5) agrees very closely with that of the *A. livula*-larva (comp. Joh. Müller, VII. Abh., Taf. II, Fig. 10), especially in the noteworthy feature that the postoral rods are fenestrated only in the point. Only the posterior transverse rod differs from that of the *A. livula*-larva in being somewhat curved and more robust, more like that of the *A. punctulata*-larva, which, on the other hand, differs from the present larva and *A. livula* in having the postoral rods fenestrated from the base.

In a plankton sample from off the Azores (36° 13' N. 33° 50' W., 15/III 1911), taken onboard the "Ingolf" by Mr. H. Blegvad, was found an Arbaciid larva which is remarkable on account of its exceedingly long postero-lateral arms (Pl. VI, Figs. 1—2). The shape of the body cannot be made out clearly on account of the rather advanced stage of metamorphosis, likewise the vibratile lobes cannot be distinguished. The preoral lobe evidently is somewhat altered by the beginning absorption; it has the appearance that the vibratile band passes all round its edge, which cannot be a normal feature in the larva. The structure of the postoral and posterodorsal rods is like that in the *A. livula* larva (both these pairs of arms are broken, so that their full length cannot be ascertained). The posterolateral rods are sparsely thorny, the thorns beginning a little outside the part that is represented in Pl. VI, Fig. 2. The posterior transverse rod is slightly curved, with no distinct hole in the middle.

It seems hardly possible that this larva might belong to *A. livula*; the posterior transverse rod is different and even in the more advanced stages of metamorphosis the larva of that species has never been observed to possess such exceedingly long posterolateral arms<sup>1)</sup>. There is then reason to suppose that this larva belongs to one of the other species of the genus *Arbacia* (*A. africana*?), or perhaps to *Arbaciella elegans*. There is also a possibility that it may belong to a deep-sea form (*Coctopleurus* or *Podocidaris*); at least such possibility cannot be rejected beforehand, so long as nothing is known regarding the character of the eggs in these deep-sea forms. Anyhow, it has seemed to me worth while calling attention to this conspicuous larval form.

<sup>1)</sup> Joh. Müller, VII. Abhandlung, Taf. II—III. L. v. Uebisch, Die Anlage und Ausbildung des Skelettsystems einiger Echiniden, und die Symmetrieverhältnisse von Larve und Imago. Zeitschr. wiss. Zool. CIV, 1913, Taf. VII.

**Tripneustes esculentus** (Leske).

Pl. II, Figs. 1—2. Pl. VIII, Fig. 2.

The development of this Echinoid was not entirely unknown previously. Tennent<sup>1)</sup>, who has used it for hybridization-experiments, has given some sketches of the skeleton of the young larva in the age of relatively 24 hours and four days, and also a short description (under the name of

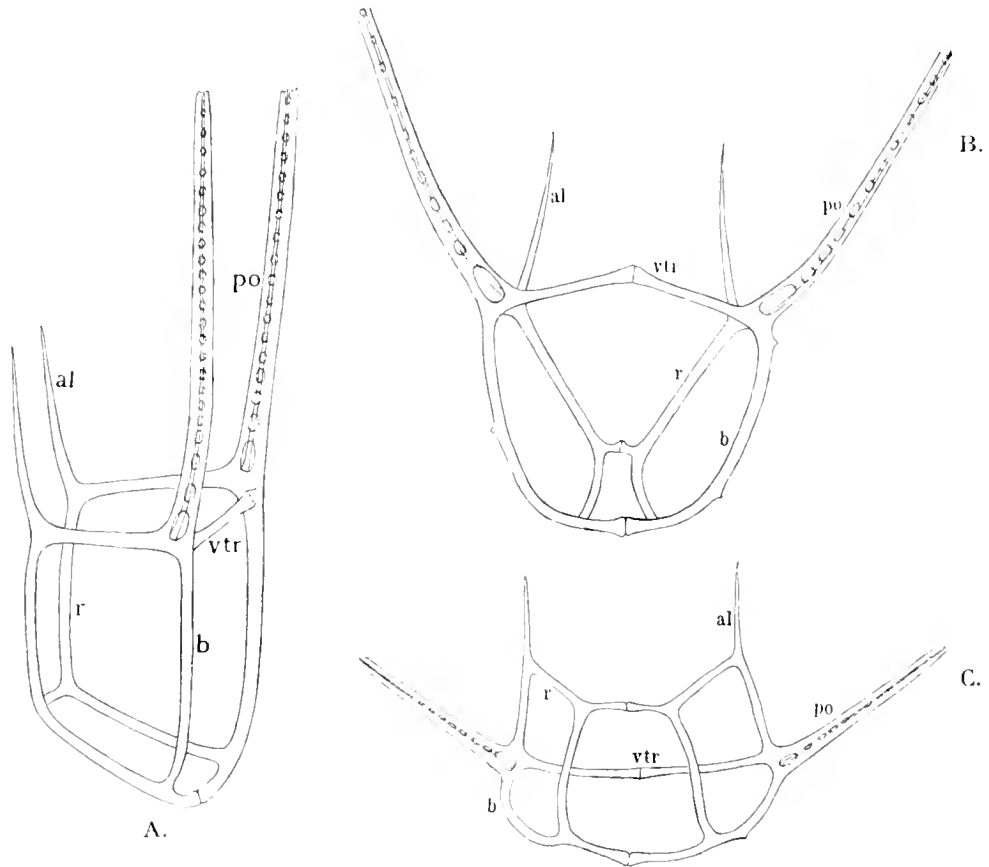


Fig. 6. Skeleton of the young larva of *Tripneustes esculentus*: A. side view; B. front view, from the ventral side; C. end view.  $\frac{300}{1}$ . Letters as in Fig. 5.

*Hipponoë*). It does not appear that Tennent has reared the larva to its full size; at least he does not give any information about the later stages.

Artificial fertilization of this species was undertaken in March and April 1916 at Tobago, B. W. I. The egg is small (I have omitted to note the exact size), and not very clear. The cleavage is of the usual modus, presenting no specially noteworthy features. Judging from Tennent's observations the young Pluteus-stage may be reached already in the

<sup>1)</sup> D. H. Tennent. Echinoderm Hybridization. Papers from the Marine Biological Laboratory at Tortugas. Publ. No. 132 of the Carnegie Inst. Washington. 1910. p. 135. Pl. I. figs. 3—4.



course of 21 hours; in my own experiments I did not find the young *Plutei* until about two days after fertilization.

As described by Tennent this first larval stage (Pl. VIII, Fig. 2) has the posterior end of the body truncated, the body skeleton forming a very regular basket-structure. The skeleton (Fig. 6) is very smooth, the body rods and ventral transverse rods, as well as the rods connecting the recurrent rods are slightly widened at the end, where they join. There is a pronounced and characteristic sinuation at the point of issue of the postoral rod from the body rod. The postoral rod, which is gracefully curved at the base, is fenestrated; but the holes are small, excepting the lowermost one, and gradually disappear towards the point. Red pigment is beginning to appear in the point of the postoral arms, and also some few scattered red pigment cells are found in the body.

In this stage the larvæ remain essentially unchanged for an unusually long time. It was not until the 12th day after fertilization that the formation of the posterodorsal arms began. That this long duration of the first larval stage is a normal feature can hardly be doubted, since the larvæ afterwards developed quite normally. Also two other cultures gave similar results, though these latter were not kept so long a time that the beginning of the second stage was reached.

At the age of 17 days the body skeleton had begun to be absorbed, and the larva was about to assume its full shape (Pl. II, Fig. 1); the vibratile band had reached the hindend of the body on the sides, being drawn out into a pair of lobes, the posterolateral processes. The posterior transverse rod was found to appear on the 20th day.

The fully formed larva (Pl. II, Fig. 2), 22 days old, is a strikingly beautiful object. The arms are all broad, especially the antero-lateral arm is broadly widened at its base; the postoral and the postero-dorsal arms are slightly and gracefully bent. The arms are all rather short, the longest, the postoral ones, only slightly exceeding the length of the body. The postero-dorsal arms are somewhat shorter, and the preoral and antero-lateral arms are generally quite short, though they vary somewhat in length. The postero-lateral processes remain short, ear-shaped lobes; above these lobes the body is distinctly narrowed, which feature, together with the concave outline of the posterior end of the body, gives the fully formed larva a very different appearance from that at the beginning of the transformation from the first to the second larval stage (Comp. Pl. II, Figs. 1 and Fig. 2). There are two pairs of vibratile lobes (auricles); the dorsal ones, at the base of the postero-dorsal arms, are outwards directed, the ventral ones, between the base of the postoral arms and the anal lobe, are forwards directed. The anal lobe is deeply concave

and has its corners produced into a pair of narrow, forward directed processes. Further there is a large fold across the dorsal side, so that the vibratile band along the dorsal side of the body is produced into a pair of processes in the middle of the body. — All the arms have a small accumulation of red pigment at the point; also in the vibratile lobes there is a series of red pigment cells under the vibratile band; few scattered pigment cells are seen in the body. The stomach is of a faint yellow colour.

The first pedicellaria has been formed; it is situated in the midline in the posterior end, deeply sunk in a groove. Also the annion has begun to form. There is thus no doubt that we have here the fully formed larva, which is about to begin its metamorphosis. The metamorphosis of the larva could not be followed, as the sojourn at Tobago ended by this time, and there were only very few larvæ left, so that it would have been useless to try to bring them along with me on the voyage.



Fig. 7. Outer end of postoral rod of the *Tripneustes esculentus*-larva. <sup>400</sup>/<sub>1</sub>.  
The unfenestrated part is shortened.

The skeleton. The postoral rods are fenestrated only in the lower part: they continue beyond as three, farther out only two, separate rods, one of them ending a little way beyond the fenestrated part (Fig. 7). The postero-dorsal rod is simple. The posterior transverse rod is a simple, thin, straight rod, ending in two simple, diverging processes, the upper quite short, the lower somewhat longer, but not nearly as long as the postero-lateral processes. The other rods, including the dorsal arch, are thin and smooth.

### ***Tripneustes gratilla* (Linn.).**

Pl. VIII, Figs. 5, 6.

Fertilization of this species was undertaken in the end of March and the beginning of April 1915 at Honolulu and at Hilo, Hawaii. At the age of three days the first larval stage was reached. In the shape of the larva and the structure of the skeleton it very closely resembles *Tr. esculentus*. The skeleton having been dissolved in the larvæ preserved, I cannot give a figure of it, but judging from my notes there would appear to be no noteworthy difference in this regard between the larvæ of these two species. The skeletal rods of the "basket" are quite smooth and the postoral rod fenestrated, as in *Tr. esculentus*. A small group of red pigment is found already at this stage in the end of the postoral arms, and small red pigment cells are found scattered in the body.

The larvæ were kept alive (in good condition) for 10 days, but did not yet show any indication of the formation of the postero-dorsal arms. The vibratile band was found to reach almost the posterior end on the sides of the body, and the postoral band to form a little fold on each side — evidently the beginning of the ventral vibratile lobes. These few facts tend to show that this larva will agree with the *Tr. esculentus*-larva also in the later stage, and also that it takes an equally long time before it develops into the full larval shape.

Although the skeleton has been dissolved, it has seemed to me not superfluous to give a pair of figures of the young larva. Partly the shape of these larvæ has been very perfectly preserved, because of the very slow dissolution of the skeleton (traces of it are still distinct), and the characteristic obliquely truncate form of the body is thus well shown; partly the figures show the suboral cavity to be very large and distinct. The same will most probably be the case in the *Tr. esculentus*-larvæ, but I have not observed it in making drawings from the living specimens, and none of the latter larvæ were preserved except a few of the oldest stage, where it cannot be distinctly observed.

### **Lytechinus variegatus** (Lamk).

Pl. III, Figs. 1—2; Pl. VIII, Fig. 1.

The larva of this species has been the object of careful studies by Tennent<sup>1)</sup> (under the name of *Toxopneustes variegatus*) partly as regards its variations under laboratory conditions, partly in regard to hybridization, for which purpose it appears a specially favourable object. Nevertheless a description of the larva has never been given; the later stages have only been mentioned quite accidentally, through the fact that in a crossing of this species with *Moira atropos* some few specimens "of a purely maternal form" were obtained; in Pl. 2 figs. 18—20 and textfigure 5, p. 138 of the paper on Echinoderm Hybridization outline figures are given of these larvæ.

The fertilization and the first embryonal stages of this species were studied by Selenka<sup>2)</sup>; he did not even rear them till they had assumed the Pluteus-shape.

<sup>1)</sup> D. H. Tennent. Variation in Echinoid Plutei; a Study of Variation under Laboratory conditions. Journ. Exper. Zoology, 9, 1910.

D. H. Tennent. Echinoderm Hybridization. Publ. No. 132 of the Carnegie Institution, 1910.

<sup>2)</sup> E. Selenka. Beobachtungen über die Befruchtung und Theilung des Eies von *Toxopneustes variegatus*. Erlangen 1877.

E. Selenka. Keimblätter u. Organanlage d. Echiniden. Z. wiss. Zool. 33, 1880.

E. Selenka. Befruchtung des Eies von *Toxopneustes variegatus*. Ein Beitrag zur Lehre von der Befruchtung und Eifurchung. Zoologische Studien, I. Taf. I—III, 1878.

Although this larva is thus comparatively well known, it does not appear to me superfluous to give a full description and figures of its different stages.

Cultures were made in March—April 1916 at Tobago, B.W.I. The fertilization was undertaken on March 29th. After 6 hours there were swimming blastulae. At the age of one day the first larval stage was reached (Pl. VIII Fig. 1)<sup>1</sup>). Its shape is the usual, the posterior end of the body being short, truncated. Scattered redbrown pigment cells have begun to appear. In regard to the skeleton it is very noteworthy that the body skeleton does not form a basket structure. There is a recurrent rod, but it does not unite at the posterior end with the body rod; it bends inwards at about the middle of the body; below this horizontal part, which represents the connecting rods (as I might term these rods connecting the recurrent rods), it continues only as a very short, small process. Both the ventral transverse and the connecting rods are pointed at the end, and they do not join in the middle line as in the *Tripneustes*-larva, but transgress one another a little with their point. The body rod normally ends in two horizontal branches, one passing towards the ventral midline, the other along the side of the body (as seen in fig. 4, p. 666 of Tennent's "Variation in Echinoid Plutei"). The postoral rod is simple, distinctly thorny, as is also the body rod.

The postero-dorsal arms begin to form at the age of about 5 days; the posterior transverse rod appears at the age of about 9 days, and at the age of 12 days the larva has reached its full shape; the first pedicellaria was formed in the 13 days old larva, and the first rudiments of the skeletal plates of the young Echinoid were seen at the age of 15 days. — The metamorphosis was not completed by any of the larvæ, evidently because I transferred them at that time to another jar with a few algæ for the purpose of giving the young urchins good conditions; but they did not stand the change and died. However, the main object was reached, the development being traced to the full shape of the larva.

The fully formed larva (Pl. III, Figs. 1—2) has, like that of *Tripneustes*, postero-lateral processes and vibratile lobes, and is, upon the whole, a no less complicate and beautiful object than the latter. The postero-lateral processes are short, earshaped, and may be obliquely forward directed. The posterior end of the body is convex, rounded, and the first pedicellaria formed is not situated in a groove. The postoral arms are the longest, of the same length as the body, while the postero-dorsal arms remain shorter, only about half that length. Possibly they may grow

<sup>1</sup>) This figure represents a 2 days old larva; it differs from that of one day only in the arms being somewhat longer.

longer during the metamorphosis; in the oldest stage represented by Tennent (Pl. 2. Fig. 20 of his "Echinoderm Hybridization"), which is somewhat more advanced in metamorphosis than the oldest larva figured here, the primary tubefeet or spines(?) of the young urchin having been formed, the postero-dorsal arms are slightly longer, though still scarcely more than half the length of the postoral arms. The vibratile lobes are rather broad. The anal lobe has not its corners produced, as is the case in *Tripneustes*. The dorsal lateral band is much folded and forms a pair of lobes almost as prominent as in *Tripneustes*. Inside the preoral arms there may be found a pair of small processes. There is a collection of red pigment in the end of each arm and a conspicuous series of such pigment cells is found below the band in the vibratile lobes and in the postero-lateral lobes. Also in the frontal area a prominent cluster of pigment cells is found in the midline, above the preoral band.

In the figure quoted from Tennent the vibratile lobes are very insignificant, but instead there is a pair of epaulets so broad as almost to join in the midline. Also in the text (p. 139) Tennent mentions the epaulets as a normal feature in this larva. There is here a discrepancy between our observations which I cannot quite explain; my preserved material of the larvæ of this species is not in a sufficiently good condition to allow a renewed careful examination; on the other hand my drawings from the living specimens are so elaborate that it would seem excluded that there could be any misrepresentation here. It is possible that the large lobes may be separated off from the vibratile band in a somewhat later stage, as appears to be the case in Tennent's figure<sup>1)</sup>, and in view of the fact that epaulets are formed in the larva of *Lytech. auaneus* (*pictus*) it is, indeed, very probable that they should also be found in this larva. Further observations will be necessary for settling this point.

In regard to the skeleton the presence of a posterior transverse rod is of special importance. It ends in two simple, diverging branches, the upper one of which is much the longer. In Fig. 5, p. 138 of Tennent's "Echinoderm Hybridization" this transverse rod is represented as having in the middle a process above and below. I have found it simple in the specimens that I have reared. On the other hand I find in a specimen of this larva found in a plankton sample from off Haiti (18° 43' N. 73° 53' W., H. Blegvad, "Ingolf" <sup>30</sup>/<sub>1</sub> 1911) the posterior transverse rod to possess a pair of similar processes, only much longer than shown in Tennent's figure. This larva, which is in beginning metamorphosis, otherwise agrees so well with the reared larvæ of *Lytechinus variegatus*, that I cannot

<sup>1)</sup> This figure is somewhat diagrammatic and perhaps not quite convincing in regard to this point.

hesitate in identifying it with this species. The only difference noticeable is this that the postoral and postero-dorsal rods are somewhat more closely thorny than was the case in the reared larvæ. (Of course, there is a possibility that this larva may really belong to one of the other species of *Lytechinus* occurring in the West Indies, viz. *L. euerces* H. L. Clark, *L. dyscritus* H. L. Clark and *L. callipeplus* H. L. Clark.) The larva is not sufficiently well preserved for showing the body shape distinctly. — In Pl. III, Fig. 2 a small rod is seen lying across the posterior transverse rod in the midline. This is, however, a separate rod, which, I suppose, represents the first rudiment of the Echinoid skeleton. The postero-dorsal rod is simple like the postoral rod. The dorsal arch is characteristic in having a pair of lateral processes, which support the lobe formed by the dorsal lateral band.

The postoral and postero-dorsal arms are generally upwards directed, but they are movable and may be directed nearly horizontally.

***Lytechinus anamesus*** H. L. Clark.

Pl. VII, Fig. 5; Pl. VIII, Figs. 3—4.

During the stay at the Biological Station at La Jolla, Cal., in August—September 1915 I had the opportunity of undertaking a fertilization of this species, which occurs in great numbers off the Californian coast in depths of ca. 40—250 meters. The fertilization was made on the 24th of August on board the ship, immediately after the dredging, and was very successful.

The eggs are small (I have no measurement of them) and perfectly clear — a most excellent object for embryological studies. After 20 hours there were swimming blastulæ (probably earlier), and after 24 hours the gastrula stage was reached. The formation of the skeleton began when the embryos were 2 days old. At the age of 7 days the postero-dorsal arms had begun to develop, with the skeletal rod, and also the preoral arms had appeared; the dorsal arch had just begun to form at the same time, its branches being still far from the preoral arms (Pl. VIII, Fig. 4), which are thus from the beginning formed independently of the rods which later on grow to support them, while otherwise the rule would appear to be that the supporting rods are so to say pushing out the arms. At the age of 11 days four epaulets had developed, and the absorption of the body skeleton had begun.

Only very few of the larvæ survived this stage. On leaving La Jolla the 17th September I carried the culture along with me to San Pedro, where I had no opportunity of paying further attention to it until the 26th. There was then found to be only one fully developed larva, which

was, however, imperfectly developed in the upper part; but the lower part was in very good condition and thus gave sufficient information of the more important features of the second stage of this larva. No full figure can, however, be given of the fully formed larva, partly because of the said incompleteness of its anterior part, and partly because the conditions (on board a small launch) did not allow me to make more than some free hand sketches from the living specimen. Although the illustrations given here of the larva of this species thus are not very satisfactory (— I regret to have drawn those of the 7 days old larva in a rather small scale —) the essential characters of the larva come out sufficiently clear from them.

In the first stage, which lasts until about the 7th day, the posterior end of the larval body is short, broadly rounded (Pl. VII. Fig. 5) and presents no essential difference from that of *Lytech. variegatus*. The upper part of the anal area, with the postoral band, is bent somewhat inwards in the middle, outwards at the sides, the beginning formation of the ciliated lobes. The skeleton is of the same structure as in that species. The postoral rod is simple, not fenestrated, and the body skeleton forms no basket-structure. The end of the body rod has some horizontal branches, very variable in shape; otherwise the body rod is smooth. At the point where the body rod and the postoral rod join there is a rather deep sinuation, generally deeper than in the specimen figured. The recurrent rod is generally bent towards the dorsal side with its point. The ventral transverse rods are transgressing with their points as in *L. variegatus*.

About this time, contemporaneously with the appearance of the postero-dorsal arms with their supporting rods and of the dorsal arch (Pl. VIII Figs. 3—4), the shape of the body becomes more complicated. On the dorsal side a saddle-shaped impression develops at the level of the lower edge of the mouth; the vibratile lobes are growing larger, and very soon epaulets begin to form, viz. about the 10—11th day. The epaulets are formed in the usual way as an outgrowth from the band at the outer corner of each vibratile lobe.

In the fully developed larva the epaulets are very large and reach to the middle of the body, where they join with that from the opposite side, so that the four epaulets form together a nearly complete band round the middle of the body, open only on the sides (Fig. 8). The posterior end of the body is almost straight, with a pair of short postero-lateral lobes (Fig. 8A). Regarding the relative length and shape of the arms in the fully developed larva nothing definitely can be said. The skeleton of the body undergoes the usual absorption and a posterior transverse rod is formed; it is short and straight, with a small process in the middle,

and branching at each end in two simple processes, of which the lowermost is the longer (Fig. 8A). Regarding the color of the larva I have noticed that red pigment cells occur scattered in the body (the small

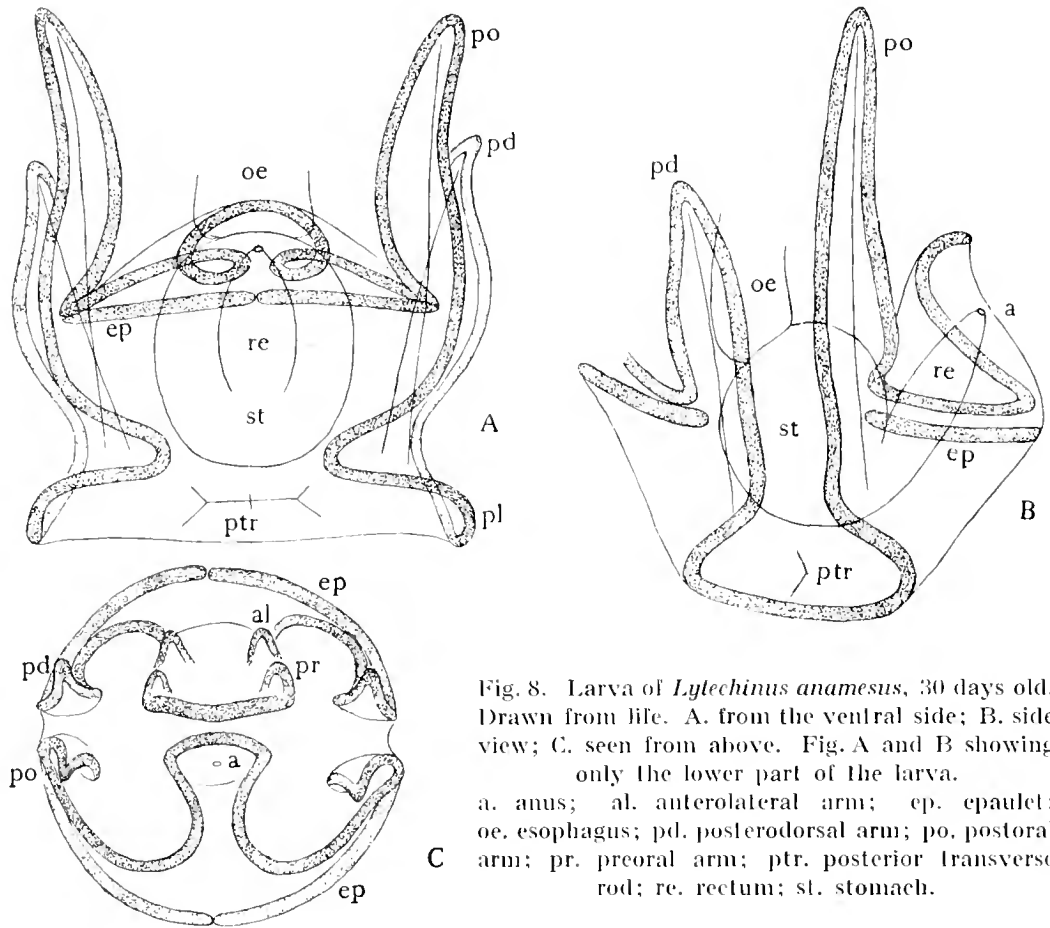


Fig. 8. Larva of *Lytechinus anamesus*, 30 days old. Drawn from life. A. from the ventral side; B. side view; C. seen from above. Fig. A and B showing only the lower part of the larva.

a. anus; al. anterolateral arm; ep. epaulet; oe. esophagus; pd. posterodorsal arm; po. postoral arm; pr. preoral arm; ptr. posterior transverse rod; re. rectum; st. stomach.

round spots seen in Pl. VIII. Fig. 1); in the grown larva such pigment cells are found especially along the epaulets and in the point of the arms.

The point to emphasize on comparing the larvae of these two species, *L. variegatus* and *anamesus*, is the presence of large, strongly developed epaulets in the latter, while such appear to be entirely absent in the former; at least their presence in this species needs to be verified. Otherwise they agree in their main features, and it is especially important to notice the close conformity of their skeletal structures, in both the first and the second larval stages.



**Lytechinus pictus** (Verrill).

On a little dredging trip to San Diego the 7th September 1915 I secured a few ripe specimens of this species; fertilization was made on board, and the culture carried to La Jolla. It proved to be very good; the larvæ developed normally until the first stage, but then came a standstill in their development, and as I had to leave La Jolla soon after, there was no possibility of starting a new culture. —

The larva was in all respects so closely like that of *L. anamesus*, that there was no reason for giving a special description or figures of it. — Perhaps the body rod is a little more branched and the recurrent rod slightly smaller than in *anamesus*, but the difference is in any case very unimportant — if at all constant.

Also the fully formed larva can be stated to be closely like that of *anamesus*. On the said dredging trip in San Diego Bay I found in a plankton sample an Echinoid-larva, fully developed, which had the same characters in shape and skeletal structure as the *L. anamesus*-larva. Since at that time no other Echini than the two above named *Lytechinus* species had ripe sexual products, it is beyond question that this larva also was a *Lytechinus* larva, and the probability is, of course, that it belonged to the species occurring at that place.

Otherwise I wish to express here my doubt of the distinctness of these two "species". I do not see that there is any reliable difference between them; the typical forms, I agree, look very different; but there are all transitions between them. In my opinion *L. pictus* and *anamesus* are only the shallow water form and the deep water form or variety of one and the same species. The close agreement of their larvæ is in conformity with this view, though in itself no proof of its correctness.

**Lytechinus panamensis** Mrtsn.<sup>1)</sup>

Pl. VII Fig. 1.

Of this, hitherto unknown, species which I discovered at Panama, specimens containing ripe sexual products were found in December 1915 and fertilization was made with very good result. The early developmental stages, which do not present any unusual features, pass very rapidly, so that at the age of only 24 hours the embryo begins already to assume the pluteus shape. The larva in its first stage (Pl. VII Fig. 1) agrees very closely with that of *Lytech. variegatus* and *anamesus*. The body is short

<sup>1)</sup> This new species is distinguished from the other *Lytechinus*-species of the West Coast of America in having the test uniformly reddish-brown coloured and the short spines somewhat banded, redbrown and white. Ocular 1 is generally insert. It is a quite small form, rarely exceeding 20 mm h. d., most specimens being only ca. 10 mm h. d.

and truncated posteriorly; the postoral rods are simple, and the body skeleton forms no basket structure (Fig. 9). The branches at the end of the body rod, as also the recurrent rods are rather strongly thorny distinctly more so than in the larva of *L. anamesus*. The larva is very transparent, with a small cluster of red pigment cells in the point of each arm and a few cells of the same colour spread irregularly in the body.

At the age of 11—12 days the larvæ showed the beginning formation of the vibratile lobes; after this they did not develop any further and soon died. I can thus give no information about the shape and skeletal structure of the fully formed larva. Especially it would be important to know whether

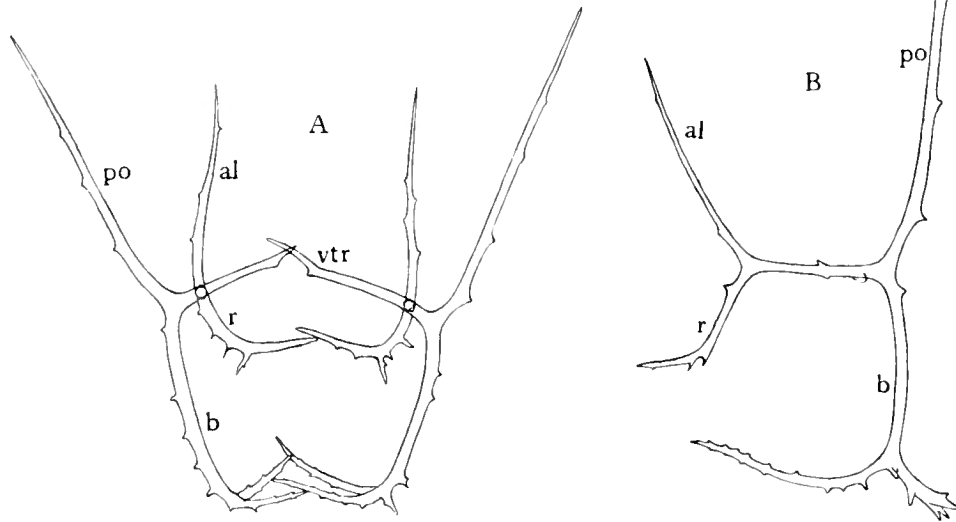


Fig. 9. Skeleton of the larva of *Lytechinus panamensis*. A. front view; B. side view. <sup>300</sup>/<sub>1</sub>. Letters as in fig. 5. vtr. ventral transverse rod.

epaulets and the posterior transverse rod are present (as is to be expected) or not. But, anyhow, the fact here made known that the larva in its first stage is in perfect accordance with that of *L. variegatus* and *anamesus* (+ *pictus*) is of considerable interest.

### ***Lytechinus verruculatus* (Ltk.)**

In the beginning of April 1915 I undertook repeatedly fertilization of this species during my stay at Hilo, on the island of Hawaii.

The eggs are small (I have no measurement of them) and very clear. The cleavage proceeds at an extraordinary speed, so that already four hours after fertilization the blastula stage is reached (though not yet swimming); the embryos are very transparent and form an excellent object for microscopical study. The first larval stage has the usual shape, with the posterior end short and truncated. The body skeleton forms

a basket structure; the postoral rod is fenestrated. The skeleton is only very slightly thorny.

Beyond this stage I did not succeed in rearing the larvæ. No figures can be given, because the "laboratory" conditions at Hilo did not permit any drawing of the living larvæ, and the skeleton has been dissolved in the preserved specimens.

The very conspicuous difference in the skeletal structure between the larvæ of this species on one hand (basket-structure and fenestrated rods) and the other *Lytechinus*-species on the other hand (no basket-structure, no fenestrated rods) would seem to necessitate the conclusion that the species *verruculatus* cannot be congeneric with the other *Lytechinus*-species, but should form a separate genus, in spite of the fact that it seems to afford no very prominent structural differences from those species.

### **Toxopneustes pileolus** (Lamk.)

Pl. VIII Fig. 8.

Fertilization of this species was undertaken repeatedly during the months April, May and June 1911 at the Biological Station at Misaki. In no case did I succeed in rearing the larva beyond the first larval stage; evidently it is not very hardy, since other Echinoid larvæ (e. g. *Helicoidaris tuberculata*) were reared to their full shape under quite similar conditions.

The gastrula stage was reached at about 21 hours age, and at the age of about two days the skeleton had begun to appear and also the first indication of the postoral arms was evident. The shape of the young larva (Pl. VIII Fig. 8) is the usual, with a short, truncated body. One of the cultures was kept for about 3 weeks, but even at that age the larvæ had not yet developed beyond the first stage, the only difference from the younger specimens being that the postoral lobe had become distinctly concave in the middle at the oral edge — an indication that vibratile lobes will be found in this larva. The pigmentation is not very prominent; there are some scattered, red pigment cells and the points of the arms are reddish. The skeleton forms a basket structure (Pl. VIII Fig. 8; Fig. 10); both the body rod and the recurrent rod are somewhat thorny. There is a deep sinuation at the point where the body rod and the postoral rod join; the latter is

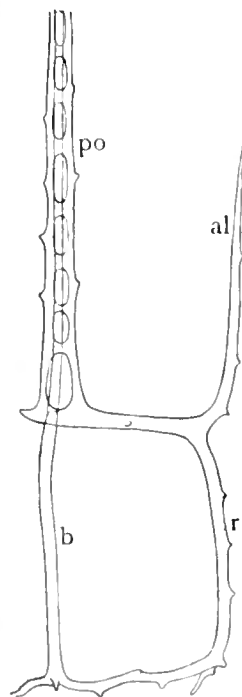


Fig. 10. Skeleton of the young larva of *Toxopneustes pileolus*. Side view;  $\frac{290}{1}$ . Letters as in fig. 5.

fenestrated. The ventral transverse rods join with their points but do not cross one another — at least not in this stage.

It should be pointed out that the figure of this larva is drawn from a preserved specimen, so that it is very probable that there is some shrinkage in the soft parts of both body and arms.

### **Toxopneustes roseus** (A. Ag.).

Pl. VIII. Fig. 7.

Fertilization of this species was undertaken on November 11th at Taboga, Panama. It was, evidently, at the end of its breeding season, most of the specimens being empty.

The eggs are of the usual small size, transparent, though somewhat yellowish. The cleavage does not present any unusual features. At the age of 24 hours the embryos show the first rudiments of the skeleton; at the age of two days they have the typical pluteus shape of the first stage. The body skeleton forms a basket structure, the postoral rods are fenestrated. — On the following day the larvæ all died, and there was no possibility of getting a new culture. No figures were drawn of the young larvæ; since the skeleton has been dissolved in the preserved specimens, there is no reason to give any figure to show the general shape of the larva, which is as usual.

Although I did thus not succeed in rearing this larva beyond the first stage, I think I can give some information also of the somewhat more advanced stage. In a plankton sample from November 1915 from near Taboga was found the larva represented in Pl. VIII Fig. 7. It is almost beyond doubt that it must be the larva of *Toxopneustes roseus*. The regular Echinoids occurring at Taboga are the following: *Eucidaris Thouarsi*, *Diadema mexicanum*, *Astropyga pulvinata*, *Toxopneustes roseus*, *Lytechinus panamensis* and *Echinometra van Bruntli*. *Diadema* was not ripe at that time and is therefore out of question; the young stages of *Eucidaris* described above are so different from this larva that it is hardly imaginable, how it could develop into a larva like the one in question. The *Astropyga*- and *Lytechinus*-larva are quite different (see Pl. V Figs. 6—7 and Pl. VII Fig. 4); also *Echinometra van Bruntli* was reared to the young Pluteus, the body skeleton of which forms a strongly thorny basket structure. Thus *Toxopneustes roseus* alone remains to which to refer this larva.

Characteristic of this larva is the considerable length of the ventral transverse rods, which are crossing one another and make the median part of the postoral band project as a pair of small lobes, supported

by these points. The posterodorsal rods have just appeared: they are fenestrated. The dorsal arch has a very long posterior process: the fact of its appearance at this comparatively young stage would seem to indicate that the arms, except the postoral ones (— they are broken in the specimen, so that their exact length cannot be ascertained; but they are fairly long, anyhow —) are, upon the whole, short. The anterolateral

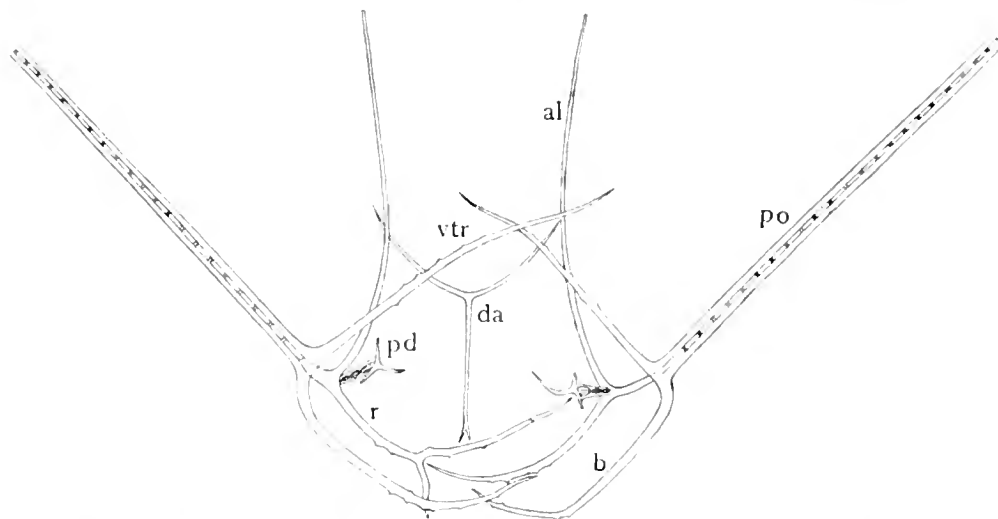


Fig. 11. Skeleton of the larva of *Toxopneustes roseus* (?).  $\frac{225}{1}$ . Letters as in fig. 5.

arms (they are broken, but somewhat restored in the figure) are evidently short. The posterior transverse rod has not yet appeared. The body skeleton is nearly smooth (Fig. 11).

### ***Pseudocentrotus depressus* (A. Ag.).**

As the breeding season of this species did not occur during my stay in Japan (April—July), I could not study its development myself. Being, however, very anxious to learn, whether the larva of this species would prove to be of the same type as the other *Toxopneustids*, as I expected, or perhaps of the *Echinus-Strongylocentrotus* type, I asked my Japanese colleagues to do me the service to try to rear the larva, when its breeding season came on. Dr. Fujita, then Assistant at the Biological Station of Misaki, kindly undertook to rear the larva, when in the end of October ripe specimens of the species were found. The preserved larvae were sent to me and received in February 1916 in Panama. On examining them I found my expectations confirmed: the body skeleton formed a basket structure as in the *Toxopneustidae* (i. e. most of them, *Lytechinus* forming a remarkable exception). The closer study of the larvae, which were reared only till the first stage (the oldest being 10 days old),

was postponed till my return. There, however, it was found that the skeleton had dissolved, except in the very youngest specimens, only one day old, where the skeleton has just appeared in the shape of a pair of three-radiate stars. Although the larvæ are otherwise very perfectly preserved there seems to me no reason to give figures of them; they do not present any noteworthy differences from the usual type of larva in regard to the shape of the body. But the information gained about the structure of the body skeleton in the first larval stage is of importance, and I beg to express my gratitude to Dr. Fujita for his kind assistance in rearing these larvæ.

### **Strongylocentrotus pulcherrimus** (A. Ag.).

Pl. IX Fig. 5.

Th. Mortensen. On the development of some Japanese Echinoderms. p. 544.

This species being among those which I had, mainly on account of the structure of its pedicellariæ and spicules, transferred to another genus (*Strongylocentrotus*) than that in which it was hitherto placed (*Sphærechinus*)<sup>1</sup>) I was very anxious to study its development and ascertain whether the structure of its larva was in accordance with that of *Strongylocentrotus drobachiensis*, — as I expected, — or not. Already on one of the first days of my stay at the Biological Station, Misaki, I had the pleasure of finding ripe specimens of the species, which is very common there under stones in quite shallow water<sup>2</sup>). Fertilization was made at once (April 28th) and proved successful.

The eggs are small yellowish, not very transparent. The cleavage does not offer anything of particular interest. The gastrula stage was reached after about 24 hours, and in the course of the second day the embryos had assumed the shape of small Plutei, rotating in the usual way, i. e. to the right, about their longitudinal axis.

The young larva agrees in its shape and structure very closely with that of *Str. drobachiensis*, as described by A. Agassiz<sup>3</sup>). The posterior part of the body is elongated (Pl. IX, Fig. 5), supported by the long body rods. The arms are rather broad and flat, narrowing towards the point. The preoral transverse band is short, rounding upwards at the corners, the frontal area being thus quite narrow. The postoral transverse band

<sup>1</sup>) Ingolf-Echinoidea I. 1903, p. 121, 138.

<sup>2</sup>) Like so many other littoral Echinoids it has the habit of covering itself with small stones, fragments of plants etc., evidently with the object of disguising itself.

<sup>3</sup>) A. Agassiz. On the Embryology of Echinoderms. Mem. Amer. Acad. Vol. IX. 1864. Figs. 1—18.

Th. Mortensen. Echinodermlarven d. Plankton-Expedition p. 90. Taf. VII. 3—4. VIII. 3—5.

has a slight sinuation in the middle. Over the whole body, as well as along the vibratile band are scattered red-brown pigment cells; in the end of the arms and in the posterior end of the body they may be lying somewhat closer, but there is never a very prominent pigment spot in the end of the arms. — The skeleton is simple. There is no basket-structure and not even an indication of a recurrent rod. The body rods are club-shaped, with some irregular, short branches at the thickened end. Otherwise the skeletal rods are very slender and very finely thorny. (Fig. 12).

At the age of ca. 3 weeks the postero-dorsal arms had begun to appear, their supporting rods being also simple and very slender. At the age of one month the posterior end of the body rods showed signs of beginning absorption; the dorsal arch had appeared and the pre-oral arms had begun to develop. A small vesicle lying opposite the hydrocoel on the left side evidently represented the beginning annion-for-

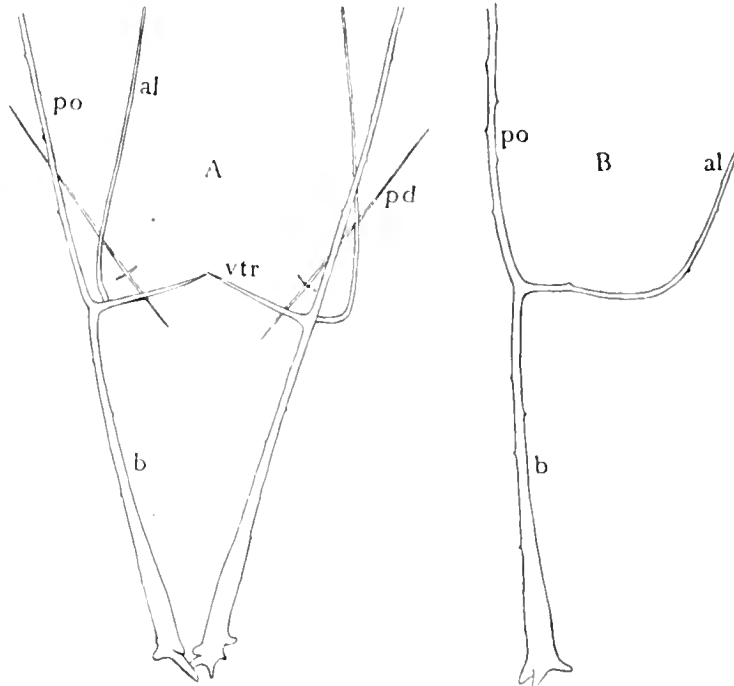


Fig. 12. Skeleton of the larva of *Strongylocentrotus pulcherrimus*. 1st stage. A. ventral view, B. Side view.  $\frac{300}{1}$ . Letters as in fig. 5. vtr. ventral transverse rod.

formation. At five weeks the body rods had been almost completely absorbed. There was otherwise no change — no posterior transverse rod and no epaulets. The larvæ still lived for nearly two weeks more, but they did not develop any further. The question whether epaulets are present in the fully developed larva of this species thus still remains open. No new culture of this species could be obtained at that time, its breeding season being over.

The larva of *Str. drobachiensis* was reared by Agassiz till the age of 1 weeks. The postero-dorsal arms and the dorsal arch had appeared, but apparently he has not observed any beginning absorption of the body rods. As for the later stages described and figured by Agassiz as be-

longing to this same larva I have shown in my "Echinodermen-Larven d. Plankton-Expedition" (p. 91) that he made a mistake. These larvæ, which were caught free swimming, evidently belong to a Clypeastroid, most probably *Echinarachnius parma*<sup>1)</sup>. But the main thing is that they are not *Str. drobachiensis*, and his statement of the presence of vibratile epaulets in the *Strongylocentrotus*-larva thus lacks real foundation. Hereby I do not mean to ascertain that there are no epaulets in the *Str. drobachiensis*-larva. On the contrary, I may take the opportunity here to state that the *Str. drobachiensis*-larva has not only the usual epaulets, but it has also a posterior pair of large epaulets, much as in the larva of *Echinus esculentus*. This statement rests, not upon the rearing of this larva, of which I have not as yet found an opportunity, but on the evidence of a pair of specimens found in a plankton-sample from Greenland, taken by Mr. K. Stephensen in Bredefjord, South Greenland, in the summer of 1912. As *Str. drobachiensis* is the only littoral Echinoid of Greenland there can be no doubt that the larva belongs to this species. Unfortunately the specimens are in a rather poor state of preservation, so that they are not fit for being figured; but the epaulets are distinct enough. — It is a pity that the larva of *Str. pulcherrimus* could not be reared to metamorphosis so that the question whether it has epaulets like *drobachiensis* could be decided. But in view of the complete accordance with the *drobachiensis* larva in the earlier stages there is every reason to expect that it will also prove to have epaulets in the same way as that larva.

### ***Strongylocentrotus franciscanus* (A. Ag.).**

Pl. IX Figs. 1—4.

The development of this species I had the opportunity of studying while staying at the Biological Station at Nanaimo, Vancouver Isl., B. C., in May—June 1915. Fertilization was made on May 26th. The eggs are small and transparent. I noticed the peculiarity that there is found a double fertilization membrane, the outer one standing far out from the egg, while the inner membrane remains close to the surface of the egg and follows the outline of the cleavage cells, as shown in the

<sup>1)</sup> In the work quoted I have suggested that they might perhaps belong to *Mellita testudinata*, pointing, however, also to their likeness to the *Echinarachnius*-larva. MacBride in his Memoir on the Development of *Echinus esculentus* (Philos. Transact. B. Vol. 195. 1903. p. 287) still states that by this work of Agassiz "for the first time a complete history of the changes in external form undergone in a single species was obtained". Evidently MacBride must have overlooked my criticism of Agassiz' work. The honour of having for the first time given the complete history of the development of an Echinoid (regarding the external form) belongs to Théel (*Echinoeyamus*), not to Agassiz.



adjoining sketch Fig. 13 (which was not drawn with the camera). I may state that I found the same peculiar membrane-formation in *Str. drobachiensis* (by a fertilization made at the same time, which, however, did not result in any rearing of the larvæ, the breeding season of that species being then already past, only few eggs remaining); I regret not having noticed whether the same phenomenon occurs in *Str. pulcherrimus*.

The gastrula stage was reached after about 24 hours, and in the course of the next day the embryos had assumed the shape of young Plutei. The postero-dorsal arms began to appear at the age of 8 days. Beyond this stage I did not succeed in rearing the larvæ, the culture dying off when the larvæ were 12 days old. A new fertilization was tried in the later part of June, but then

the breeding season was past and only few eggs could be found, which did not develop normally. However, I can give some information also of the fully formed larva of *Str. franciscanus*, having found a specimen in the plankton. As no other species of Echinoids occur there, besides *Dendraster excentricus* — the larva of which I have also reared, and which has no resemblance to the present larva — and a Spatangoid, *Brisaster latifrons* (A. Ag.) — which was not ripe and which has, moreover, probably not pelagic larva — there cannot be any doubt that this larva really belongs to *Str. franciscanus*.

The larva of *S. franciscanus* in its first stage differs from that of *drobachiensis* and *pulcherrimus* in the posterior end of its body being distinctly less elongated and more rounded (Pl. IX, Figs. 1—3). The arms are not so broad as in the said species. As in these species the body skeleton does not form a basket structure. The body rod is clubshaped, rather strongly thorny at the thickened end, which curves somewhat inwards; it is distinctly shorter than in the two other species. Furthermore this larva differs from the two other larvæ known of this genus in having a well

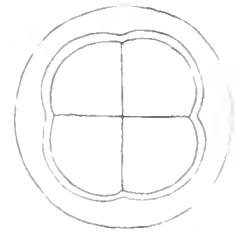


Fig. 13. Egg in the 1-cell stage of *Str. franciscanus*; showing double membrane.

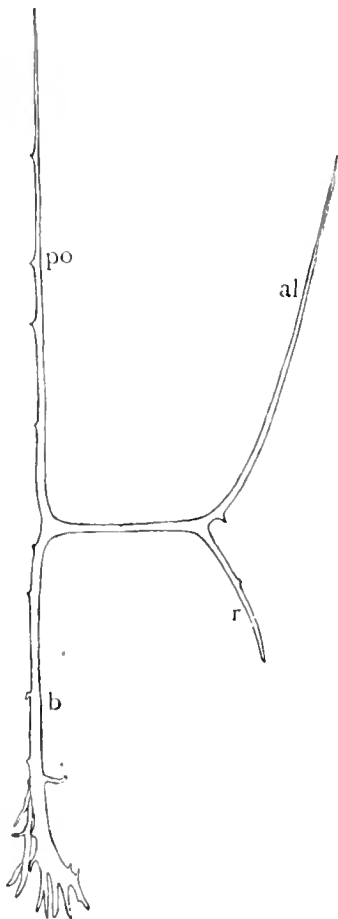


Fig. 14. Skeleton of larva of *Strongylocentr. franciscanus*. 1st stage. Side view.  $\frac{300}{1}$ . Letters as in fig. 5.

developed recurrent rod (Fig. 14), which may even sometimes reach the posterior end of the body. It was, however, never found to unite with the body rod, so that no basket structure is formed. The rods of the postoral and posterodorsal arms are simple, slightly thorny. Only scattered red pigment cells are found, no accumulation of pigment in the point of the arms.

In the stage where the posterodorsal arms are beginning to develop, which occurs already at the age of 8 days, — much earlier than in *S. pulcherrimus* — the postoral ciliated band assumes a characteristic appearance (Pl. IX, Fig. 2), with a median and two lateral sinuations. These gradually grow deeper, and in the fully formed larva (Pl. IX, Fig. 4) the median sinuation forms a deep excavation, while the two lateral sinuations form a pair of large epaulets (or vibratile lobes). The body is very wide in the middle, while the oral part remains narrow, the dorsal ciliated band thus making a deep sinuation at the level of the postoral band. The preoral band has the same shape as in *pulcherrimus*, the frontal area being very small. The postero-dorsal rod has appeared in the specimen figured in side view. In this specimen this rod lacks the usual sidebranches at its base, but in sketches from other specimens I have represented these small branches in the same form as in *pulcherrimus*, which is then evidently the normal feature.

The fully formed larva (Pl. IX, Fig. 4) has the posterior end shortened in the usual way through the absorption of the body rods, the hind edge being nearly straight. It carries a pair of epaulets at the posterior end, besides those at the base of the postoral and postero-dorsal arms, as is the case also in the *S. drobachiensis*-larva. The arms are fairly broad and flat, not very long, the postoral arms being the longest. The postoral area is very much concave, the frontal area is very small. There are only scattered pigment cells. There appears to be no posterior transverse rod; in the said figure, it is true, a small rod is represented lying in the place usually occupied by the posterior transverse rod. It can, however, hardly be doubted that it is only a part of the body rods broken off in the course of their absorption; its irregular shape would seem to preclude the idea that it could be a true posterior transverse rod. Of course, however, researches on living material will be required for definitely settling this important point.

The figure of the fully formed larva is partially reconstructed. No doubt the outline of the living larva will prove somewhat different, especially the body will probably be somewhat broader. Still, as the specimen from which the figure was drawn is fairly well preserved, I have thought

it worth while giving this figure, since otherwise no figure exists of a fully formed larva of a true *Strongylocentrotus*-species.

Concerning the four anterior epaulets I may point out that it cannot be decided from the single specimen in hand, whether they have been separated off from the vibratile band or not; in the latter case they will be no true epaulets, but only the band along the vibratile lobes.

*Strongylocentrotus franciscanus*, together with the other Californian species *S. purpuratus*, has been the object of a great many experimental studies, especially by Loeb. In spite of this the larvæ of these two species have not been described hitherto in any way adequately; only some outline figures have been given of the first larval stage for the sake of comparison with hybrid larvæ of the two said species, while no information at all is given of the later larval stages. But at least we may gather from these papers<sup>1)</sup> the important information about the larva of *Strongylocentrotus purpuratus* that in its first stage it agrees closely with the larva of *S. drobachiensis* and *pulcherrimus* in having a long, clubshaped body rod; there may be an indication of a recurrent rod, much smaller than in *franciscanus*, and there is, accordingly, no basket-structure. — The species breeds during the winter season. I had therefore no opportunity myself of studying its development.

### **Temnopleurus toreumaticus** (Klein).

Pl. X, Fig. 6. Pl. XII, Fig. 6.

Fertilization of this species was undertaken at Misaki on June 25th and again on the 29th, the first culture being unsuccessful. The eggs are very small and transparent. The cleavage and the first developmental processes go very rapidly, so that already after about 12 hours the embryos leave the egg-membrane in the shape of blastula, and at the age of ca. 22 hours the embryos were found to have assumed the Pluteus-shape (Pl. XII, Fig. 6). A conspicuous feature of the young larva is the very

<sup>1)</sup> J. Loeb, W. O. R. King & A. R. Moore. Über Dominanzerscheinungen bei den hybriden Pluteus des Seeigels. Arch. f. Entw. Mechanik. Bd. 29. 1910. p. 351—362. Taf. XI—XII.

J. Loeb. Über die Natur der Bastardlarve zwischen dem Echinodermenei (*Strongylocentrotus franciscanus*) und Molluskensamen (*Chlorostoma funebrale*). Arch. f. Entw. Mech. Bd. 26. 1908. p. 476—82. 13 figs.

J. Loeb. Weitere Versuche über heterogene Hybridisation bei Echinodermen. Arch. f. d. ges. Physiologie. Bd. 101. 1901. p. 325—50.

J. Loeb. Die chemische Entwicklungserregung des tierischen Eies. 1909. (On p. 7, Fig. 17 is represented a young Pluteus of *Strongyloc. purpuratus*).

A. L. Hagedoorn. On the purely motherly character of the Hybrids produced from the eggs of *Strongylocentrotus*. Arch. f. Entw. Mechanik. 27. 1909. p. 1—20.

small size of the stomach, oesophagus and rectum, the more conspicuous since the body is fairly elongate. The arms are still quite short; the anterior edge of the oral lobe is rather thickened, the preoral vibratile band being not yet very distinctly differentiated. The skeleton is very characteristic, the elongated body rods being rather coarsely thorny and ending in two serrated branches<sup>1)</sup> (Fig. 15); the postoral rod is fenestrated. There is a small recurrent rod, with the end curving forward, and the body

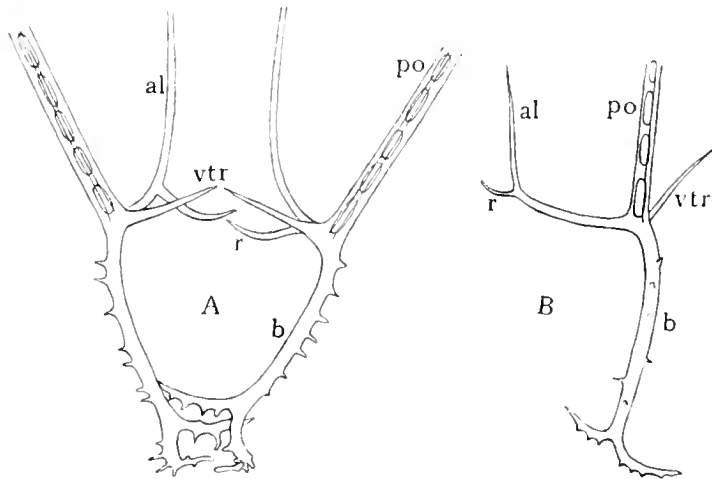


Fig. 15. Skeleton of larva of *Temnopleurus loreumaticus*, 1st stage. A. from the ventral side; B. side view. <sup>300</sup>/<sub>1</sub>.  
Letters as in fig. 5. vtr. ventral transverse rod.

skeleton accordingly does not assume a basket structure.

After 8 days the larvæ had reached the shape shown in Pl. X, Fig. 6. The postero-dorsal arms have developed, their rods being fenestrated. All the arms are fairly broad, but somewhat abruptly narrowed towards the point.

There is a small prominence on each side

at the anterior end, indicating the place of the future preoral arms, and further there is a characteristic small thickening on the postoral band where it bends out along the postoral arm. Vibratile lobes or epaulets have not yet been formed, and it then remains undecided whether they exist in this larva; judging, however, from the presence of epaulets in the *Mespilia*-larva as also in the undetermined *Temnopleurid* larvæ described below it can scarcely be doubted that epaulets, but no vibratile lobes, will be found also in this larva. (Cf. the larva from the Gulf of Siam, mentioned below.) There are only scattered pigment cells, no prominent pigment spot in the point of the arms.

In the skeleton (Fig. 16) there is still only little change. The absorption of the body rods has begun, one of the end branches having disappeared.

<sup>1)</sup> In the preliminary notice "On the development of some Japanese Echinoderms" p. 546. it is stated that the main rod of the body skeleton in the *Temnopleurid* larvæ "has a median process off the posterior end of the stomach, and beyond this process there is a short prolongation, which becomes absorbed in the later stages". While it really has this appearance when seen from the ventral or dorsal side, the side view of the body makes it evident that it is more correct to say that the body rod ends in two branches, one of which (the ventral) may be directed more or less directly downwards; this latter appears to be the first to be absorbed, when the full larval shape is about to be formed.

The dorsal arch has not yet been formed, and there is as yet no trace either of a posterior transverse rod. That this latter rod will prove to exist may be supposed from its existence in the two related forms described below, and especially in the larva from the Gulf of Siam, which probably belongs to *T. loreumaticus*.

At the age of 12 days the larva had not developed beyond this stage, and as I had then to leave Misaki, there was no possibility of studying its further development. I tried to carry the culture along with me; but while I succeeded in carrying some other cultures in good condition to Australia, this one succumbed.

In a plankton sample from the Gulf of Siam (off Koh Kam, 4. II. 1900) I have found an Echinoid larva which is so very similar to the larva of

*Temnopl. loreumaticus*<sup>1)</sup> that it seems almost justified to refer it to this species. This larva is only

in a slightly more advanced stage than the oldest stage of the *T. to-*

*reumaticus* larva reared. Vibratile epaulets are beginning to develop. A posterior transverse rod has appeared and also the dorsal arch; on the other hand the body rods have apparently not yet begun to be absorbed. Posterolateral processes are indicated, which will be supported by the branches of the transverse rod; that this rod has branches at its ends can be seen, but their definite form is not yet to be ascertained.

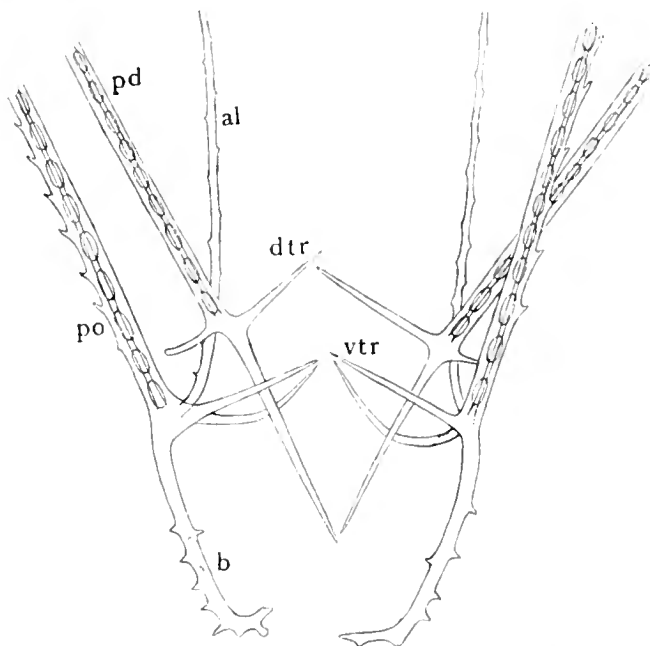


Fig. 16. Skeleton of larva of *Temnopleurus loreumaticus*, 9 days old.  $\frac{300}{1}$ . Letters as in fig. 5. dtr, dorsal transverse rod.

<sup>1)</sup> The fact that this larva was taken in the beginning of February, while the fertilizations were undertaken in the end of June, does not render the reference of the larva to this species impossible, since some specimens taken off Koh Kong in the Gulf of Siam on the 25th of January 1900 prove to contain ripe sexual products. Whether this species has then a breeding season so long as indicated by these dates, or its breeding season is perhaps not so early in Japan as farther South, remains to be ascertained.

**Temnotrema sculpta** A. Ag.

Pl. VI, Fig. 4.

This species, which occurs — though in rather small numbers — under stones or among *Laminaria*-roots along the shores at Misaki, was found to be ripe in the end of April. Fertilization was undertaken on the 26th and later on again in the end of May, 1914. The cultures were not quite as good as desirable, and the larvæ could not be reared till the full shape was reached; still valuable information was obtained, showing that the shape and structure of this larva is in conformity with that of the other *Temnopleurid*-larvæ here described.

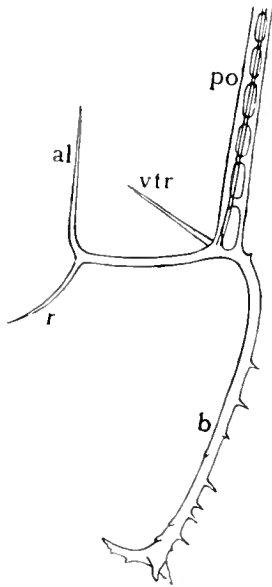


Fig. 17. Skeleton of larva of *Temnotrema sculpta*, 2 $\frac{1}{2}$  days old; side view.  $\frac{300}{1}$ . Letters as in fig. 5.

The eggs are very small, and the first developmental processes occupy a very short time only. The embryos were found to have assumed the shape of young *Plutei* at the age of 36 hours (probably it does not really take so long time to reach that stage). The shape of the young *Pluteus* is very much like that of *Temnopleurus toreumaticus*; the body is elongate on account of the long body rods; the ventral side of the body is distinctly concave. The stomach, oesophagus and rectum are small but hardly so small as in *Temnopleurus toreumaticus*; the anterior border of the oral lobe is thickened as in that larva. The skeleton (Fig. 17) is of the same type as in the *Temnopl. toreumaticus*-larva; the body rod is elongate, thorny, ending in two or three horizontal branches; the recurrent rod is quite small, curved; no basket structure is formed. The postoral rod is fenestrated.

The most advanced stage reached is that figured in Pl. VI, Fig. 4, from a larva 18 days old; the arms are broad, rather abruptly narrowing towards the point; the posterodorsal arms have appeared, but not the preoral ones. The postoral ciliated band bends somewhat downwards in the middle, and the anal area is slightly concave here. Along the sides of the body the ciliated band goes far downwards — which indicates that postero-lateral lobes will develop as in the *Mespilia*-larva. — Conspicuous red pigment cells are distributed along the vibratile band and over the body; in the point of the arms a few pigment cells occur. — Vibratile epaulets have not been formed.

In the larva figured the body rods had begun to be absorbed, but no

trace of a posterior transverse rod was seen; the dorsal arch had been formed. The postero-dorsal rods are fenestrated as the postoral ones.

In the second culture many of the larvæ were more or less abnormal, the body skeleton forming a more or less developed meshwork.

### *Mespilia globulus* (Linn.).

Pl. VII, Figs. 1—2.

Th. Mortensen. On the development of some Japanese Echinoderms. p. 546.

Although this species<sup>1)</sup> is fairly common in shallow water near the Biological Station at Misaki, it was quite difficult to get a culture of it, partly because its breeding season appears to be somewhat later in the summer, partly because it was found to be very generally infested with a Trematod living in its genital organs and destroying these more or less completely. I succeeded, however, in getting a fertilization of it on June 25th 1914, which gave a small, but sufficient number of larvæ. They developed quite normally until beginning metamorphosis, when the surviving specimens had to be preserved on my depart from the station.

The developmental processes do not go on so fast as in *Temnopleurus torenimaticus*; the embryos had not yet passed the blastula stage at the age of ca. 24 hours. The young Pluteus does not afford any very marked features; the body is not quite so elongate as in the two other Temnopleurid-larvæ described above, and the stomach is not quite so small as in these. Pigmentation is very scarce.

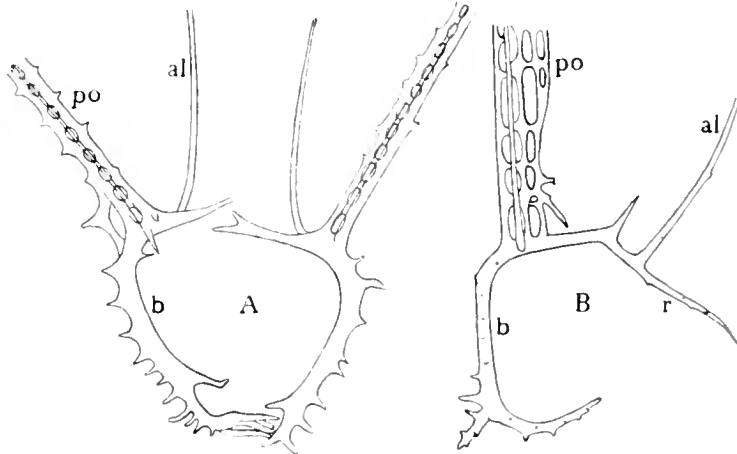


Fig. 18. Skeleton of larva of *Mespilia globulus*, 1st stage. A, front view; B, side view.  $\times 300$ . In fig. B, the postoral rod is abnormally widened into a fenestrated plate; also in fig. A there is a slight abnormality at the base of the right postoral rod. Letters as in fig. 5.

<sup>1)</sup> Yoshiwara (Preliminary Notice of new Japanese Echinoids. Annot. Zool. Japonenses. II, 1898, p. 58) has established the species *M. levituberculata* for the Japanese form of *Mespilia*. H. L. Clark (Hawaiian and other Pacific Echini. The Pedimidae . . . Echinidae, Temnopleuridae . . . Mem. Mus. Comp. Zool. XXXIV, No. 1, 1912, p. 322) maintains that it cannot be separated from the typical *M. globulus* (L.). On adopting the name *M. globulus* for it here I must state that it is on the authority of H. L. Clark, having not yet had the opportunity of critically examining the question myself.

The skeleton (Fig. 18) is of the same type as in the *Temnopleurus* and *Temnotrema* larva, the body rod being only somewhat less elongate; it is strongly thorny. There is no basket structure. The recurrent rod is not curved forwards (at least in the single young larva preserved; I have omitted to observe how it was in the specimens examined alive). The postoral rod is fenestrated. (Some irregularities are seen in the skeletal details figured, but not so much as to obscure the main features.)

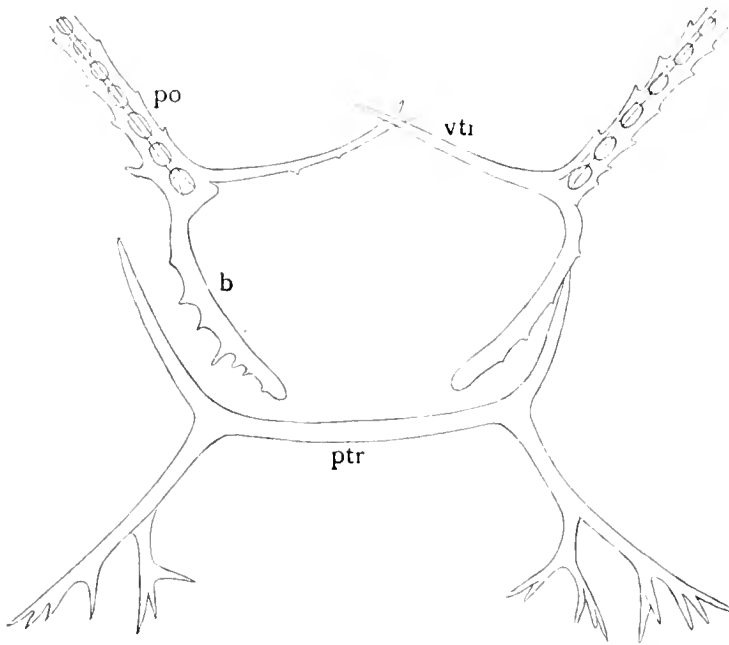


Fig. 19. Part of the skeleton of a fully formed larva of *Mespilia globulus*; front view. <sup>300</sup>/<sub>1</sub>. Posterodorsal and anterolateral rods as well as the dorsal arch have been omitted. b. body rod; po. postoral rod; ptr. posterior transverse rod; vtr. ventral transverse rod.

At the age of 15 days the larvæ had reached their full size and were in the beginning of metamorphosis. It is now a most striking object and one of the most beautiful Echinoderm larvæ. The postoral and postero-dorsal arms are very wide at their base, rather abruptly narrowed towards the point. They are held almost horizontally and thus directly serve as a floating apparatus. The figures do not show these arms in their

natural position; Pl. VII, Fig. 1, which was drawn from a living specimen, shows the larva in half dorsal view; the postoral arms are seen in their full breadth, while the postero-dorsal arms are seen half in profile; in reality they are as wide as the postoral ones. Pl. VII, Fig. 2 is drawn from a preserved specimen; the postoral and postero-dorsal arms have contracted to less than half their natural width and also the position is more upright than normal.<sup>1)</sup> Across the base of each of these arms is a large ciliated epaulet. In the preserved specimens the epaulets

<sup>1)</sup> I have thought it of some interest to represent the larva in preserved condition beside the figure of the living larva in order to show directly the amount of shrinkage due to preservation. Such shrinkage appears to be unavoidable, especially in larvæ with broad arms, e. g. *Ophiopluteus paradoxus*, and must, of course, be taken into consideration when such larvæ are described from preserved material.



are seen to consist of two parallel, closely apposed parts, which fact most probably indicates their origin as a fold of the ciliated band. The process of their formation was not observed on the living material. There is a pair of small, ear-shaped posterolateral processes, supported by branches from the posterior transverse rod. No antero-dorsal arms are developed, and there are no processes from the dorsal arch to support lobes of the dorsal vibratile band. The antero-lateral and preoral arms are rather short and narrow. The preoral band is almost straight, the postoral band slightly concave in the middle, bending rather abruptly downwards at the sides, whence it passes into the band of the postoral arms. There are no vibratile lobes. Pigmentation is inconspicuous; there are no large pigment spots in the point of the arms, only scattered pigment cells in the body and along the arm rods.

In the body skeleton absorption has begun in this stage (Fig. 19) and a posterior transverse rod has been formed. This is very characteristic; it is a little curved and ends in two branches, one simple, slightly curved, upwards directed, the other larger, obliquely downwards directed; this latter branch bifurcates, the divisions again branching somewhat irregularly. It is this branch which supports the postero-lateral process. Both the postoral and the posterodorsal rods are fenestrated and rather strongly thorny; the simple rods supporting the anterior arms are finely thorny, judging from the young larva preserved; the skeleton has been dissolved in the preserved specimens of the fully formed larva, and it was omitted to make notes or figures thereof from the living specimens. — Pedicellariæ have begun to develop in some of these 15 days old larvæ (Pl. VII, Fig. 2), and also the rudiment of the sea-urchin is distinct.

#### **Echinopluteus of Temnopleurid (?), Species a.**

In a plankton sample from off Jolo, taken the 20th of March 1914, an Echinoid larva was found which agrees in the essential features of its skeletal structure so closely with the *Mespilia*-larva, that it can hardly be doubted that it must belong to a related form. It is, of course, impossible to ascertain which form this is, and at present no more can be said than that it belongs most probably to one of the numerous Temnopleurids occurring in these seas. It is very tempting to suggest that it might belong to one of the *Salmacis*-species; but there is no real support, at present, for such suggestion. The larva is, unfortunately, in too poor a state of preservation for giving a whole figure of it; but its main features are distinctly seen, and the skeleton is well preserved; it presents some very marked features by which the larva may be easily recognized.

The larva is in beginning metamorphosis; the absorption of the body

rods has begun and a pedicellaria has appeared in the middle of the posterior end. There are epaulets across the base of the four main arms as in the *Mespilia*-larva, and posterolateral processes are developed,

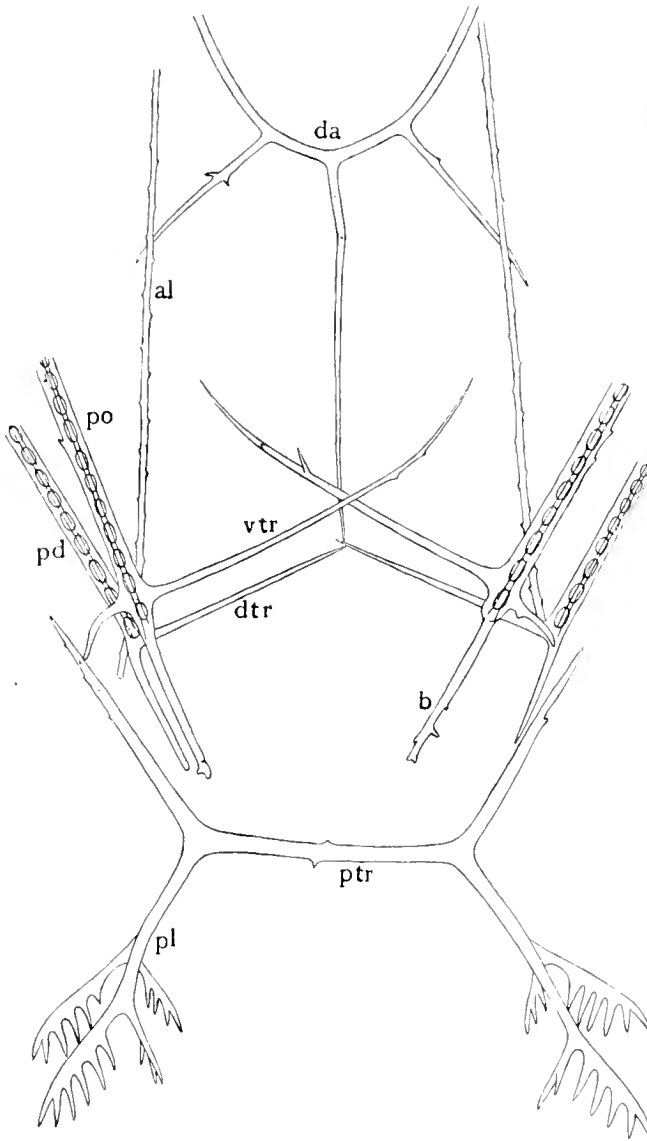


Fig. 20. Skeleton of Temnopleurid larva, species a; front view.  $\frac{220}{1}$ . al. anterolateral rod; b. body rod; da. dorsal arch; dtr. dorsal transverse rod; pd. posterodorsal; pl. posterolateral; po. postoral; ptr. posterior transverse; vtr. ventral transverse rod.

being supported by the branches of the posterior transverse rod as in the *Mespilia*-larva. The shape of the arms cannot be ascertained. The anal lobe is not very high, such as is the case in the species c; there are no vibratile lobes, but there appears to be a lobe on the dorsal side, although apparently not supported by a branch from the dorsal arch.

In the skeleton (Fig. 20) the eminently characteristic feature is the posterior transverse rod, which branches at the ends, the upper branch being simple, pointed, with only a few small thorns, while the lower branch bifurcates twice, terminating in two larger, outer, and two smaller, inner branches, each set along its posterior edge with long thorns, the whole structure recalling the antlers of a deer. The postoral and posterodorsal rods are fenestrated in their whole length, sparsely thorny. The absorption of

the body rods is so far progressed that nothing can be said with regard to their shape. The dorsal arch has a very long posterior prolongation from its middle and a pair of rather long lateral branches directed obliquely outwards. The preoral and antero-lateral rods are finely thorny.

**Echinopluteus of Temnopleurid (?), species b.**

From the Gulf of Siam (off the North of Koh Kut, 27/1. 1900), there are two larvæ in an advanced stage of metamorphosis, which represent another closely related species (Fig. 21). The posterior transverse rod is shorter and the lower branches have fewer thorns than in species a; the small inner branches are lacking. The irregularities of the upper branch seen in the figure are, evidently, abnormal; they are not seen in the second specimen. The posterodorsal rod is distinctly curved

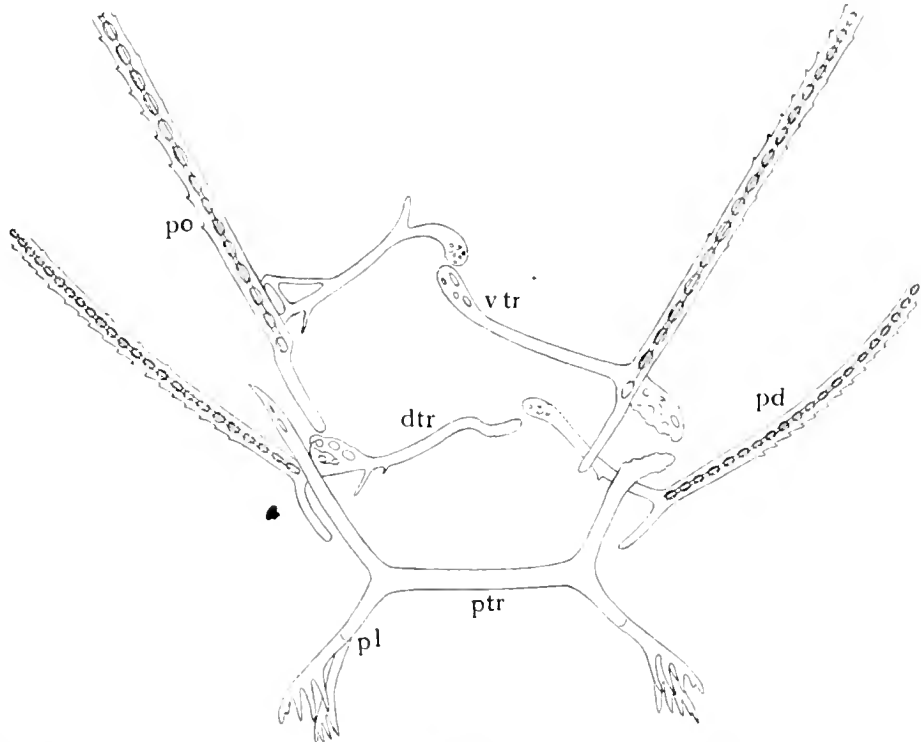


Fig. 21. Skeleton of Temnopleurid larva, species b: front view. <sup>220</sup><sub>1</sub>. The widening of the dorsal and ventral transverse rods are probably due to the beginning metamorphosis. Letters as in fig. 20.

and, like the postoral rods, densely serrate. Both these rods are fenestrated in their whole length. The dorsal arch has the same shape as in species a, only the posterior prolongation appears to be shorter. In one of the specimens muscles are seen very distinctly to pass between the ends of the body rods, which proves that the four main arms in this species may be moved and probably are kept in a nearly horizontal position while swimming, as in the *Mespilia*-larva. That vibratile epaulets are present as in the *Mespilia*-larva can be ascertained, otherwise the shape of the larval body cannot be seen distinctly on account of the advanced stage of metamorphosis.

As with species a it can only be said that, judging from the close resemb-

lance to the *Mespilia*-larva, this larva must in all probability belong to some Temnopleurid, possibly a *Salmacis*.

**Echinopluteus of Temnopleurid (?), species c.**

Pl. XI, Fig. 3.

Together with the specimen of the species **a** were found, in the same plankton sample from off Jolo, three specimens of another *Echinopluteus* species, which must be assumed to belong likewise to a Temnopleurid, and which I shall designate as species **c**. One of these specimens has not yet begun to metamorphose, the two others are in the beginning of metamorphosis. Although not in a very good state of preservation the younger of these specimens shows several very characteristic features well; it was therefore thought desirable to give a whole figure of it, although it had to be partly restored: thus the vibratile band is preserved only in the lower part of the arms, so that the true shape of the arms cannot be seen; likewise it is impossible to ascertain the exact shape and size of the epaulets.

As seen in Pl. XI, Fig. 3 the absorption of the body rods has not yet begun, in spite of the fact that the posterior transverse rod has already been formed. The body is thus seen to be somewhat elongated as in those Temnopleurid-larvæ of which the young larval stage is known. A very characteristic feature of this larva is the shape of the anal lobe, which is very high, being supported by the very long ventral transverse rods; it is concave in the middle, the corners being rather prominent. On the dorsal side the vibratile band is produced into a small lobe, supported by a process from the dorsal arch. The postero-lateral process is very short and small, but it is quite possible that it is considerably larger in the living larva.

The skeleton (Fig. 22) affords several very characteristic features. The body rods are branched at the end in the same way as appears to be the rule in Temnopleurids. The postoral rod is fenestrated, but the holes, which are very small, disappear completely a little above the middle of the rod, and the outer part is simple, the three component rods coalescing so completely that there is no trace of a compound structure. The postero-dorsal rod is simple, slightly curved. Both these rods are very sparsely set with fine thorns. There are two sets of ventral transverse rods, one very long, upwards directed, supporting the high anal lobe, the other transversely directed, short; the latter may perhaps really represent the recurrent rod. The posterior transverse rod is very peculiar, formed like a bow, with no posterior branch at the ends; on the other hand it has a long posterior process in the middle, somewhat curved, and a small anterior process. In Pl. XI, Fig. 3 it is seen to have developed before the absorption of the body rods has begun; a similar case was found in the

larva mentioned above sub *Temnopleurus loreumaticus* (p. 53), so that this may well be supposed to be a normal case. The place of the posterior transverse rod, as shown in Pl. XI, Fig. 3 is somewhat unusual, so that one might be tempted to suggest that it has been somewhat transplaced upwards on preservation. I would, however, be inclined to think that it lies in its normal position, especially since it lies in the same way in the above mentioned larva of *Temnopleurus loreumaticus*(?): but this can, of course, only be decided through observations on the living larva. The dorsal arch has a very characteristic shape; there are two rather long lateral processes; at the point where they proceed the arch makes an obtuse angle, and the part beyond (the preoral rod) makes a graceful bending. The posterior median process is short. All the simple rods are nearly completely smooth.

The branching end of the body

rods, the existence of vibratile epaulets, but apparently not of vibratile lobes, and the presence of a posterior transverse rod is a combination of features which appears to be characteristic of the Temnopleurids: it seems therefore justifiable to suggest that also this larva belongs to a Temnopleurid. Any suggestion of the species or genus to which it belongs would appear to be hopeless: it may only be said that it may probably belong to another genus than the larvæ described as species **a** and **b**, its very peculiar

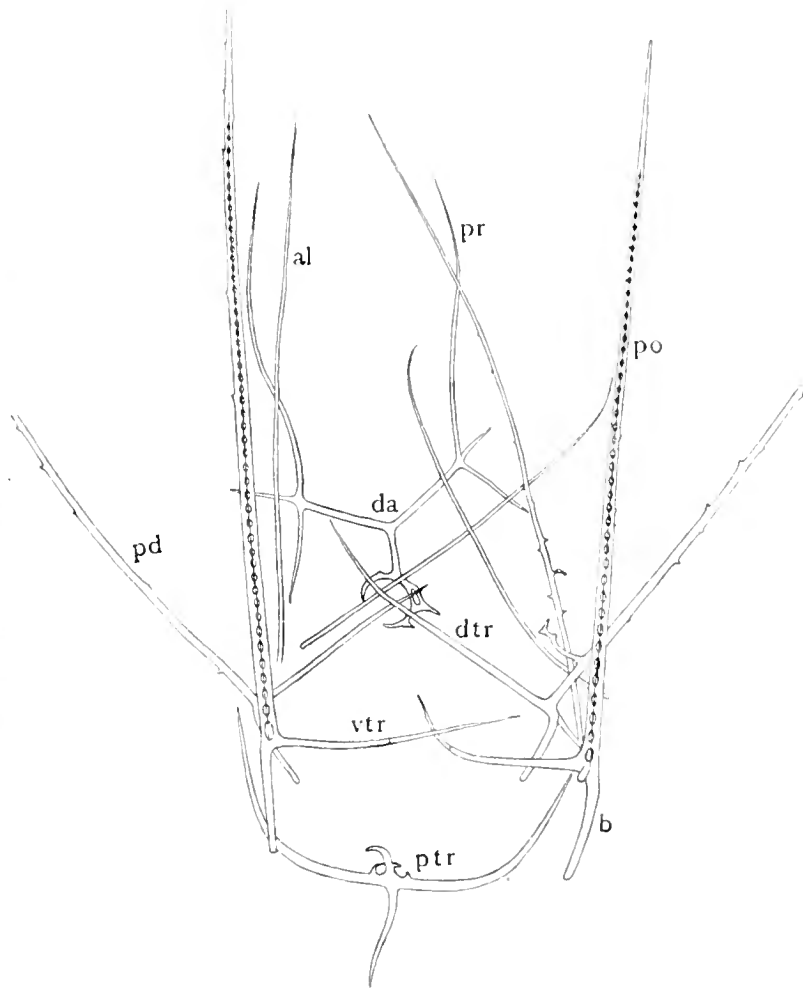


Fig. 22. Skeleton of Temnopleurid-larva, species **c**. Front view, slightly oblique. <sup>225</sup>/<sub>1</sub>. Letters as in fig. 20.

posterior transverse rod especially indicating that it can hardly be so very closely related to those forms.

***Evechinus chloroticus* (Val.).**

Pl. X, Figs. 1—5.

During a trip round the North Island of New Zealand, onboard the N. Z. G. S. "Hinemoa" I had the opportunity of rearing the larva of this species. Fertilization was undertaken on the 18th of December 1914. The culture of the larvæ was kept until the 22nd of January 1915; the larvæ had attained their full size by that time, but metamorphosis had not yet begun. The development of this species then goes on rather slowly, though perhaps not quite so slowly in nature. The conditions under which the cultures had to be kept onboard the small steamer were not the very best, and this may perhaps have had some delaying influence on the development, as also the fact that not few of the larvæ showed more or less pronounced abnormalities most probably is due to some extent to these conditions. The fact that the two cultures which were made showed a rather marked difference in the time of appearance of the skeleton indicates that this supposition is correct. But, anyhow, a good number of the larvæ developed normally, and a fairly complete description of the larva of this species thus can be given. — Unfortunately there was no possibility of making drawings from the living specimens, and moreover it happened that in all the specimens of the more advanced larvæ preserved the skeleton had been dissolved (while the shape was preserved quite exceptionally well); only in some larvæ of the first stage the skeleton remained intact — but all of them present some abnormalities. The description of the skeleton thus cannot be quite satisfactory; but the main features at least can be ascertained from this material combined with the notes put down after observations on the living specimens.

The cleavage is quite regular; the 8-cell stage was reached in the course of 4 hours; swimming blastulæ were found ca. 16 hours after fertilization, and the gastrula stage was reached at the age of about 24 hours. They were not very clear and evidently do not form a very good object for microscopical study. The skeleton had appeared on the 3rd day and the embryos were beginning to assume the *Pluteus*-shape. In another culture the skeleton began to form in the course of the second day. At the age of 6 days the larvæ were found to be well developed *Plutei* in the first stage; in this stage they remained apparently unaltered for about 8 days more; at the age of nearly two weeks the first indication of the postero-dorsal arms appeared. At the age of three weeks the stage shown in Pl. X, Fig. 2 was reached, and the fully formed larva shown in Pl. X, Fig. 3

is five weeks old. This larva is, accordingly, among those which, like e. g. *Strongylocentrotus pulcherrimus* and *Heliocidaris tuberculata*, take a comparatively long time to develop; but, as stated above, it is hardly justifiable to conclude that the development normally proceeds quite so slowly.

In the young Pluteus stage (Pl. X, Fig. 1) the body is short, in accordance with the character of the body skeleton. There is a very distinct suboral cavity. No pigment spots in the point of the arms, only few scattered pigment cells in the body and arms. — The body-skeleton (Fig. 23) forms a basket structure; in the figure A the frame is not complete, the recurrent rod not having united with the body rod; but since I have noticed after observation on the living specimens that "the body skeleton is like that of *Heliocidaris tuberculata*" it can hardly be doubted that normally the recurrent rod unites with the body rod to form a complete basket structure as it does also in fig. B. In some of the specimens with the skeleton preserved the body skeleton is considerably more complicate than in the specimens after which Fig. 23

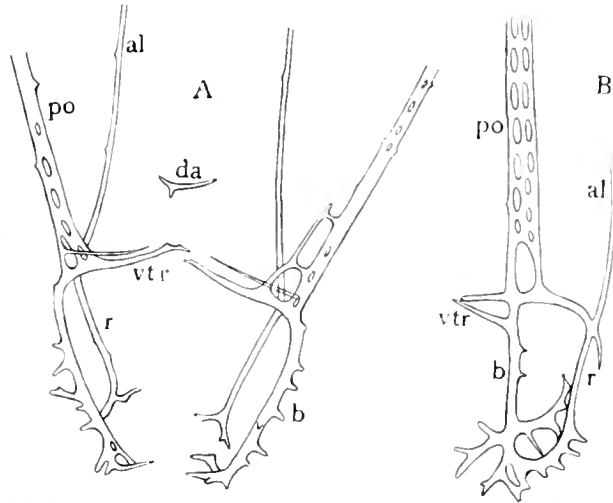


Fig. 23. Skeleton of the larva of *Euechinus chloroticus*, 1st stage. Slightly abnormal. <sup>225</sup>1. A. front view; B. side view. Letters as in fig. 20.

was drawn, looking more or less distinctly like the structure found in *Heliocidaris tuberculata* and *Echinometra lucunter* (Figs. 24, 25). It is impossible to ascertain from this material what is really the normal structure of the body skeleton in this larva, but, in any case, it is important to notice that there is a distinct tendency in this larva towards forming a complicate body skeleton similar to that occurring in the two forms mentioned; in the Fig. 23 B there is seen an indication of a double recurrent rod. The body rod is rather coarsely thorny. The postoral rod is fenestrated; in the specimens where the skeleton is preserved it shows more or less pronounced abnormalities. It is seen to consist only of two component rods in the outer part; I would, however, not venture to ascertain that this rod is normally thus constructed — it is only safe to say that the postoral rod is fenestrated. The anterolateral rod is almost smooth.

The fully formed larva (Pl. X, Fig. 3) has two pairs of vibratile lobes and short, earshaped postero-lateral processes. On the dorsal side the vibratile band forms a pair of lobes, supporting a raised wall across the

dorsal side. There are no epaulets. The arms are of medium length, fairly broad. The pigmentation consists of scattered red pigment cells; no prominent pigment spots in the point of the arms.

Regarding the skeleton full information cannot be given, because it has been dissolved in all the specimens preserved. In my notes from the observation of the living specimens it is stated that the posterodorsal rod is fenestrated, as may also be ascertained from one of the young specimens with the skeleton preserved, showing these rods in beginning formation. It is very regrettable that I have forgot to state anything about the posterior transverse rod. That this rod is present can, however, not be doubted, partly because the shape of the posterior end of the larva is in conformity with that of other larvæ possessing this skeletal rod, partly because in one of the specimens preserved traces of this rod — and other parts of the skeleton — are distinct, made up by the organic matrix of the calcareous substance. Judging from this specimen — as also from the fact that nothing is said about this skeletal part in my notes — it would appear that the ends of this rod are simply dichotomous, probably the upper branch the longer.

Some few of the abnormal larvæ in the cultures of this species were so remarkable that I have thought it worth while to mention and figure them (Pl. X, Figs. 4—5). They are quite flat, with the arms radiating horizontally. In the middle of the flat body are seen the rudimentary stomach and mouth. — These remarkable forms might possibly indicate that this species would be a favourable object for experimental studies.

### ***Heliocidaris tuberculata* (Lamk.)**

Pl. VI, Fig. 3. Pl. XI, Figs. 1—2.

Th. Mortensen. On the development of some Japanese Echinoderms. p. 545. (*Toxocidaris tuberculatus*.)

This species, which occurs abundantly on the rocky shores near the Biological Station at Misaki, was found to be sexually ripe early in the summer, and artificial fertilization was undertaken on May 22nd. The cleavage is total and regular; developmental processes are not passing very rapidly. Swimming blastulæ were found 20 hours, gastrulæ 24 hours after fertilization. At the age of 30 hours the skeleton had begun to form, and at the age of two days the embryos had assumed the shape of small plutei. On the eleventh day the posterodorsal arms had begun to form; at the age of 21 days the larva had the posterodorsal and preoral arms fully developed, while there was as yet no transformation of the body skeleton; at the age of 5 weeks the larvæ were found to have begun metamorphosis and thus reached their full shape. As only few larvæ remained



at that time, they were preserved, no attempt being made to have them metamorphose completely. Whether the larva will take so long time to develop under better conditions (more food, more congenial temperature?) must be left undecided.

The first larval stage (Pl. XI, Fig. 1) shows the typical form, offering no marked special features. The body is short, the arms rather long. There is a very distinct suboral cavity. Pigment very scarce; a few pigment cells, mainly in the point of the anterolateral arms. The skeleton

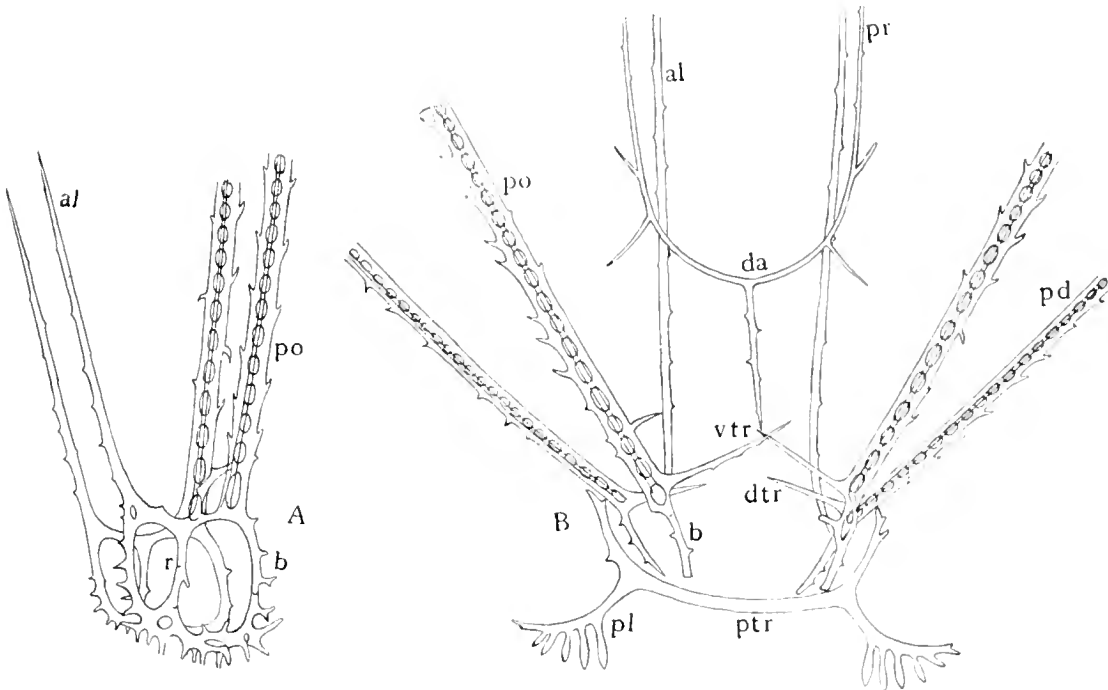


Fig. 24. Skeleton of larva of *Heliocidaris tuberculata*: A. of young larva, side view; B. of fully formed larva, front view. <sup>225</sup>/<sub>1</sub>. Letters as in fig. 20.

(Fig. 24 A) is very complicated. The body skeleton forms a basket structure, but not in the usual simple way; there are two recurrent rods, so that two large meshes are formed in each side of the body. In the end of the body there are three transverse connecting rods, all strongly thorny along the hind edge; also the body rod and the recurrent rods are rather strongly thorny. The postoral rod is fenestrated, with many thorns along the outer, fewer — sometimes none — along the inner side.

The fully formed larva (Pl. XI, Fig. 2) is provided with four vibratile lobes, but there are no vibratile epaulets. The anal area is somewhat concave. At the anterior edge there is a pair of small ciliated protuberances. The vibratile band is arranged along the dorsal side so as to form a pair of small lobes. The arms are fairly long, narrow; the postero-lateral

processes are short, earshaped. The pigmentation is very slight, with no prominent spots in the point of the arms. There is a very distinct transverse muscular band connecting the ends of the postoral and posterodorsal rods, these pairs of arms being thus actively movable, as is apparently the general rule in those larvæ provided with a posterior transverse rod.

The skeleton (Fig. 24 B). The most conspicuous feature is the posterior transverse rod, which ends in two branches, the lower of which carries along its lower side 5—6 lancet-shaped branches, the whole structure recalling a pair of antlers of a stag. The middle part of this rod may be quite smooth or provided with some small processes. The posterodorsal rods are fenestrated and thorny along the outer edge like the postoral ones, only the holes are slightly smaller. The dorsal arch has two lateral processes. Both the preoral and the anterolateral rods are distinctly thorny.

### ***Heliocidaris erythrogramma* (Val.)**

PL. XVII—XVIII.

This species, which occurs abundantly along the rocky shores of Port Jackson, Sydney, was found to have ripe sexual products in February (— most probably its breeding season will prove to continue during a greater part of the summer —). The development proved to be of such exceptional interest that it was thought advisable to give a preliminary report of it<sup>1</sup>). The fuller record given here is also rather summary and by no means complete. The preserved material is not sufficient for an elaborate study of all the internal transformations; moreover, the skeleton has been dissolved so that this part of the development must be entirely left out, the conditions under which the larvæ were reared not having allowed to draw the living objects or to undertake a careful microscopical study of them. Neither is it within the scope of the present work to give a detailed description of the development of the internal organs and all the complicated transformations connected with the process of metamorphosis. The matter is merely indicated here. But it is evident from the facts here recorded that the development of this species really deserves to be made the object of a detailed monographic study, since it presents so many novel and exceptionally interesting features, being upon the whole, so entirely different from that of any other Echinoid hitherto

<sup>1</sup>) Th. Mortensen. Preliminary note on the remarkable, shortened development of an Australian sea-urchin, *Toxocidaris erythrogrammus*. Proc. Linn. Soc. N. S. Wales. XL, 1915, p. 203—6.

I have adopted in the present work the name *Heliocidaris* instead of *Toxocidaris*, in agreement with H. L. Clark (Hawaiian and other Pacific Echini. The Pedinidæ etc. Mem. Mus. Comp. Zool. XXXIV. 1912. p. 281).

studied with regard to its development. It is to be sincerely hoped that some Australian naturalist will take up this matter for a complete study, which will need a rich supply of material and also constant access to living material.

Fertilization was undertaken on Febr. 25th 1915. The development proceeded at no exceptional speed; the gastrulation took place at the age of ca. 18 hours, while the first metamorphosed specimens were found after 4—5 days. The eggs are large, ca. 0.5 mm, red-yellowish and quite opaque. They float at the surface of the water; this is the case also in *Phyllacanthus parvispinus*, while it is otherwise unknown in Echinoids. It is evidently due to the fact that the egg contains some fatty substance; though I did not observe this in the living objects, it is easily seen in the preserved eggs that they have a vacuolated structure, and it can hardly be doubted that these vacuoles must contain some fatty substance which makes the eggs lighter than the water. The same vacuolated structure was found in *Phyllacanthus parvispinus* (p. 21—25).

The cleavage is total and perfectly regular. It appears that the blastula is not folded, as is the case in *Phyllacanthus*. The formation of the mesenchyme could not be followed in detail. It is seen to begin very early; in the stage represented in Pl. XVIII, Fig. 1, which is 6 hours old and apparently either in the 32- and the 64-cells stage (this cannot be definitely ascertained from the sections), one cell is seen lying in the middle of the blastocoel cavity, which must, evidently, be a mesenchyme cell. Pl. XVIII Fig. 2, representing an 18 hours old blastula, shows the blastocoel cavity completely filled up by vacuolated mesenchyme cells: they are still undifferentiated and of the same general aspect as the ectoderm cells, which latter do not yet form a regular epithelial layer. The whole of the embryo is full of large and small vacuoles, which must, evidently, undergo divisions together with the cells, as is apparent from the fact that they are much more numerous and, upon the whole, smaller in the older than in the younger stages. (Comp. Pl. XVIII, Figs. 1—2.)

A further advanced stage, from a culture 18 hours old, is shown in Pl. XVIII, Fig. 3, representing the fully formed blastula. The ectoderm is now a typical, high epithelium, slightly higher in one side, where the gastrula-invagination is to take place. The mesenchyme has undergone a noticeable differentiation, the cells forming now merely a fine reticulum between the vacuoles, which have partly united into some very large ones. Some few vacuoles are still found in the ectoderm. This peculiar structure of the mesenchyme, recalling a parenchymatous plant tissue, is retained during the whole process of the embryonal development, until the metamorphosis has been completed.

The gastrulation, which proceeds in the usual way (Pl. XVII. Figs. 1—2) begins at the age of about 18 hours. The blastoporus is sometimes pushed out towards the side (Pl. XVII. Figs. 2—3); this is, however, hardly anything but an individual variation; generally it is in the middle of the hind end of the body, and in this place a trace of it is generally found in the more advanced stages (Pl. XVII. Figs. 5—6; Pl. XVIII. Fig. 7). The gastrulae are not bound to the surface, but swim freely in the water, with the usual rotating movement, the aboral end always being turned upwards, as a necessary consequence of the fact that the vacuoles containing the light, probably fatty substance are in the main confined to this part of the body, and it remains so during the whole course of the development. It seems beyond doubt that the substance contained in these vacuoles forms the nourishment on which the embryo subsists until the young sea-urchin has got its mouth and is able to feed actively; the embryo itself is perfectly unable to feed, the gastrula mouth closing very early, sometimes already at the age of only 30 hours (Pl. XVII. Fig. 7) and no larval mouth being formed.

In embryos 30 hours old the archenteron begins to differentiate (Pl. XVII. Figs. 3—4), its upper end widens, and gradually the widening pushes itself downwards, the wall of the archenteron making a fold on one side. The pouch thus formed, representing the rudiment of the hydrocoel, is still in open connection with the archenteron, but in embryos of 42 hours it has been separated from it (Pl. XVII. Fig. 6; Pl. XVIII. Fig. 7). The formation of the enterocoel cannot be made out in the material available. Judging from this material it would appear to originate as schizocoel spaces in, not as pouches from the entoderm; but I do not venture to ascertain as a fact that it does originate in this exceptional way. A rich and most perfectly preserved material would be needed for giving full evidence of such a surprising statement, and my material cannot be said to be of such eminent quality. Also the question of the formation of the hydro-pore must remain unsettled; in fact, I have been unable to find the slightest trace of it, and it would appear that also in this regard the development of this species is exceptional among Echinoderms. (Comp. below, sub *Peronella Lesueuri*).

As already stated the blastoporus may close completely already at the age of 30 hours (Pl. XVII. Fig. 7), the archenteron completely separating from the ectoderm. In most cases, however, the separation is not complete, a fine strand remaining as a connection between the entoderm and the ectoderm (Pl. XVII. Figs. 5—6). Within the cavity of the archenteron a distinctly limited mass of a substance is generally seen which stains very strongly in hematoxylin or safranin; it may perhaps be an agglutinated

mass of cilia: but the fact that it is always distinctly separated from the epithelium of the archenteron would seem to point towards its being more probably some slimy secretion. Anyhow, it is very useful for identifying the entoderm in the sections.

At the age of about 12 hours the embryos have reached their full shape, which is, indeed, most surprising for an Echinoid larva (Pl. XVII. Figs. 5—6, 8). It is a simple, elongated, worm-shaped body, rounded at the anterior end, truncated at the posterior end. There is nothing to remind one of a *Pluteus*. A little below the middle there is generally a ring-shaped widening; in the preliminary notice I have said that this might perhaps represent a rudiment of the postoral larval processes. After a closer examination of the larva I do not see any sufficient reason for this supposition. If rudiments of the larval skeleton could be found at this widening, that would serve to support the said suggestion; but it appears that there is no trace of a larval skeleton. The body is covered by a uniform ciliation, not provided with distinct ciliated bands, as it is otherwise generally found in the Echinoderm-larvæ of the simple worm-shaped type (Crinoids, Dendrochirote Holothurians). In a somewhat later stage there may, however, be found a rather distinct ciliated band on the ring-shaped widening (Pl. XVII. Fig. 8) and also the oral end may show an indication of a ciliated ring; but this appears to be no constant feature. Red pigment also begins to appear about this time. It is especially prominent round the oral end; in the later stages it may form a very prominent ring just above the widening, and also in the anterior part of the body it may be more or less distinctly arranged in rings (Pl. XVII. Figs. 10, 12, 11). Scattered pigment cells otherwise are found all over the body. Some of the embryos have scarcely any pigment at all; these latter probably give rise to the very light-coloured specimens which are often found among the otherwise generally dark coloured specimens of this species.

{The first indication of the metamorphosis was observed in embryos 12 hours old. Below the thickened wall a slight invagination is seen (Pl. XVII. Figs. 5, 6), which gradually widens so as to go nearly round the body (Pl. XVII. Fig. 8). This represents the amniotic invagination: being at first a simple fold (Pl. XVIII. Fig. 4) it gradually develops into a true amniotic cavity, which, however, apparently never closes completely, a small pore remaining open (Pl. XVIII. Figs. 5—6). Contemporaneously the hydrocoel differentiates and the five primary tubefeet are formed (Pl. XVII. Fig. 11). These, together with the first spines, formed also by this time, protrude into the amniotic cavity (Pl. XVIII. Figs. 5—6) and soon push out through the opening, which widens more and more,

and ultimately the embryo splits open here along the whole ventral side. At first the tubefeet and the spines are arranged in a single row in the rather narrow slit (Pl. XVII. Fig. 10), but gradually the slit opens more and more, giving room to the tubefeet and spines, which assume a more or less distinct circular arrangement (Pl. XVII. Fig. 14), and ultimately the slit becomes so wide that the upper and lower ends of the embryo are pushed up on the back of the urchin; the small part left untouched by the amniotic invagination acts by this process as a hinge between the upper and lower parts. In fact, it has the appearance that the young sea-urchin creeps out of the embryo as of an egg-shell, carrying now the rests of it on its back (Pl. XVII. Fig. 9, 12).

All the processes of transformation connected with the metamorphosis are limited to the very small part just below the widening of the embryonal body. The large aboral part remains perfectly passive during the whole process of the development from the gastrula stage unto the metamorphosis. It is simply a reservoir of food to the embryo, and the metamorphosing sea-urchin thus literally carries a wallet along with it on its back. Gradually, as the food is absorbed, the "wallet" shrinks (Pl. XVII. Figs. 12—13; Pl. XVIII. Figs. 8—9) and finally it disappears completely, the young sea-urchin at the same time assuming its regular shape. — In the preliminary notice (p. 205) it is stated that the aboral part of the embryo "gradually becomes completely overgrown by the young urchin and enclosed within its body". This expression is not quite correct; the aboral part is not overgrown by the sea-urchin but simply absorbed, and its skin becomes directly part of the skin of the young urchin.

The sections of the metamorphosing sea-urchin represented in Pl. XVIII. Figs. 8—9 show the stone canal and its outer and inner opening, the body cavity etc.; but there is no reason to enter on a detailed description of all these various structures, since it has not been possible to trace them from their first origin. The character of the aboral part as a simple food reservoir, containing no special structures, comes out very distinctly.

As already stated, the calcareous structures have been completely dissolved in all the specimens; accordingly no information can be given of the development of the skeleton of the young sea-urchin. It should only be mentioned that the first spines to appear are of the trifold, embryonal type, which appears to be of general occurrence in the young of all regular Echinoids.

**Echinometra lucunter** (Linn.)

Pl. I, Figs. 1—2; Pl. XII, Fig. 1.

During my visit to Tobago B. W. I. with the Carnegie Expedition in 1916 I had the opportunity of rearing this species. Fertilization was undertaken on the 24th of March and again on the 2nd of April; by this time the breeding season was in the main over, only some few small specimens still having ripe sexual products. Both cultures were perfectly successful, metamorphosed young being obtained from both. On leaving Tobago I carried some of these onboard the steamer to New York; during the time from the 9th to the 18th of May they were kept in the New York Aquarium and thereafter again carried onboard the steamer to Copenhagen. At the arrival there, on June 1st, two specimens were still alive, although they had hardly grown, which is naturally explained by the fact that it was impossible to procure a good food supply for them; it was also impossible to secure a constant, congenial temperature. That it was possible to carry them so far, in spite of these adverse conditions, is of considerable interest and plainly indicates that much more may be done in this way.

The eggs are small, ca. 0.12 mm, opaque, and the embryos are likewise very opaque and no good objects for microscopical study. I have omitted to note the time it takes to pass the different developmental processes, but the first pluteus stage is reached on the second day. At the age of 4 days the postero-dorsal arms began to appear, and in the 7 days old larvæ (Pl. XII, Fig. 1) I found the absorption of the body skeleton in progress. The posterior transverse rod appeared on the 10th day and metamorphosis was completed or nearly so at the age of 19 days.

In the first Pluteus stage the larval body is short, obliquely truncated. The young larva is rather strongly pigmented by red pigment cells and not very transparent. In specimens 6—7 days old a distinct nerve band was noticed across the corners of the anal lobe (Pl. XII, Fig. 1). Although this structure cannot be observed in the preserved specimens, I would venture to see herein an indication that this larva (and probably many others) has a nervous system similar to that of the larva of *Echinocyannus pusillus* as recently described by me<sup>1)</sup>.

The skeleton (Figs. 25 A—B) forms a complicated basket structure: the recurrent rod is double, two large meshes being thus formed on each side of the body, sometimes also some smaller additional meshes at the lower end, on account of secondary ramifications. The body rod is strongly thorny. The postoral rods are fenestrated, rather strongly thorny. — Judg-

<sup>1)</sup> Notes on the development and the larval forms of some Scandinavian Echinoderms. Vid. Medd. Dansk Naturh. Foren. 71. 1920, p. 157.

ing from a sketch (not reproduced) from a living specimen there are only two transverse connections between the two halves of the body skeleton, not three as in *Heliocidaris tuberculata*; this point, however, cannot be settled, the skeleton having been dissolved in the preserved specimens of the young larva (while it has remained perfectly intact in all the other stages preserved).

The fully formed larva (Pl. I, Figs. 1—2; textfigure 26) is provided with four well developed vibratile lobes, but has no epaulets. The anal area is rather deeply concave. The postero-lateral processes are short,

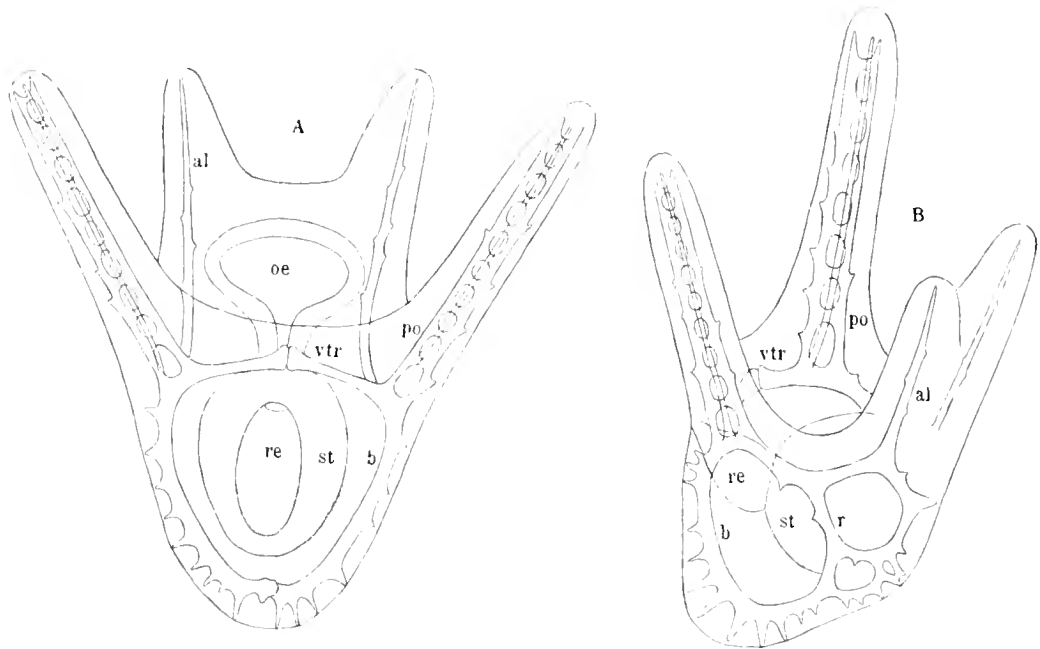


Fig. 25. Larva of *Echinometra lucunter*, 2 days old, showing skeletal structure. A, seen from the ventral side; B, side view.  $\frac{300}{1}$ . Letters as in fig. 20. Further: oe, mouth; re, rectum; st, stomach.

earshaped. In the larva in beginning metamorphosis (when the first pedicellaria has appeared in the midline in the posterior end) the vibratile band in the constriction above the postero-lateral processes widens towards the midline, so that it has almost the appearance of forming a closed ring round the posterior end of the body. Whether it may ultimately form a really closed ring I have been unable to ascertain. Also the vibratile lobes gradually become so broad as almost to join in the midline of the body and thus to form an apparent transverse band about the middle of the body. Along the dorsal side the vibratile band is raised into a pair of lobes, supporting a wall across the dorsal side of the body. At the anterior edge there may be a pair of small processes formed by the vibratile band, where it bends from the preoral over to the antero-



lateral arms. The arms are of medium length, narrow, with a more or less distinct widening at the point. There is a not very conspicuous cluster of red pigment cells in the point of the arms; series of pigment cells are also seen along the vibratile band in the lobes, in the postero-lateral processes and along the postoral and preoral band. In the body and arms

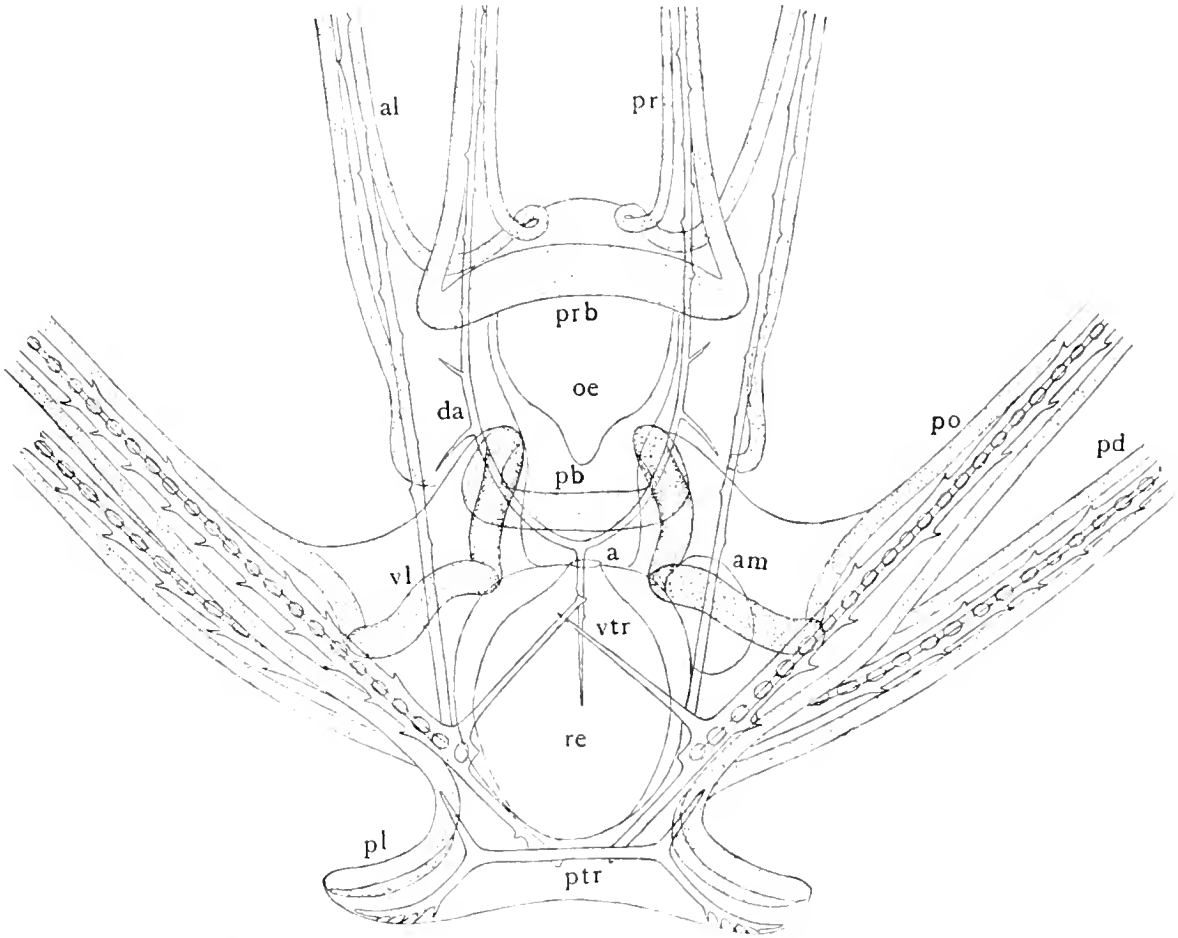


Fig. 26. Larva of *Echinometra lucunter*, 15 days old; ventral view.  $\frac{20}{1}$ . a. anal opening; al. anterolateral arm; am. amnion; da. dorsal arch; oe. mouth; pb. posterior ciliated band; pd. posterodorsal arm; pl. posterolateral process; po. postoral arm; pr. preoral arm; prb. preoral ciliated band; ptr. posterior transverse rod; vl. vibratile lobe; vtr. ventral transverse rod.

some irregularly scattered pigment cells are also found. The stomach is yellow.

In the skeleton the most noteworthy feature is the structure of the posterior transverse rod, which ends in the two usual branches, the lower of which is the longer and set with a series of 4–5 thorns along its lower edge (Fig. 27). The postero-dorsal rod is fenestrated, distinctly curved in the basal part. The dorsal arch has a rather long, simple median process

and two short lateral processes, the lower of which is backwards directed and supports the dorsal lobes. The antero-lateral and preoral rods are more or less thorny.

The young sea-urchin carries the typical embryonal spines on the apical plates; they end in four, smooth thorns. The spines of the normal type are characteristic in having a very long central thorn (Fig. 28). The

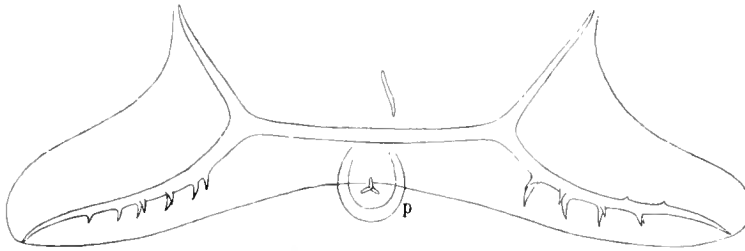


Fig. 27. Posterior transverse rod of the larva of *Echinometra lucunter*;  $^{290}/_1$ . p. the first rudiment of a pedicellaria.

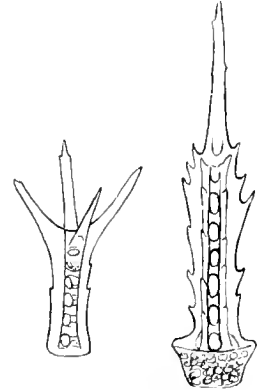


Fig. 28. Spines of the young *Echinometra lucunter*; the left an embryonal spine, the right a spine of the adult type.  $^{225}/_1$ .

Fig. 28.

sphæridia are remarkably spinelike. Of pedicellariæ only the ophicephalous form has appeared even in the oldest of the specimens. For the rest I cannot enter on the study of the postlarval development on this occasion.

### ***Echinometra oblonga* (Blv.)**

Pl. XII, Figs. 2—3.

In the rock ponds at the coast of Hawaii, near Hilo, this species occurs in considerable numbers, together with the other pacific species, *Echinometra Mathæi*. It was found to have its breeding season at the time of my stay there, in April 1915; fertilization was undertaken on the 6th, and proved to be successful. The eggs are very small, opaque. In the course of 4 hours the 16—32 cell-stage was reached, and after about 16 hours the gastrula stage. On account of its opaqueness it forms a poor object for microscopical examination in these young stages of development. On the second day the embryos had assumed the Pluteus shape; for a few days more the larvæ were thriving well, but then the culture degenerated, doubtless because the water was not very good. In spite of repeated attempts I did not succeed in getting another culture, so that information can be given only of the first larval stage.

The shape of the larva (Pl. XII. Figs. 2—3) is somewhat unusual, the upper edge of the anal lobe projecting almost at a right angle from the body, like a lip. The postoral band does not follow the edge of the anal lobe, or rather it has the appearance that it does not do so, the part inside

the band rising over it — in the preserved specimens at least. The suboral cavity is very distinct. The body is short, obliquely truncated as in *Ech. lucunter*. The postoral arms are somewhat unusually long. On the sides of the body the ciliated band reaches far backwards. The pigmentation is not very conspicuous; there is an indication of pigment spots in the point of the arms and scattered red pigment cells over the body.

No figures can be given of the skeleton on account of its having been almost dissolved in the preserved specimens; but I have noticed that the body skeleton forms a complicate basket structure, the recurrent rod being double; it is not very thorny. The postoral rods are fenestrated.

As seen in Pl. XII, Fig. 2 there are still traces of the skeleton preserved, showing the double recurrent rod, but it is insufficient for giving detail figures. The postoral rods have been restored in the figure, but it is distinctly seen in the specimen that they are fenestrated and also that they are somewhat thorny.

### **Echinometra Mathæi** (Blv.).

Fertilization of this species was undertaken repeatedly in April 1915, but never very successfully, only once the young Pluteus-stage being obtained. Moreover, the skeleton has been completely dissolved in the specimens preserved; no more information can therefore be given than what is found in my notebook, namely that the body skeleton forms a basket structure, very thorny, and very oblique, the recurrent rod being considerably shorter than the body rod. — Unfortunately it is not stated in my book, whether the recurrent rod is double as in *E. oblonga* and *lucunter*. The postoral rods are fenestrated. The larva is rather much pigmented, almost opaque.

In view of the fact that de Meijere<sup>1)</sup> and H. Lym. Clark<sup>2)</sup> are inclined to regard *Ech. oblonga* only as an extreme form of *Ech. Mathæi*, while Döderlein<sup>3)</sup> makes it the type of a separate genus (on account of its peculiar triradiate spicules), it is interesting to notice that there appears to be quite a conspicuous difference between the larvæ of the two forms, which is decidedly in favour of their being, at least, distinct species. Even in the first cleavage processes I noticed a marked difference between them, the cleavage cells lying much more closely pressed against one another in *E. oblonga* than in *Mathæi* (while the eggs did not appear to be different in size or color). On account of the incompleteness of this record of

<sup>1)</sup> Siboga-Echinoidea 1901, p. 101.

<sup>2)</sup> Hawaiian a. other Pacific Echini. The Pedinidae . . . and Echinometridæ. Mem. Mus. Comp. Zool. XXXIV. 1912, p. 370.

<sup>3)</sup> Echinoidea d. deutschen Tiefsee-Expedition. p. 233.



their development the question cannot, of course, be regarded as settled; but there is reason to expect that a complete study of their development will show them to be quite distinct.

### ***Echinometra van Brunti* A. Ag.**

Fertilization of this species was tried repeatedly in the beginning of November 1915 at Taboga, Panama, but always with poor success, it being at the end of its breeding season. Some of the embryos reached the young *Pluteus* stage. In the few preserved specimens the skeleton has been dissolved. No remarks about its structure being found in my notebook, I can only state from memory that the body skeleton forms a basket structure, but whether the recurrent rod is double or not, unfortunately, must remain uncertain. The body is very obliquely truncated.

### ***Colobocentrotus atratus* (Linn.)**

Pl. XII, Figs. 4—5.

This species occurs in great numbers on the rocky coasts of Hawaii, near Hilo, always in places exposed to the most violent surf. Fertilization was undertaken on April 4th; the culture proved successful. About the early development stages I have only noticed that gastrulation had taken place at the age of 24 hours and that the young *Pluteus* stage was reached on the second day. The larvæ developed normally for about two weeks, when all died away. New fertilization was then undertaken, but with poor result, it being about the end of its breeding season. Information can thus be given only of the first larval stage, and, moreover, only incomplete, the skeleton having been completely dissolved in all the preserved specimens. (There was no possibility of making drawings from the living specimens).

The shape of the larva in the first stage is quite characteristic on account of the unusual width of the posterior end (Pl. XII, Fig. 5). A sketch made from a living specimen shows that the skeleton passes close to the stomach, the posterior end of the body being thus much broader than the supporting skeletal structure. The body is otherwise short, obliquely truncate as in the *Echinometra* larva. The postoral band has a downward sinuation at each side, which indicates the presence of ciliated lobes; on the sides of the body the vibratile band goes down almost to the posterior end, which fact, combined with the unusual width of the posterior end, indicates the presence of posterolateral processes in the fully formed larva. The postoral arms long, diverging, rather broad (probably somewhat broader than shown in the figure). The suboral cavity is very deep, with a little eleva-

tion in the middle above the stomach. The digestive organs show the unusual feature of a small intestine, well separated from the rectum by a constriction. The pigmentation consists of scattered, red grains; there are no distinct pigment spots in the arm points.

Regarding the skeleton I can only quote from my notebook, that it is very robust, forming a basket structure, "somewhat extra complicate" and strongly thorny. (This probably means that the recurrent rod is double as in other Echinometrids). The postoral rods are fenestrated, the anterolateral rods somewhat stronger than usual. In one of the oldest specimens the posterodorsal rods had begun to form, so that it could be ascertained that also these rods are fenestrated. — That the fully formed larva will prove to have a posterior transverse rod there is not the slightest reason to doubt, but none of the larvæ developed far enough to show it.

It is quite a problem to understand how the young metamorphosing Echinoid can succeed in attaching itself to the rocks, without being washed off or otherwise crushed by the surf. Also the development of the peculiar spines, so well adapted to its unique habits<sup>1</sup>), would be exceedingly interesting to follow.

#### **Heterocentrotus mamillatus** (Klein.)

Fertilization of this species, which was found here and there under stones and coral blocks in the rock ponds near Hilo, Hawaii, was undertaken on the 8th of April. The culture was not very successful, but some specimens developed normally and reached the first Pluteus stage, but not beyond that stage. For want of sufficient material no new culture could be started. The skeleton of the preserved specimens of the larva having been dissolved, no information can be given beyond the observations from the living specimens stated in my notebook.

About the first developmental processes it is only noticed that the embryos were in the gastrula stage 24 hours after fertilization; they were rather opaque. — The young Pluteus is only slightly pigmented, some scattered red grains are found in the body, nothing in the point of the arms. Judging from the preserved specimens the shape of the young Pluteus appears to be much like that of *Colobocentrotus*. The body skeleton forms a complicate basket structure. The postoral rods are fenestrated.

The statement that the basket structure of the body skeleton is "complicate" makes it highly probable that also this species has a double recurrent rod like the other Echinometrids.

<sup>1</sup>) The same habit of living on rocks exposed to the surf was most probably adopted by the extinct Hemicidarid, *Acrocidaris nobilis* Ag. as also by the peculiar extinct Asteroid, *Sphaeraster*.

**Echinopluteus transversus** nova forma.

Pl. XIII, Figs. 1—4.

In the material collected by Mr. Blegvad in the West Indies in the early part of 1911 there was a number of specimens of that most remarkable Echinoid larva (Fig. 29) which I described in 1912 in the "Festschrift für Spengel"<sup>1)</sup> and which I thought must be the larva of *Echinometra lucunter*. That this reference was erroneous I have proved myself by rearing the larva of that Echinoid from the egg through metamorphosis. It therefore still remains an open question to which Echinoid this larva belongs. — Meantime I have found in the plankton samples collected in the Indian Ocean on my Expedition to Siam in 1900 a specimen of a larva

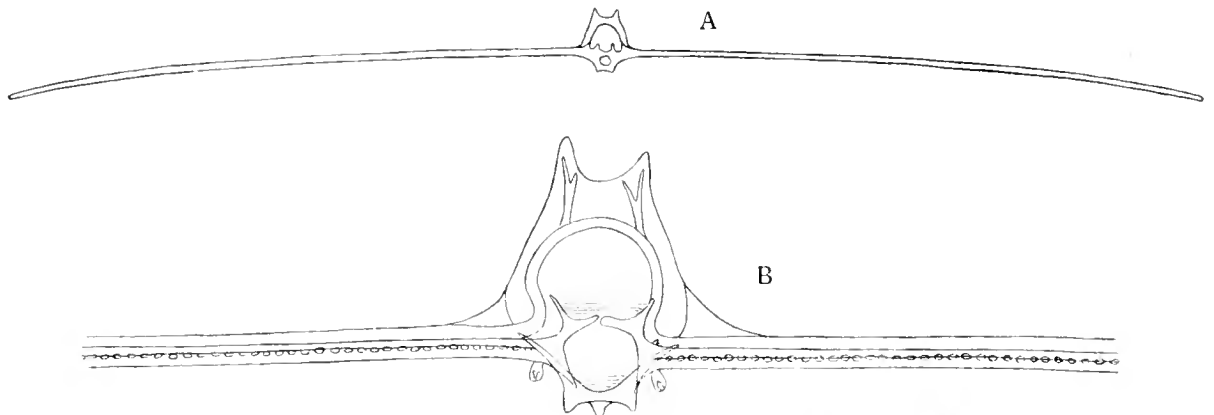


Fig. 29. *Echinopluteus transversus*, species e. A.  $\frac{14}{1}$ , B.  $\frac{65}{1}$ . Figure A shows the excessive length of the postoral arms, which are not even quite complete here, the point being broken in the specimen from which the figure was drawn.

exactly similar to the Westindian form, and another one was taken there in 1914 on my way to the Pacific. Furthermore two related forms were taken in the Gulf of Panama in 1916, and two more were found in the material collected in the West Indies by Mr. Blegvad and Mr. Faye. Thus I have now no less than six different species of this interesting larval form, which I shall designate as *Echinopluteus transversus*. The species described in the paper quoted above is, together with the one from the Indian Ocean, the most specialized of all, the other forms showing more or less primitive features. Still they all have so many characteristic features in common that I have deemed it desirable to keep them together under the same name, even though it may seem very probable that they will prove to belong to different genera, but within the same family, beyond doubt.

This larval type is eminently characteristic through the excessive development of the postoral arms, while the other arms remain undeveloped,

<sup>1)</sup> Th. Mortensen. Über die Larve von *Echinometra lucunter* (L.) (?). Zool. Jahrb. Suppl. XV. 2. Bd. 1912, p. 275—88. Taf. 19—20.

excepting only the antero-lateral arms, which are well developed, though small, in the four first species. The postoral rod is fenestrated, the rudimentary posterodorsal rod is simple. There is a recurrent rod, but no typical basket-structure. The posterior transverse rod has a very peculiar bow-shape. A small, unpaired, posterior process (perhaps a spine of the young sea-urchin) is present in species **e–f**; whether it is present also in the other species remains uncertain. The vibratile band is not strongly developed on the body, in accordance with the reduced state of the arms; there are no vibratile lobes or epaulets. In species **a–d** the preoral lobe has the typical shape; in species **e–f** it bends forwards so as to cover the mouth and the oral area. In the two latter species the esophagus appears to be folded. The stomach is very wide; it has been impossible to distinguish with certainty the rectum and the anal opening.

The postoral arms are directed outwards so as to recall the posterolateral arms of Ophiurid larvæ, to such a degree even that in young stages, where the characteristic skeletal parts of Echinoplutei (dorsal arch, posterior transverse rod) have not yet been formed, it is really very hard to see, whether it is an Echinoid- or an Ophiurid-larva. From the ventral transverse rods, which are more or less transformed, a supplementary transverse rod proceeds, serving for the attachment of an adductor muscle, which (in the species **e–f**) together with a similar muscle on the dorsal side, serves as antagonist to a powerful abductor muscle connecting the ends of the short, widened body rods. By means of this muscular apparatus the long postoral arms can be moved actively and thus apparently serve as an active locomotor organ, besides the usual ciliary movement of the vibratile bands. The immense length of the postoral arms together with the active swimming movements, which the strong development of the musculature in the species **e** and **f** indicate almost certainly to take place, make this larva one of the organisms most highly adapted to pelagic life.

**Species a.** (Pl. XIII. Fig. 2). The single, well preserved, specimen of this species, which was found in a plankton sample from the surface taken by Mr. Blegvad in the West Indian Sea, at 18°59' N. 65°05' W. (a little to the North of the Virgin Islands), (I/III. 1911), is a young one, not yet having the hydrocoel distinctly differentiated. The postoral arms are ca. 1.5 mm long, or nearly 7 times the length of the body (the point is broken, so that the total length remains unknown, but it is not likely to be much more than the preserved part). The antero-lateral arms are well developed, a little more than body length. They are somewhat widened at the base and with a slight widening at the point. The preoral ciliated band is well developed and forms a beautiful curve; the postoral band forms a simple

bow and passes nearly straight on to the postoral arms<sup>1</sup>). Along the dorsal side the band goes almost straight down to the base of the postoral arms, where it then makes an almost right angle before passing out along the arms. There is no indication of ciliated lobes or epaulets. The oral area is very large, the large mouth opening lying free, contrary to what obtains in the species *e* and *f*, where it is covered by the preoral lobe. The rectum I have not been able to distinguish with certainty, but it seems that the

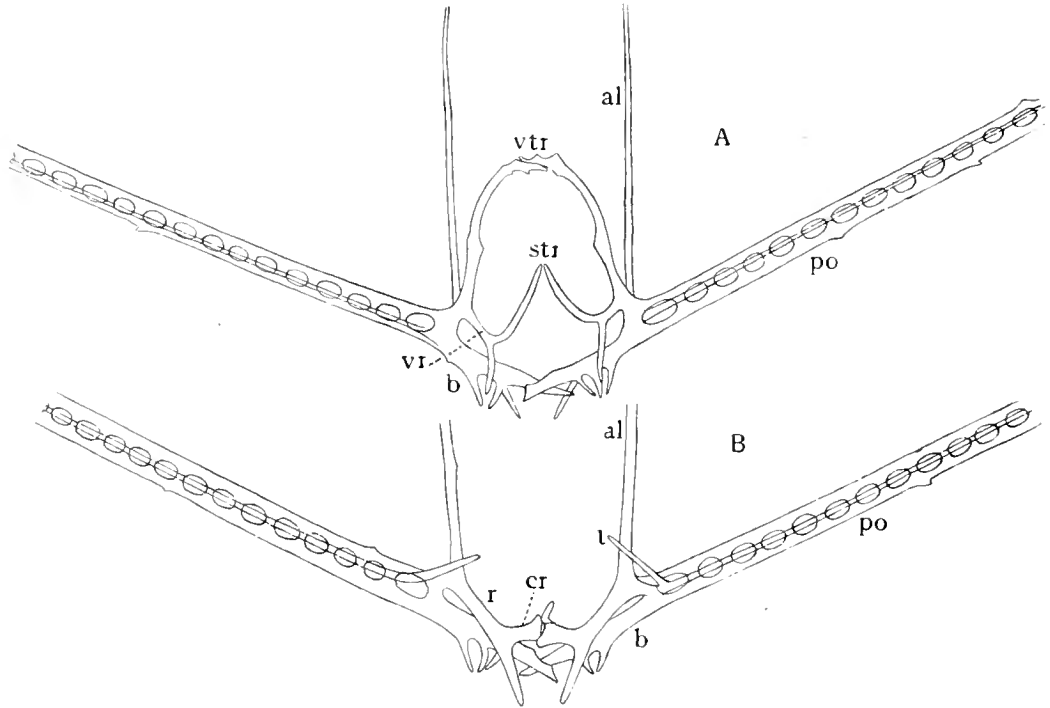


Fig. 30. Skeleton of *Echinopluteus transversus*, species *a*. A. from the ventral, B. from the dorsal side. <sup>280</sup>/<sub>1</sub>. al. anterolateral rod; b. body rod; cr. connecting rod; po. postoral rod; r. recurrent rod; str. supplementary transverse rod; t. thorn; vr. ventral recurrent rod; vtr. ventral transverse rod.

anal opening lies in the posterior part of the body, below the pair of supplementary transverse rods lying here over the middle of the stomach. — No trace of pigmentation is seen.

The skeleton (Fig. 30). The postoral rods are of the usual fenestrated type, with rather large holes and with some few, small thorns along both edges. The body rod is short, with some irregular thorns along its outer edge, and apparently with a simple, not widened point, showing no special adaptation for the attachment of the abductor muscle. The ventral

<sup>1</sup>) In the preserved specimen the postoral band is even more straight than in the figure, passing somewhat below the points of the ventral transverse rods. That this is due to contraction on preservation is evident, the natural position of the band being above the point of the ventral transverse rods; in that position it is also seen in species *c* and *d*. I have therefore not hesitated in showing the band in its natural position in the figure.



transverse rods are directed nearly straight upwards, bending inwards at the point, so that they meet and together form an elegant arch; they are slightly widened and serrated at the point. From their base issues a backward prolongation, a "ventral recurrent rod", which soon bifurcates, each sending one branch, the "supplementary transverse rod", upwards, where they join over the middle of the stomach, the other branch going straight downwards, crossing the body rod. Both these branches are simple rods in this species, while in the other species they undergo a remarkable specialisation, species **b** being, however, peculiar in this regard. The antero-lateral rods are well developed, simple, with few small thorns irregularly disposed. The recurrent rod is well developed, smooth, slightly longer than the body rod; from about its middle a short, simple, somewhat widened transverse rod proceeds recalling the transverse rod of an *Ophiopluteus*, with which it is, however, not to be compared, of course; it is homologous with the connecting rod of Echinoid larvæ with a typical basket structure, as e. g. the larvæ of *Astropyga* or *Tripneustes*. At the base of the postoral rod, close outside the point of issue of the antero-lateral rod, a rather long, simple thorn is found. The postero-dorsal rod, the posterior transverse rod and the dorsal arch have not yet appeared.

There is some probability that the "*Auricularia paradoxa*" (from 0°4' N, 16°6' W) which I described in the "Echinodermlarven der Plankton-Expedition" (p. 21 Taf. I, Fig. 7) really is a decalcified specimen of this species. It may seem strange that an Echinoid-larva should have been mistaken for an *Auricularia*; but a glance at the figure will show that there is really nothing which could indicate that it might be an Echinoid-larva, the shape being just as unusual for an *Echinopluteus* as it is for an *Auricularia*; as long as the *Echinopluteus transversus* was unknown, hardly anybody could have fancied that this might be an Echinoid-larva. Now it is easy to see that a form like *Echinopluteus transversus*, species **a**, when decalcified and otherwise not too well preserved — as was the case with that larva — would get very much the same appearance as the "*Auricularia paradoxa*". The complicated folds of the vibratile band, of course, do not very well suit the rather simple course of the band in the single specimen of the present species of *Echinopluteus transversus*; as, however, this is a younger stage, it is quite conceivable that the band may be more developed in the older stages of this larva. — The species **c** would hardly come into consideration, the band being simple there also in a further advanced stage, so that it could certainly not give rise to the complicated folds of "*Auricularia paradoxa*" when decalcified; the postoral arms of this species are also much longer.

Although still somewhat problematical I have deemed it well worth

while to offer this suggestion as to the true nature of the rather mysterious *Auricularia paradoxa*. For the definite solution of the problem direct observations of the living larvæ or, at least, considerably more material than at present available will be necessary.

Species **b**. A single specimen of this species, which is, evidently, closely related to species **a**, was found in a plankton sample from the Gulf of Panama, at Taboga, (January 1916). It is in a poor state of pre-

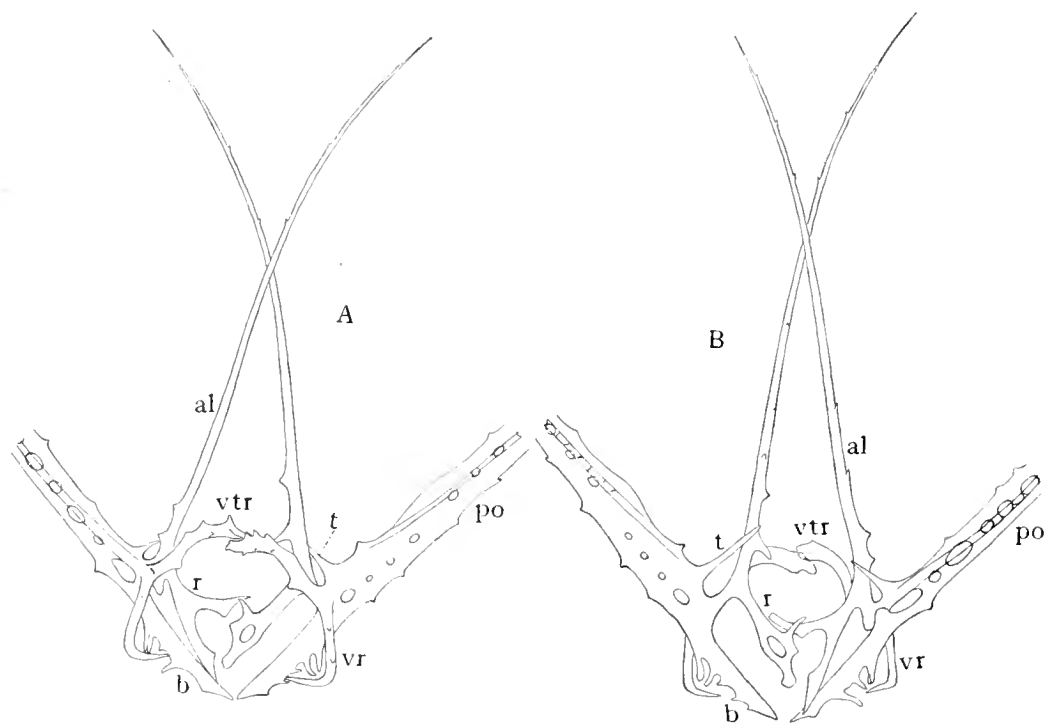


Fig. 31. Skeleton of *Echinopluteus transversus*, species **b**. A. From the ventral, B. from the dorsal side. <sup>290</sup>/<sub>1</sub>. Letters as in fig. 30.

servation so that only the skeleton can be figured and described; but there is no reason to expect that it would show noteworthy differences from the species **a** in regard to the general shape of the larval body. Apparently it differs markedly in shape from species **a**, the postoral arms being nearly erect; this, however, evidently is due only to muscular contraction (comp. species **c**, Pl. XIII, Fig. 1).

The skeleton (Fig. 31), although in its main features like that of species **a**, shows some very characteristic differences from that species. The ventral transverse rods form an arch as in that species, but are not so high and somewhat more widened and thorny at the end. The ventral recurrent rods are especially characteristic, being hookshaped, not bifurcating at the point, with one or two small thorns along the sides. They

are directed obliquely outwards, projecting considerably from the body; it seems fairly certain that a muscle is passing between the ends of the hooks. The body rods are simple, with irregular thorns along their outer edge, not widened in the point, which is apparently not specially adapted to the attachment of an abductor muscle. The postoral rods are in the main as in species **a**; only the left being slightly abnormal in its basal part. Both these rods are broken so that their length cannot be ascertained. The anterolateral rods are well developed, slightly thorny. The recurrent rods are somewhat irregular; the right one bifurcates, one branch going medially, the other backwards, reaching the end of the body rod; the left ends with a widening in which a rather large hole. A somewhat long thorn proceeds from the base of the postoral rods, just outside the point of issue of the anterolateral rod. Posterodorsal rods, dorsal arch and posterior transverse rod are not yet developed.

Species **c**. (Pl. XIII. Fig. 1). One beautifully preserved specimen of this larva was found in a plankton sample from Christiansted, St. Cruz, West Indies, taken on the 16. VI. 1915 by Mr. H. Faye.

In its main features it agrees with species **a**, but the postoral arms are very much longer, no less than 12 times the body length; moreover the point is broken off, so that they must be rather considerably longer. The preserved part is 3 mm long. The specimen has been preserved in such a state of contraction of the adductor muscle, that the arms are directed almost straight upwards, which gives the specimen an aspect very different from that of the other species. That this is, however, really due only to muscular contraction is beyond doubt, as is evident only from a comparison with the two related species, **b**. and **d**., from the Gulf of Panama, of which species **b** has the arms in the same upright position, while the other, species **d**, has them horizontally directed. The contraction of the muscle connecting the two body rods (which is quite distinctly seen in the specimen) would give the postoral rods the usual horizontal position. The anterolateral arms are distinct but considerably shorter than in species **a**, hardly more than one fourth of the body length, while in the latter species they are somewhat more than body length. The preoral band is well developed, though not so strongly curved as in species **a**. The postoral band has a concavity in the middle and makes a rather deep downwards bend before passing on to the postoral arms; however, this configuration may probably be due only to the upward direction of the postoral arms; it seems certain that on the postoral arms being horizontally directed the postoral band must assume the same simple shape as in species **a** and probably also be lowered down to the level of the

ventral transverse rods, while in the present state of preservation it passes at a distance above these rods. The band along the dorsal side is straight and simple; there is no indication of vibratile lobes or epaulets. No indication of pigmentation is seen. The oral area is very wide as in species **a**, the mouth opening remaining uncovered. The rectum and anal opening are not to be distinguished. Nothing can be discerned of the enterocoel or hydrocoel.

The skeleton (Fig. 32). The postoral rods are of the same character as

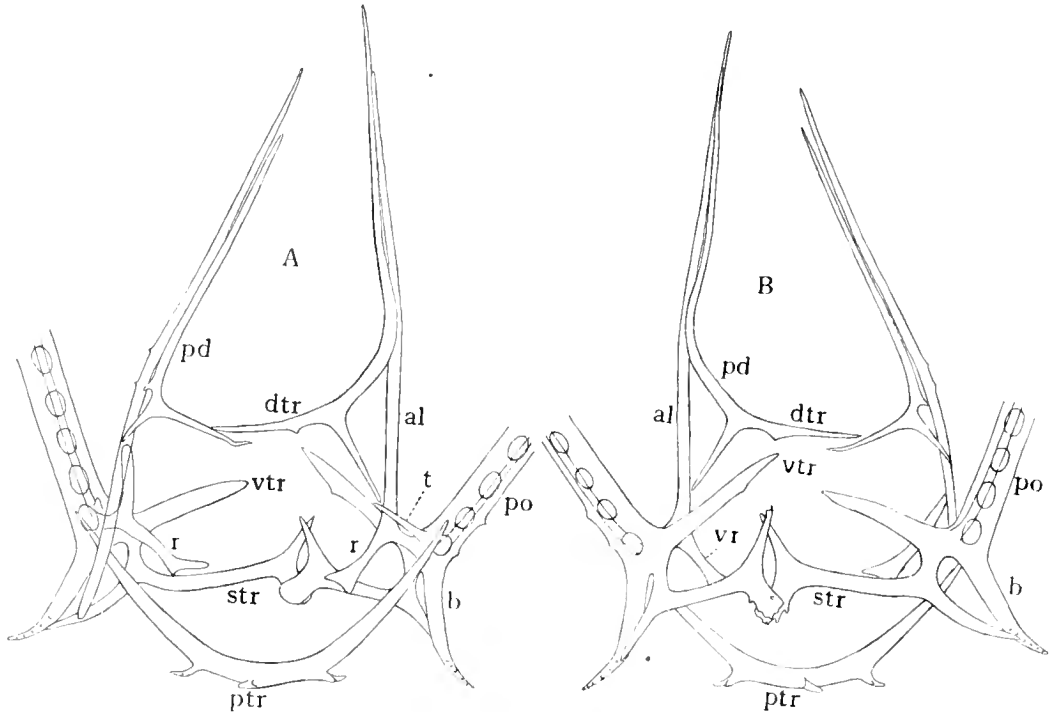


Fig. 32. Skeleton of *Echinopluteus transversus*, species **c**. A. from the dorsal, B. from the ventral side.  $\frac{290}{\mu}$ . Letters as in fig. 30; further: dtr. dorsal transverse rod; pd. postero-dorsal rod; ptr. posterior transverse rod.

The left anterolateral rod is broken and pushed some way backwards (Fig. A).

in species **a**, fenestrated, with rather large holes; they are set with some few small thorns in the lower part, entirely smooth in the outer part. The body rod is short, smooth; the point bent a little outwards, apparently somewhat widened: it appears to be finely fenestrated, or perhaps only irregularly serrate — this cannot be definitely ascertained in the side view presented by the single specimen at hand. But, at any rate, it is clear that there is some adaptation for the attachment of the abductor muscle. The ventral transverse rod is short, robust, with a simple, straight point. The ventral recurrent rod is short, bifurcating, one branch going along with the body rod and perhaps uniting with it at the point — this cannot be definitely ascertained, but it looks so — the other branch, the sup-

plementary transverse rod, proceeding over the stomach, where it meets the corresponding rod from the other side in the midline. The end of this supplementary transverse rod again bifurcates, one branch going upwards, the other downwards; the latter branch is somewhat widened, flat, with some few thorns along the edge, whereas the upwards directed branch appears to be simple or at most carrying a single small thorn. To this branch the ventral adductor muscle is attached in the species **e** and **f**; it seems beyond doubt that there must also be such adductor muscle attached to these rods in the present species, but on account of its excessive contraction it is impossible to see it. The anterolateral rods are fairly robust, simple, or with a very few small thorns. Just outside the point of issue of the anterolateral rod a fairly long thorn proceeds from the postoral rod. The recurrent rod is short, simple, with a small medially directed branch at the end. The posterodorsal rod is fairly well developed, almost as long as the anterolateral rod; it is simple and smooth; at the base it is somewhat curved, with a well developed medially directed process, the dorsal transverse rod, and another downwards directed process. Its whole shape is somewhat unusual for a posterodorsal rod, recalling to some degree an irregularly shaped dorsal arch; but I have hardly any doubt that it is really the posterodorsal rod, — especially because it is a paired structure — the dorsal arch not having made its appearance as yet. However, attention must be called to the fact that in species **d**, which is evidently in the same stage of development, the dorsal arch is well developed, while there are no posterodorsal rods. Full certainty regarding the true interpretation of these skeletal parts can hardly be acquired from the scanty material available at present. — The posterior transverse rod is bow-shaped, with a few small thorns along the posterior edge. The ends of this rod appear to be simple, not widened or fenestrated as in species **e** and **f**.

**Species d.** One specimen was found in a plankton sample taken at Taboga, Gulf of Panama, in January 1916. The state of preservation is not good enough to allow giving a full figure of it, especially because the preoral lobe is destroyed. But it is evident that this larva resembles the species **c** very closely in the shape of the body. The postoral arms are horizontally directed, thus giving the larva a very different aspect from the specimen of species **c** shown in Pl. XIII, Fig. 1; but this depends, as stated above, only on the state of contraction of the muscles moving these arms. The arms are broken, the remaining part being 7 times the body length; that they must be really a good deal longer is evident, but whether as long as in species **c** cannot be ascertained. The anterolateral arms are

well developed, longer than in species **c**, nearly as long as the body. The postoral band makes a simple curve above the ventral transverse rods, apparently rather unusually broad.

The skeleton (Fig. 33). The postoral rods are like those of the species **a—c**, with few small thorns and fairly large holes. The body rod is short,

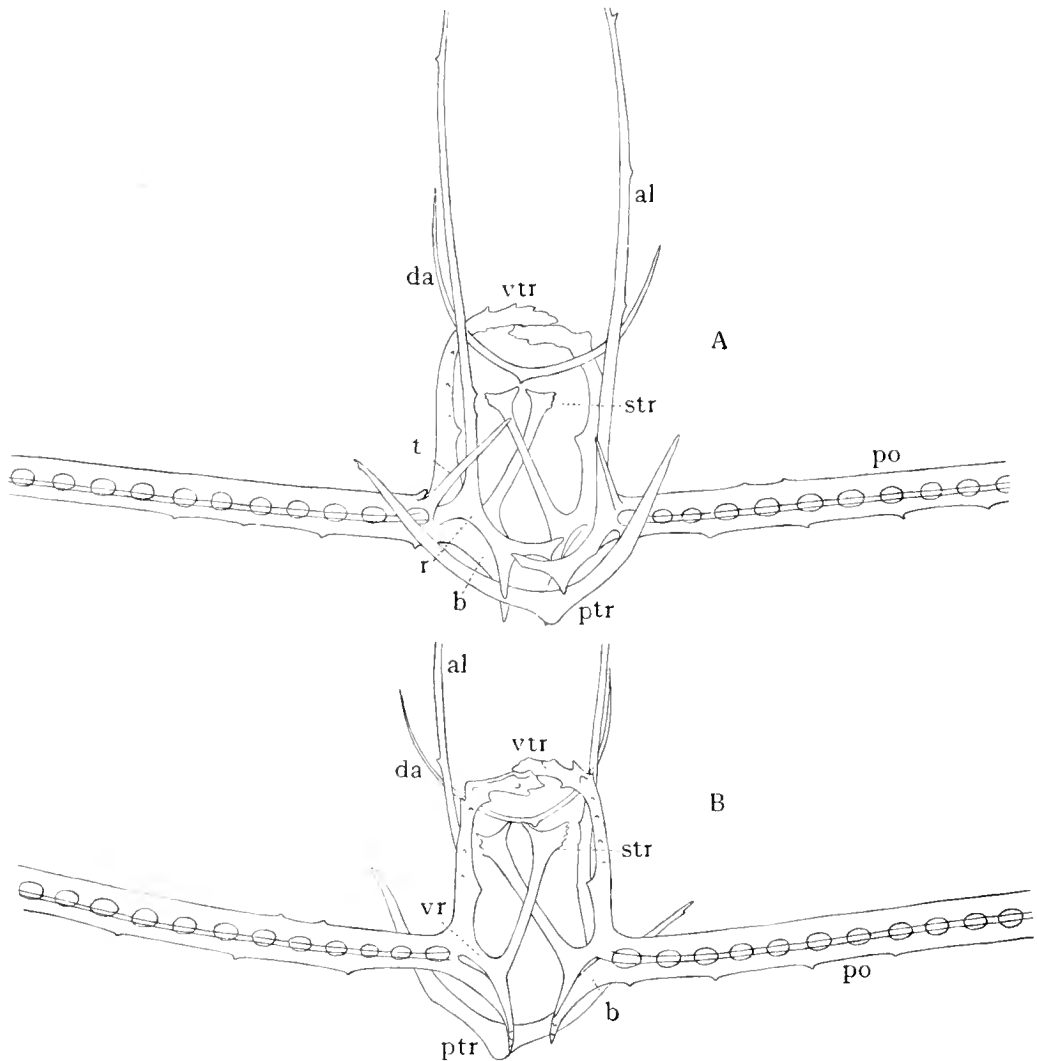


Fig. 33. Skeleton of *Echinopluteus transversus*, species **d**. A. from the dorsal, B. from the ventral side. <sup>290</sup>/<sub>1</sub>. Letters as in fig. 30; further: da. dorsal arch; ptr. posterior transverse rod.

a little curved at the point, which appears to be somewhat widened, probably fenestrated, and somewhat specially adapted to the attachment of the abductor muscle. The ventral transverse rods are developed so as to form a high, beautiful arch; the point is bent inwards, so that they overlap one another in the middle. They are somewhat thorny, a little widened at the base and towards the point. From the ventral recurrent

rod a large, upwards directed supplementary transverse rod proceeds; in the specimen they are broken at their base, but it appears that their position must be as shown in the figure 33, crossing one another over the middle of the stomach. The point is widened and has an indication of the same structure as in species *c* and the species *e-f*, viz. a simple, outer process and a widened, somewhat serrate inner process. (On account of the crossing of the rods the latter branch here becomes the outer one). By this position of the rods it is hard to see how the adductor muscle could be attached here (perhaps to the outer side of the simple process, not to the inner side as in the other species (?); the muscle cannot be observed in the specimen). Another branch of the ventral recurrent rod goes downwards, where it meets (and joins?) the end of the body rod. The anterolateral rods are well developed, slender, with few small thorns. Just outside their base a long simple thorn proceeds from the postoral rod. The recurrent rod is fairly long, smooth, bifurcating at the end. The posterior transverse rod is simple, bowshaped, with a small prominence in the middle of the posterior edge, otherwise smooth; the ends are not widened. Posterodorsal rods have not been formed, but there is a well developed, quite normally shaped dorsal arch; its branches are simple and smooth; there is a small median backward prominence, as usually found in the dorsal arch.

**Species e.** This is the species which was described in the paper quoted above. Several specimens were taken by Mr. Blegvad off the South Coast of Haiti and off the West Coast of Portorico in the end of January and the beginning of February 1911. Furthermore some specimens were found in plankton samples taken by Mr. P. Kramp off Madeira (32°10' N. 17°20' W.; 30/ N. 1911) and off the Canaries (27°10' N. 21°53' W.; 3/ XI. 1911) and in the same neighbourhood (31°22' N., 14°57' W., and 28°13' N. 20°10' W.) by Mr. H. Fogh in October 1912 (on the 16th and 22nd). A pair of specimens were also taken by Mr. H. Faye in the harbour of Christiansted, St. Cruz, on the 9th and 16th of June 1915. The larva is thus seen to occur nearly all the year round.

Referring to the paper quoted I may give here only a pair of textfigures (Fig. 29 on p. 78) in order to show the general appearance of this extraordinary larva, which, with its extremely long horizontally directed, slightly downwards curved postoral arms, in fact reminds one of a rope-dancer with an immense balancer. In the specimen with the arms best preserved they are 12 mm long, no less than 21 times the body length, and still the point is broken off. The body has the shape of a truncated four-sided pyramid. The postoral arms alone are developed; a pair of

short processes from the anterior end of the body cannot really be regarded as antero-lateral arms, partly because the irregular rods by which they are supported cannot be homologous with the anterolateral rods, partly because they appear not to be bordered by the vibratile band. The post-

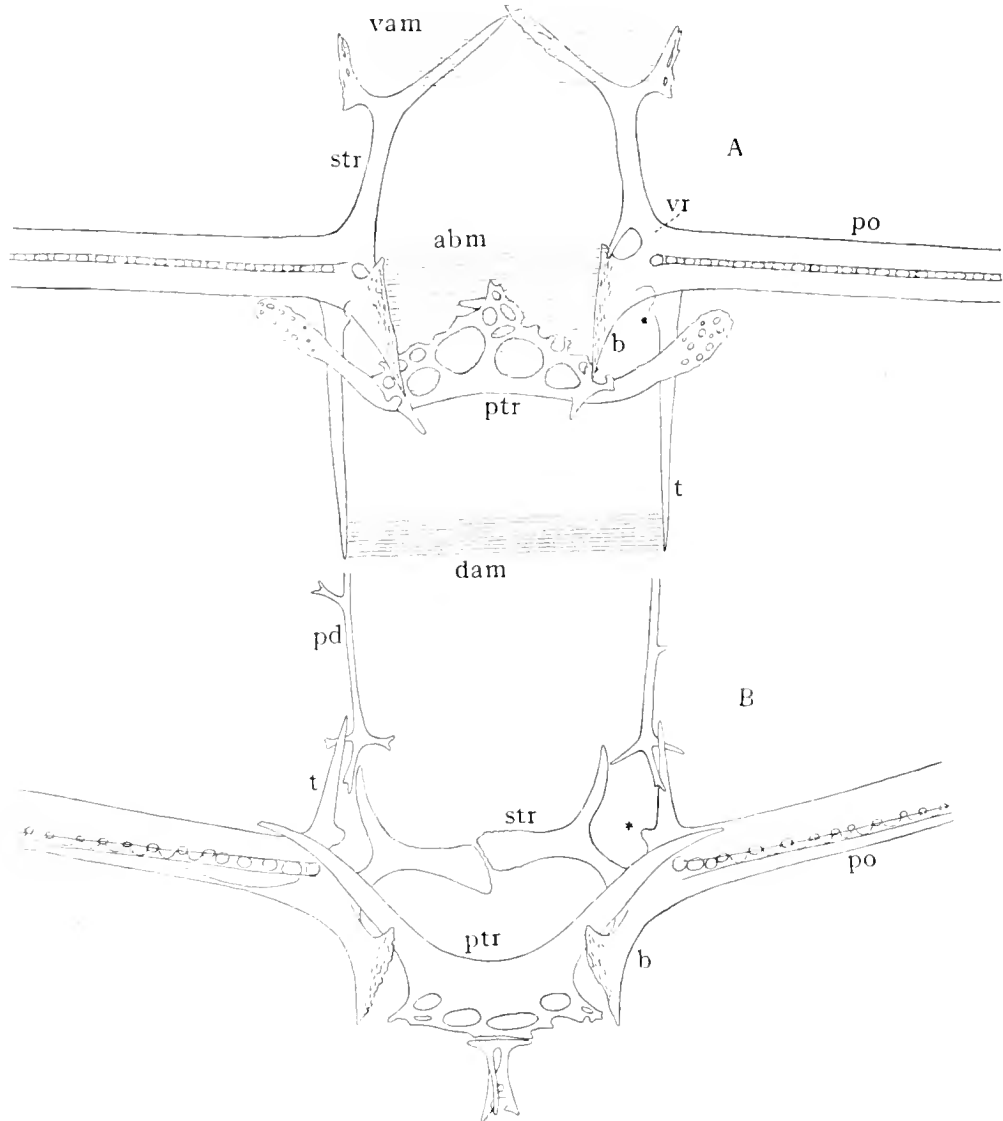


Fig. 34. Skeleton of *Echinopluteus transversus*, species e. A. seen from behind; B. from the dorsal side.  $\frac{180}{1}$ . abm. abductor muscle. b. body rod; dam. dorsal adductor muscle; pd. postrodorsal rod; po. postoral rod; ptr. posterior transverse rod; str. supplementary transverse rod; vam. ventral adductor muscle; t. thorn; \* rudimentary anterolateral rod.

oral band makes an elegant curve or rather half circle round the whole anal lobe, and then makes a nearly right angle in passing out along the postoral arms. Along the dorsal side it makes a pair of folds. The preoral band is difficult to observe; it passes close along the postoral band, the



preoral lobe bending downwards over the oral area so as to cover the mouth opening completely, the entrance to the mouth being the narrow slit left between the anal area and the projecting frontal area. The esophagus is short, somewhat folded (comp. Species *f*, Pl. XIII. Figs. 3—4); the stomach is very large, filling almost the whole body; the rectum appears to be small and short, situated in the lower part of the body, apparently within the space limited by the posterior and the supplementary ventral transverse rods. I have, however, been unable to make out its shape quite distinctly, and likewise the anal opening could not be located. The development of the enterocoel and hydrocoel could not be made out; a single specimen in a younger stage is, unfortunately, in too poor a condition for showing anything of the enterocoel or hydrocoel formation; it does, however, show that the oral lobe is quite narrow and somewhat elongate, so that from the beginning the mouth-opening is free, the oral area being not yet covered up by the preoral part of the body. This then takes place in a somewhat later stage, though still rather early, being completed already before metamorphosis is beginning (Fig. 29).

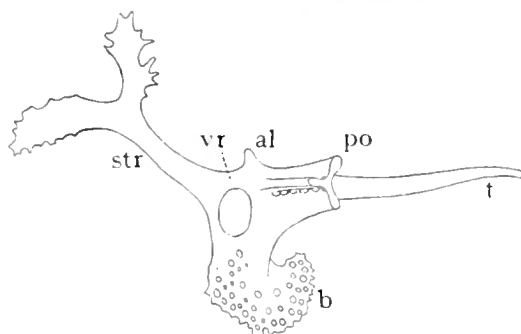


Fig. 35. Half of the body skeleton of *Echinopluteus transversus*, species *e*, seen from the side; showing the widening of the body rod (b.). The postoral rod (po.) has been cut close to its base. al. the rudimentary anterolateral rod; t. the thorn to the point of which the dorsal adductor muscle is attached; str. supplementary ventral transverse rod. vr. ventral recurrent rod. <sup>180</sup>/<sub>1</sub>.

In the course of the proceeding metamorphosis the body becomes quite oblique, the whole anterior part being pushed over to the right side, as seen in the figures of species *f*.

The skeleton (Figs. 34—35). The postoral rods differ markedly from those of species *a—d* in having only very small holes, the unfenestrated part of the component rods being considerably larger. They are entirely smooth. The body rod is quite short, at the point widened into a large fenestrated plate (Fig. 35), to which the abductor muscle is attached. Seen in ventral or dorsal view this plate appears as a thin, slightly outwards curving rod; seen from the hind end of the body (Fig. 34 A) it is found to be directed somewhat towards the dorsal side. The ventral transverse rods are entirely lacking; the ventral recurrent rod is quite short. The supplementary ventral transverse rod is highly developed, dividing in the end into two branches, one upwards directed apparently having the shape of a simple thorn, but really, as may be seen in side view, having the shape of a small, mostly fenestrated plate, to which the ventral

adductor muscle is attached, the other medially directed, having the shape of a thin plate with serrate edges, but otherwise unfenestrated. No muscle is attached to this plate. The posteriorly directed branch from the ventral recurrent rod coalesces with the end plate of the body rod. (In the paper referred to above the supplementary transverse rod was regarded as the true ventral transverse rod; this was the only possible explanation at that time, before the more primitive forms of this larval type were known. The presence of both the supplementary and the true ventral transverse rods in the species **a—d** leaves no doubt that the interpretation of these skeletal parts in species **e** (and **f**) given here is the correct one). The anterolateral rods are quite rudimentary. As will be remembered there is in the species **a—d** just outside the base of the anterolateral rod a long thorn proceeding from the postoral rod. In the present species there is only a thorn at the corresponding place, but generally a distinct knob is seen on the proximal side of the base of this thorn. Very probably this knob is all that remains of the anterolateral rod, the thorn itself corresponding to the thorn outside the anterolateral rod in the other species. The point of this thorn serves for attachment of the dorsal adductor muscle. If it could be proved that this thorn also in the other species serves for attachment of this muscle, the interpretation here suggested would be definitely proved to be correct; unfortunately I have been unable to ascertain the presence of such dorsal adductor muscle in any of the four other species, so that this point must remain unsettled for the present. — The postero-dorsal rods are simple, somewhat irregularly thorny. The posterior transverse rod is situated somewhat dorsally, not in the middle line (Fig. 34 A). It is a most elegantly shaped piece of calcareous structure, a gracefully curved bow, the ends of which are slightly widened and fenestrated. In the middle part it bends over ventrally, forming a triangular fenestrated plate, which covers the abductor muscle. At its posterior side a small separate skeletal part is situated resembling a small young spine (also recalling the posterior process of the Spatangoid larvæ, with which it can, however, scarcely be homologous, the latter being in direct connection with the posterior transverse rod and an outgrowth therefrom, while in the present case it is a separate piece, independent of the posterior transverse rod). Whether a dorsal arch is present or not is hardly ascertainable. The upper part of the body contains some irregular branched rods supporting the processes at the anterior edge, which look like but are not really rudimentary anterolateral or preoral arms. It is quite possible that one of these rods really represents the dorsal arch (see Pl. XIII, Fig. 4 of species **f**); that it is in a nearly vertical position may not be a serious objection to regarding it as homologous with the dorsal arch of other Echinoid

larvæ, where it is always found in a horizontal position; but the fact that there is a piece exactly corresponding to it on the ventral side makes the homology more doubtful. The question must remain unsettled for the present.

Species **f** (Pl. XIII, Figs. 3—1, Textfigure 36). One specimen was taken off Minicoy (Maldive Islands; 73° E. 7° N.; 26/IV. 1900), another in the Bay of Bengal (89° E. 6° N.; 5/I. 1911). Both specimens are in beginning metamorphosis; in both of them the postoral arms are broken, so that their length cannot be ascertained; the remaining piece of one of them is

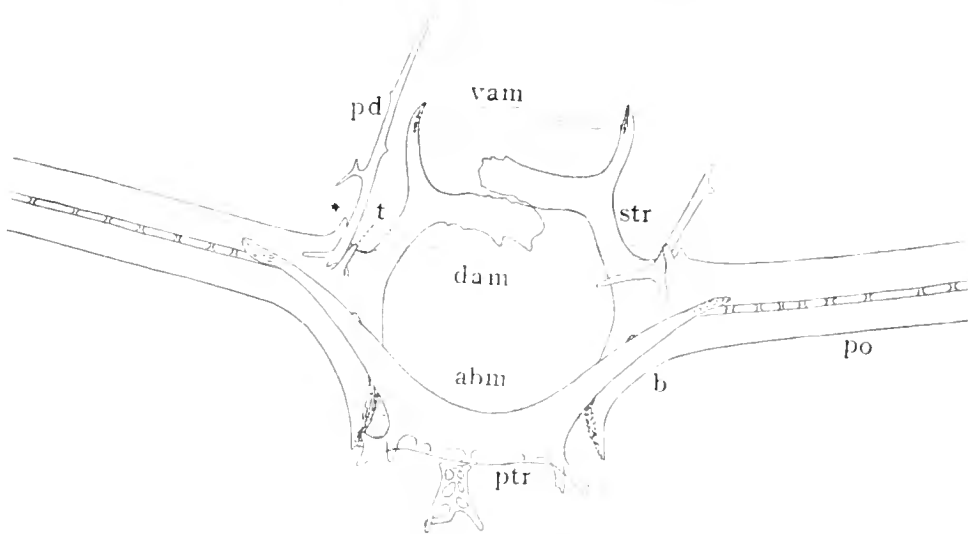


Fig. 36. Skeleton of *Echinopluteus transversus*, species **f**. Seen from the dorsal side.  $\frac{100}{4}$ . Letters as in Fig. 34.

6 mm long. There is evidently no reason to doubt that they will prove to be of about the same length as in species **e**. The two species are so very closely alike that it is hardly possible from the scanty material available of the species from the Indian Ocean to point out specific differences. That they are, however, really different species is evident from the fact that there are no species of regular Echinoids known to occur both in the West Indian Sea and the Indian Ocean. To enter on a detailed description of the present species seems entirely unnecessary; reference to the figures must be sufficient.

The interesting problem to which Echinoids these remarkable larvæ must be referred now needs some discussion. As mentioned above I came to the result, when describing the first of these larvæ, the species **e**, that it was probably the larva of *Echinometra lucunter*. The fact that it has in the metamorphosis-stages ophicephalous pedicellariæ of the type

found in the regular Echini at once excludes both the Spatangoids, the Clypeastroids and the Cidarids, the two former having quite another type of ophicephalous pedicellariæ, the latter being entirely devoid of that type of pedicellariæ. Reviewing the regular Echini, other than Cidarids, occurring in the West Indies, it seemed evident that *Echinometra lucunter* was the only form that could come into consideration, taking for granted that only littoral forms could come into regard when seeking for the parental origin of these larvæ, which were found to occur in fairly good numbers in the littoral waters. The premises were apparently quite correct. Nevertheless the conclusion was wrong. It is not the larva of *Echinometra lucunter*; that larva, reared from the egg through metamorphosis, as described and figured in the present work (p. 71; Pl. I, Figs. 1—2) has quite the typical shape of Echinoid larvæ. — There was at that time also some uncertainty regarding the larva of *Diadema antillarum*, it being only from inference concluded that the *Diadema*-larva would be found to resemble the *Echinopluteus Mülleri*, viz. that larva from the Mediterranean which has been, though without sufficient evidence, referred to *Centrostephanus longispinus*, a near relative of *Diadema*. Although the development of *Diadema* is still only incompletely known, the shape of the young larva, reared by the present author (see above, p. 25

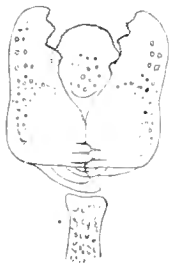


Fig. 37. Ophicephalous pedicellaria of *Echinopluteus transversus*, species e.  
250/1.

Pl. V, Fig. 5) gives sufficient evidence that it has nothing with the *Echinopluteus transversus* to do, and *Diadema* is then also really out of question as the parent of this larva. There must therefore be something wrong in the premises, either so that the type of ophicephalous pedicellariæ found in the larva may be found also in other forms than the regular Echini, save the Cidarids, or that the larvæ may belong to deep-sea forms. Regarding the latter eventuality I would say that — although it can scarcely be doubted any more that some deep-sea Echinoids have true pelagic larvæ — the fact that two species of this larval type were found near the island of Taboga in the inner part of the Gulf of Panama, very far from the deep sea, decidedly speaks against the suggestion that the larvæ might belong to deep-sea forms.

The ophicephalous pedicellariæ (Fig. 37) are decidedly of the type known to occur only in the regular Echinoids. Of these *Arbacia*, *Diadema*, *Tripneustes*, *Lytechinus* and *Echinometra* are all excluded, their larvæ being known more or less completely. The fact that there are two species of larvæ from the Gulf of Panama very closely related to two other species from the Westindies would seem to preclude the idea of taking forms like *Salenia*, *Coelopleurus*, *Podocidarid*, or any of the Echinothurids or the

Aspidodiadematids into consideration. But then no other regular Echinoids are left, and we are forced to assume the possibility that ophicephalous pedicellariæ of the shape occurring in these larvæ may perhaps occur as a sort of embryonal organs, corresponding to the embryonal spines of young regular Echinoids, in young, just metamorphosed urchins, being very soon lost, like the embryonal spines. If that were the case, also Cidarids, Clypeastroids, Echinoneids and Spatangoids would come into consideration. Of the Clypeastroids so many different larvæ are known from previous researches or described here, all being of a very uniform type, that it is exceedingly improbable that the *Echinopluteus transversus* could belong to that family. Of the Echinoneids there are not sufficient forms known to account for the presence of two species of larvæ in the Gulf of Panama closely related to two West-Indian species. If the larvæ species **a** and **c** were really only one species in different stages of development, and in the same way species **b** and **d** only one species, we would have a species of *Rhyncholampas* (*Cassitululus*) corresponding to each of them, and then species **e** and **f** might be referred to *Echinoneus*, the West-Indian species of which is — according to H. L. Clark — identical with the indopacific *Echinoneus cyclostomus*. This would also account well for the fact that the larvæ **e** and **f** are so similar that they seem hardly distinguishable. But I fail to see how the species **a** and **c** or **b** and **d** could possibly be the same species. That would require a so remarkable transformation of the different skeletal parts that it is hardly conceivable. It would not consist in the resorption of some parts and new formation of others, as is the case in so many Echinoid larvæ on their passing from the first to the second larval stage; but it would be a real and complete transformation of the same skeletal parts, especially the body rod, the ventral and supplementary transverse rod, and even in the course of very short time, the specimen of species **c** being only in a very slightly more advanced stage of development than that of species **a**, as is also the case with the specimen of species **d** in comparison with that of species **b**. The idea of the identity of species **a** and **c**, or of species **b** and **d** then evidently must be dropped, and also the suggestion that these "species" might represent only individual variations of one species would seem equally absurd. — Against the idea that these larvæ might belong to *Echinoneus* and *Rhyncholampas* the fact also speaks that the larva of *Oligopodia* (*Echinobrissus*) *recens* is of the type of the Clypeastroid larvæ (comp. below), so that it is highly improbable that the closely related *Rhyncholampas* should have a larval form so entirely different.

That the *Echinopluteus transversus* might belong to some Spatangoid is by no means more probable. All the Spatangoid larvæ known belong to

the well known type characterized by the presence of an unpaired posterior process, and as we now know the larvæ of the genera *Spatangus*, *Echinocardium*, *Moira*, *Brissus*, *Brissopsis* and *Meoma* it is certainly not unreasonable to conclude that this larval type will be found in all those Spatangoids that have typical pelagic larvæ. (*Brisaster lalifrons* and *fragilis* most probably have no pelagic larvæ, their eggs being large and rich in yolk). It is true, we do not know the larva of any of the Palæopneustidæ or of the Meridosternata. But these again would seem to be out of question, because none of these occur in the Gulf of Panama which might account for the two larval species occurring there.

Then the Cidaridæ alone remain. Of these there are, at least, forms enough to account for the different species of the larvæ, also those of the Gulf of Panama, although there is only one strictly littoral species there, *Eucidaris Thouarsii*; but the *Cidaris panamensis*, with a known bathymetrical range of 66—112 fathoms occurs at the coast of Columbia and might thus far very well come into consideration when looking for the parental origin of the second of the larvæ found in the Gulf of Panama. Moreover, the young stage of the larva of *Eucidaris Thouarsii* described above (p. 22, Pl.V. Fig. 2) really suggests a larval shape like that of *Echinopluteus transversus*. There are, however, some great difficulties in referring these larvæ to Cidarids. One is that the larva of *Cidaris cidaris* (*Doricidaris papillata*), reared by Prouho, is of the typical Echinopluteus shape, not in the least recalling the *Echinopluteus transversus*. It is also, a priori, very improbable that the most primitive of all Echinoids should have one of the most specialized and transformed larval types. And then, of course, the ophicephalous pedicellariæ are the chief difficulty. It is, no doubt, possible that such may occur on the newly metamorphosed Cidarid, but are lost very soon. But nobody has found them there as yet. I have examined some young specimens of *Eucidaris Thouarsii*, only 3—4 mm in diameter, but there was no trace of ophicephalous pedicellariæ (they should, of course, be looked for on the apical system, as that is their place in the metamorphosing larva); however, there is no definite proof that they may not be found in still younger specimens<sup>1)</sup>. Embryonic spines of the shape known from other regular Echini, with 3—4 points, highly different from the typical secondary spines of Cidarids, were found on the apical system of these specimens. The presence of such embryonic spines, which soon disappear, is certainly in favour of

<sup>1)</sup> In very young specimens from the marsupium of *Notocidaris gaussensis* there are no ophicephalous pedicellariæ, so that it seems fairly certain that such do not occur in this species at least, which is not in favour of the suggestion that they might possibly occur in other species.

the suggestion that also embryonic ophicephalous pedicellariæ might be found in Cidarids.

The possibility that *Echinopluteus transversus* may belong to Cidarids is thus not entirely excluded. But at present the interesting problem of the parentage of this remarkable larva is insolvable.

### **Clypeaster japonicus** Döderlein.

Pl. XIV, Figs. 2—3.

Th. Mortensen. On the development of some Japanese Echinoderms, p. 547.

Fertilization of this species was undertaken at Misaki on May 24th and again on June 18th, the embryos in both cultures developing until the beginning formation of the posterodorsal arms, but no further. The full larval shape was accordingly not reached, but still the larvæ were sufficiently advanced to show that they are in the main like those of the other Clypeastroids thus far known.

The eggs are extraordinarily clear and must be especially good objects for cytological studies. They appear to be normally surrounded by a wide, quite transparent mucilaginous coat, which may, however, easily break, when the eggs are taken from the ovary, so that both entirely naked eggs and such as are surrounded by the mucilaginous coat are found among one another. Both are fertilized, though not quite so fast in the case of those with the coat. — The cleavage does not present any specially noteworthy features. Swimming gastrulæ were found after ca. 11 hours. They are oblong, showing a great number of mesenchyme cells wandering into the blastocoel cavity from the oral pole, where a very active multiplication of the cells must take place. In embryos a little more than two days old the formation of the skeleton is beginning; they are still in the gastrula stage, the larval mouth having not yet been formed; the archenteron is very narrow, and upon the whole the shape is rather characteristic, as seen in Pl. XIV, Fig. 2. Some red pigment has appeared in the point of the beginning postoral arms. Four days old embryos have assumed the typical *Pluteus* shape. In larvæ eleven days old the posterodorsal arms had begun to appear; beyond this stage they did not develop.

The shape of the larva (Pl. XIV, Fig. 3) appears to be that typical of Clypeastroid larvæ, so far as can be judged from the stage of development reached. The body is short, the oral lobe fairly high. The arms are broad and flat, of the same width in their whole length. The postoral band is slightly concave in the middle, making a deep curve on each side before passing on to the postoral arms. A distinct line is seen passing from the lower point of these curves across the esophagus, indicating the

lower limit of the suboral cavity. There is a conspicuous patch of red pigment in the point of the postoral arms.

The skeleton (Fig. 38) is notable for its smoothness, scarcely an indication of a small thorn being found on any of the rods. The body skeleton forms a basket-structure, the ends of the body rod and recurrent rod having a few irregular branches; but they do not develop into such large, fenestrated plates as is otherwise the rule in Clypeastroid larvæ. The postoral rods are fenestrated, the holes being distinctly smaller in the outer part of the rod than in the basal part. The posterodorsal rod appears

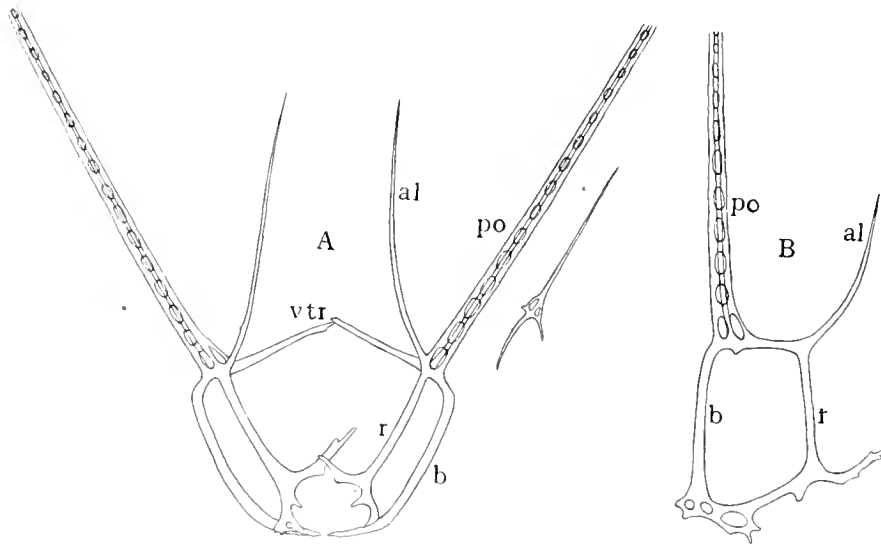


Fig. 38. Skeleton of larva of *Clypeaster japonicus*;  $180/1$ . A. from the dorsal side, B. side view. To the right of Fig. A the beginning posterodorsal rod is represented separately. Letters as in fig. 20.

to be simple; still a few holes were found at the base, so that perhaps they will be found to be fenestrated to some extent in the fully formed larva. The dorsal arch had not yet appeared in the oldest stage reached.

### **Arachnoides placenta (L.)**

Pl. X, Fig. 7.

On an excursion to Napier, New Zealand, on January 29th 1915 I found this species to occur in great numbers in quite shallow water in the lagoon, buried in the sandy mud, generally so deep that not even a slight elevation indicated the place where a specimen was found. As they appeared to have ripe sexual products I thought it worth while trying, whether I could make an artificial fertilisation, although I had no microscope with me, only a pocket lens, and in spite of the fact that I would



have no opportunity of changing the water, being at that time on a visit in the interior of the country. Only a bottle of water was carried along for removing the young embryos from the water in which the fertilization was made, which would, of course, be necessary, if there should be any prospect of keeping the embryos alive for more than a very short time. In spite of these unfavourable conditions the experiment proved quite successful, the larvæ developing quite normally until nearly full size. The character of the egg could, of course, not be ascertained, so that I have to leave undecided the question, whether it is surrounded by a mucilaginous coat as appears otherwise to be the rule among Clypeastroids. Also the cleavage could not be observed. Swimming gastrulæ were found after 16 hours, and at 27 hours the postoral processes had begun to form. At the age of  $2\frac{1}{2}$  days the posterodorsal arms began to appear; the first indication of metamorphosis — the formation of the amnion — was found in the larvæ when  $3\frac{1}{2}$  days old. Beyond this stage the larvæ did not develop, excepting a slight prolongation of the arms, although they lived apparently in full health for more than two weeks. No doubt, the lack of food was the reason for their failing to develop further. Evidently, it must be very easy to rear this larva through metamorphosis under suitable laboratory conditions.

The shape of the larva (Pl. X, Fig. 7) is that typical of Clypeastroid larvæ, the body only being slightly longer than usual. The arms are apparently not widened; their length in the fully formed larvæ will probably be found to be somewhat larger than shown in the figure, it is especially to be expected that the posterodorsal and the preoral arms will be longer. There is no indication of the formation of vibratile lobes. No pigment spot in the points of the arms (— so far as could be ascertained without microscopical examination —). — In the interior structure there are some unusual features. The esophagus shows a clear space in its lower part, apparently representing a kind of gizzard — a structure otherwise unknown in Echinoderm larvæ. The stomach has a rather characteristic, nearly rectangular shape, which may, of course, be due to contraction on preservation; but as such shape is not found in other preserved Echinoderm larvæ, it appears rather to be due to some special structure. From its lower corners a string of cells is seen to proceed towards the ectoderm, like a pair of strands by which the stomach is suspended in the very spacious body cavity, which it is very far from filling out. To this band the angular shape of the stomach would appear to be due, it being prevented from contracting on the point where the string is attached. The hydrocoel has not yet begun to form lobes. A hydropore canal is fairly distinct, opening apparently in the midline on the dorsal side; the opening has,

however, not been distinctly observed. — Across the edges of the anal area a fairly regular series of nuclei is seen, evidently representing the nervous system, as observed in the larva of *Echinocyamus*<sup>1)</sup>. A very distinct line a little below the postoral band indicates the lower limit of the suboral cavity. The lower end of the posterodorsal rods are connected by what would appear to be a strand of muscles, these arms being thus evidently movable.

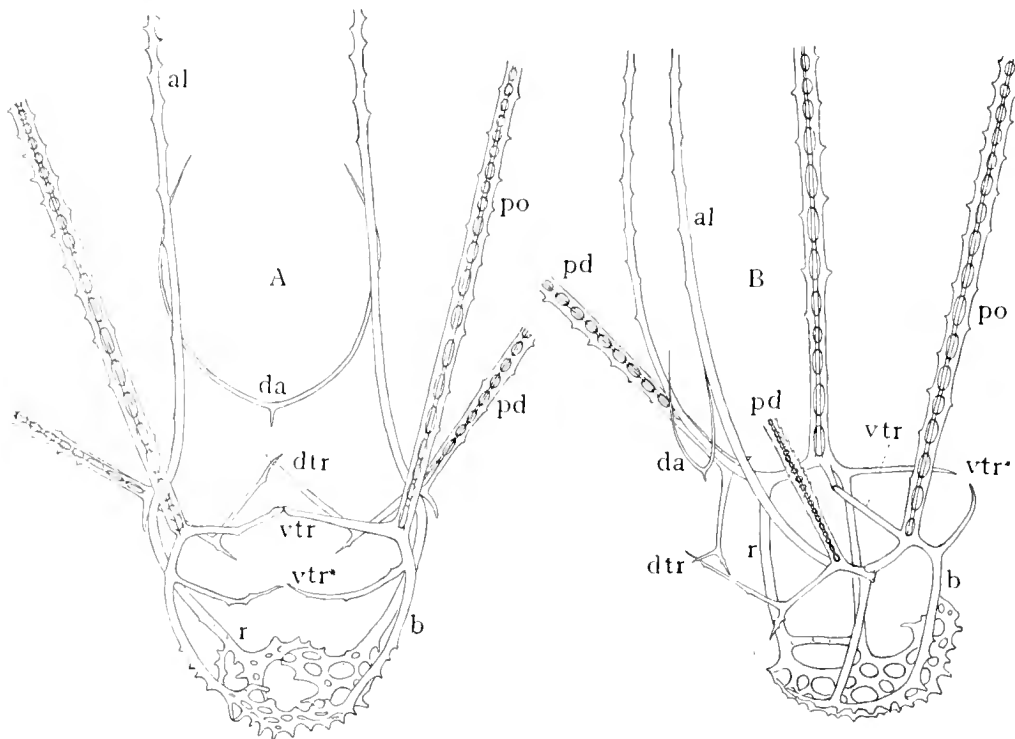


Fig. 39. Skeleton of the larva of *Arachnoides placenta*.  $\frac{250}{1}$ . A. from the ventral side; B. side view. vtr\*. lower ventral transverse rod. Other letters as in fig. 20.

The skeleton (Fig. 39) is of the typical Clypeastroid structure, the body skeleton forming a basket structure, which develops in the posterior end of the body into an irregular, fenestrated plate. The body rod and recurrent rod otherwise nearly smooth, except towards the end, where the fenestration begins. From the body rod proceeds, besides the usual ventral transverse rod, another similar rod somewhat lower down, so that there is a double set of ventral transverse rods. The upper one, corresponding to that normally occurring in Echinoid-larvæ<sup>2)</sup> passes somewhat inwards,

<sup>1)</sup> Th. Mortensen. Notes on the development and the larval forms of some Scandinavian Echinoderms. Vid. Medd. Dansk Naturh. Foren. Kobenhavn. Bd. 71. 1920, p. 156.

<sup>2)</sup> Also in the larva of *Echinocyamus pusillus* we may find both these ventral transverse rods, only the upper one appears to be quite inconstant. It seems beyond doubt that it is the upper one which corresponds to that normally occurring in Echinoid-larvæ, while the lower

between the stomach and the rectum, while the lower one lies on the outside of the rectum. The postoral and posterodorsal rods are fenestrated; they are slightly narrower in the basal part, the holes being there also narrower and longer than in the outer part. Both are rather much thorny, the posterodorsal rods are, however, nearly smooth along their inner side. The anterolateral rods are distinctly thorny in their outer part: the dorsal arch is very slender, smooth, often bent at an angle at the level of the preoral band.

**Echinarachnius mirabilis** (A. Ag.)

Pl. XIV, Fig. 4.

Fertilization of this species, which occurs in quite shallow water, among *Zostera*, near the Station at Misaki, was undertaken on June 1st 1914. Unfortunately the culture was destroyed already the next day, and no further opportunity was found for starting a new culture until towards the end of the month, and then the breeding season of the species had passed; at least, I did not find any specimens with ripe sexual products by that time. Accordingly only very little information can be given about the development of this species, and especially the characters of the larva remain unknown. Still it may be worth while recording the few observations that were made.

The eggs are surrounded by a mucilaginous coat with some red pigment cells. This coat may be found floating empty in the water after the embryo has been hatched, which does not happen till the embryo has reached the gastrula stage, at the age of ca. 18 hours. The gastrula has an unusual shape, like a pear (Pl. XIV, Fig. 4); on leaving the egg-membrane the pointed end is foremost. — The skeleton had not yet begun to form, when the embryos died (probably because of the water being very impure in those days).

**Echinarachnius (Dendraster) excentricus** (Esch.)

Pl. XIV, Figs. 5—6.

This species was found in great numbers in a locality near the Biological Station, Nanaimo, viz. at Gabriola Island, in quite shallow water. While some specimens were found buried in the sand, several inches deep, so that no trace of them could be seen and they could be found only by

one is a special formation, apparently of general occurrence among Clypeastroid-larvae. Thus far it was unfortunate that in the "Echinodermenlarven d. Plankton-Expedition" (p. 74), where the skeleton of the *Echinocyamus*-larva was used as an example, this lower rod was designated as the "ventral transverse rod". — It should still be pointed out that this lower ventral transverse rod does not correspond to the supplementary transverse rod of *Echinopluteus transversus*, which latter proceeds from the ventral recurrent rod.

digging, the majority of them were sitting obliquely in the sand, only half buried, the darker posterior end being above the sand. In places they were found so close together that they were touching one another, sometimes over several square meters. They were found to be ripe in May—June, and fertilization was undertaken on May 29th. The egg is surrounded by a mucilaginous coat with purple pigment spots. About the first developmental processes I have omitted to make any notices. The embryos had assumed the shape of small Plutei at the age of two days. In eight days old larvæ the first indication of the metamorphosis (formation of the annion) was found; none of the specimens, however, developed through metamorphosis; but, anyhow, the full larval shape was reached.

The shape of the larva (Pl. XIV, Figs. 5—6) is very much like that of *Echinarachnius parva* (comp. especially Pl. VII, Fig. 1 of Fewkes' paper on the development of that species<sup>1</sup>). The arms are rather narrow, not widened at the base; they have all of them a prominent red pigment spot at the point, while the larva is otherwise without color. (A noticeable fact is that it turns green when preserved in alcohol; this fact was observed also in several other Clypeastroid larvæ and probably will prove to hold good for all of them, in accordance with the fact that Clypeastroids upon the whole generally turn green when preserved in alcohol; also when otherwise damaged the tissue on the damaged place turns green<sup>2</sup>). The posterodorsal rods have their lower ends connected by a muscular band and are thus movable; the same holds good for the postoral arms in the later stage, when the lower part of the body skeleton has been absorbed. — On the sides of the anal lobe the vibratile band makes a downward curve, thus forming a pair of small vibratile lobes; a corresponding pair of lobes is found on the dorsal side and also on the side of the body the band forms a pair of small, posterolateral lobes. As seen in the figures there is an indication of a ciliated band going from the corner of the preoral band obliquely downwards towards the band along the dorsal side. This band, which I have also observed in other Clypeastroid larvæ (and which is also seen in the larva of *Echinocyamus pusillus*, comp. Pl. VI, fig. 90 of Théel's Monograph), is probably a special feature of the Clypeastroid larvæ and may have something to do with the oral nervous system occurring in the *Echinocyamus*-larva and probably in Clypeastroid larvæ in general (comp. p. 71); but this needs a closer investigation. — The esophagus shows an indication of the structure observed in the larva of

<sup>1</sup>) I. W. Fewkes. Preliminary observations on the development of Ophiopholis and Echinarachnius. Bull. Mus. Comp. Zool. Harvard Coll. XI. 4. 1886.

<sup>2</sup>) Some interesting observations on this remarkable property of Clypeastroid tissues are given by W. I. Crozier in a paper "On the pigmentation of a Clypeastroid *Mellita sesquiperforatus* (sic!) Leske". American Naturalist, Vol. LII. 1918. p. 553.

*Arachnoides placenta* and regarded as a kind of gizzard; the stomach and rectum are somewhat peculiarly shaped, especially the rectum with its conspicuous widening. Of course, it is impossible to decide how much of this is due to contraction on preservation, but it is evident that the shape is not that of a simple oval sac. The ventral and dorsal transverse rods give the body a characteristic prominence on the ventral and the dorsal sides. — It was observed that this larva has the habit of swimming close to the surface of the water; often it comes up and touches the surface film with the arm points, whereupon it suddenly sinks as if it had got a shock.

The skeleton (Fig. 40) is of the usual Clypeastroid type. The body skeleton forms a basket structure, the body rod and recurrent rod forming together at their posterior end a large, fenestrated plate, which is, however, unusual through the holes in it being very small, so that the plate is nearly compact. There is both an inner (upper) and an outer (lower) ventral transverse rod. The postoral and posterodorsal rods are fenestrated, the latter with distinctly smaller holes than the former; both are thorny, the posterodorsal, however, almost exclusively along the outer side. The anterolateral rods are also rather much thorny. The basal part of the anterolateral rod has a small process with which one of the basal processes of the posterodorsal rod joins so that here is formed a sort of articulation about which this rod may move. Whether this is a constant feature, I do not, however, venture to ascertain. — In some cases I have found some irregularities in the body skeleton, as in that figured, where the lower ventral transverse rod has some branches, one of them proceeding, like an extra recurrent rod, downwards to the basal plate, with which it joins.

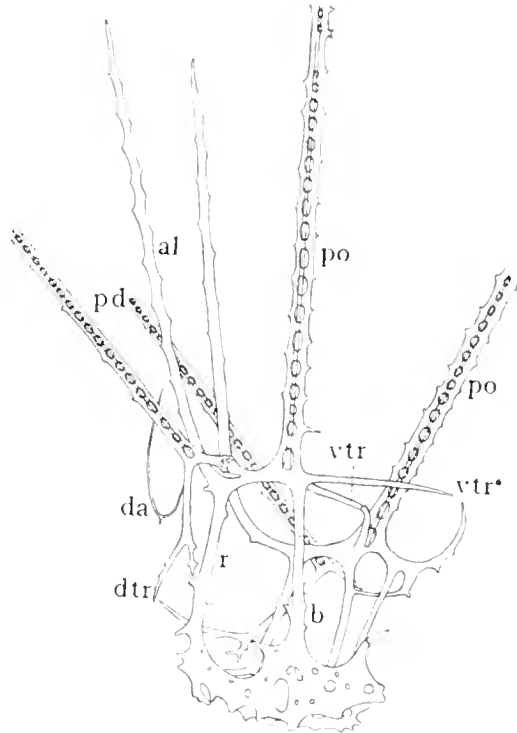


Fig. 40. Skeleton of the larva of *Echinarachnius excentricus*. Side view.  $\frac{250}{1}$ . Letters as in fig. 20.

This larva resembles to a striking degree that of *Echinarachnius parma*. It is not easy to designate the characters by which to distinguish them, especially because Fewkes does not give any detailed and exact figures of the skeleton of the latter larva. It appears, however, that the plate

in the posterior end of the body is much more openly fenestrated in *E. parva* than in *E. excentricus*.

I may add here an observation regarding the rate of growth of this sea-urchin. On the place mentioned above, where the species was found in such vast numbers, careful search was made also for the young specimens, the sand being sifted through a sieve, the meshes of which were only 1 □ mm. No specimens smaller than 4 mm length were found. As it was just in the breeding season of the species, it was, evidently, impossible that the brood of that year could already have reached a size of 4 mm or even more, so that these young specimens must represent the brood from the foregoing summer, being thus one year old.

When measuring the whole material collected at this locality (in the end of June and the beginning of July) the arrangement of the sizes shown in the adjoining table resulted. It is quite evident therefrom that the group from 4—17 mm represents the one year old specimens, the main number of them measuring 5—10 mm. Another group from 20—52 mm, with the maximum from 30—40 must represent specimens two years old, while the specimens from 55—70 must be, at least, three years old. There is, however, no distinct limit between these two groups and the possibility that the larger specimens are more than three years old cannot be denied. — As we do not otherwise possess any definite knowledge of the rate of growth in Echinoids, the facts given here may claim some interest.

Table of measurements of specimens of *Echinarachnius excentricus* from Gabriola island, June—July 1915.

mm	Number of specimens	mm	Number of specimens	mm	Number of specimens
3		26.....	1	49	
4.....	2	27.....	3	50.....	3
5.....	16	28.....	3	51	
6.....	33	29		52.....	4
7.....	54	30.....	4	53	
8.....	35	31.....	4	54	
9.....	34	32.....	1	55.....	2
10.....	18	33.....	6	56	
11.....	10	34.....	4	57.....	5
12.....	6	35.....	2	58	
13.....	5	36.....	2	59.....	2
14.....	4	37.....	1	60.....	3
15.....	2	38.....	5	61.....	3
16.....	1	39.....	2	62.....	2
17.....	1	40.....	6	63.....	1
18		41.....	2	64.....	3
19		42		65.....	4
20.....	2	43.....	2	66.....	5
21		44.....	4	67.....	6
22.....	1	45.....	2	68.....	2
23		46.....	3	69	
24.....	1	47.....	2	70.....	2
25		48.....	2	71	

**Encope micropora** Agass.

Pl. XIV, Fig. 7.

On the sandy shore of the little island Taboguilla in the Gulf of Panama this Clypeastroid was found in considerable numbers, living buried in the sand in shallow water, about low-water mark. It was found to be ripe, and fertilization was undertaken on January 7th 1916. Owing to the exceedingly strong development of the calcareous substance in this species, the gonads being so to say infiltrated in the calcareous mass it was impossible to take out pieces of the gonads as usually done by artificial fertilization in Echinoderms; it had to be done in this way that the specimens were broken to pieces and laid in water, male and female together. The sexual products were thus emptied and fertilization took place. By this procedure, however, the water became nearly black from the intensive black coloration of the sea-urchin, and it was necessary to decanter off the water many times, before the culture was in good order.

The eggs are surrounded by a thick, somewhat irregular mucilaginous coat without pigment spots. The first developmental processes went on very rapidly, so that already after twelve hours the embryos had begun to assume the Pluteus-shape and the skeleton had begun to form. At the age of four days the posterodorsal arms had appeared, and in the course of two weeks the larva had reached its full shape. The metamorphosis was not accomplished by any of the — rather few — larvæ surviving thus far.

The shape of the larva (Pl. XIV, Fig. 7) is that typical of Clypeastroid larvæ, presenting no specially noteworthy features. A small downward curve of the ciliated band at the base of the postoral and posterodorsal arms represents ventral and dorsal ciliated lobes, and a similar curve between these arms on the side of the body the posterolateral lobes, but all of them are small and inconspicuous. The arms are narrow, of the same width throughout. There is no pigment spot in the point of the arms.

The skeleton (Fig. 41) also shows the typical Clypeastroid structure, the body rod and recurrent rod developing in the posterior end of the body into a complicated fenestrated plate, strongly thorny along the posterior edge. There is both an upper and a lower ventral transverse rod, the former being entirely smooth, the latter very thorny along its posterior edge; the same holds good for the dorsal transverse rod. Postoral and posterodorsal rods fenestrated, the latter having distinctly smaller holes than the former; in both of them the holes are somewhat larger at the base, gradually diminishing in size upwards, but then remaining of the same size till the end: both rods are strongly thorny, the posterodorsal rod, however, mainly along the outer side. It appears that there

is a kind of articulation between the base of the posterodorsal rod and the anterolateral rod, but it is not so distinctly seen as in *Echinarachnius excentricus*. The anterolateral rods are strongly thorny in their outer part, and also the preoral rods have a few thorns; they proceed at an obtuse

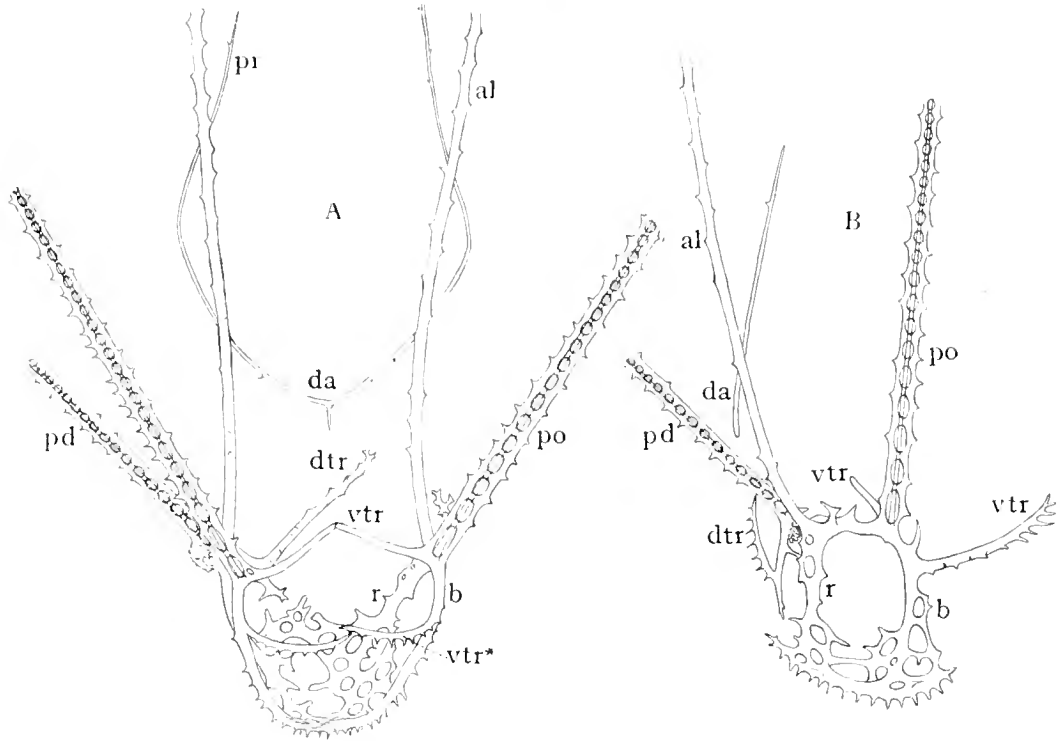


Fig. 41. Skeleton of the larva of *Encope micropora*. A. from the ventral side; B. side view. <sup>250</sup>/<sub>1</sub>. In figure A, the left posterodorsal rod is lacking. Letters as in fig. 20. vtr\* the lower ventral transverse rod. The asterisk has been omitted by a mistake in fig. B; it is the outward directed rod in the right side of this figure which represents the lower transverse rod.

angle from the dorsal arch. — The specimen from which the skeleton was drawn, shows the peculiar anomaly of having only the left posterodorsal arm developed, being otherwise quite normal.

### *Mellita sexies-perforata* (Leske).

Pl. IV, Fig. 2; Pl. XIII, Figs. 5—6.

A few specimens of this species containing ripe genital products were obtained at Tobago, B. W. I., on the 8th of April 1916 and fertilization was made, which proved successful. The eggs<sup>1)</sup> are surrounded by a pig-

<sup>1)</sup> W. I. Crozier, in his paper "On the pigmentation of a Clypeastroid *Mellita sesquiperforatus* Leske" (*American Naturalist*, Vol. LII, 1918, p. 554) states the egg of this species to be "apparently larger than any other Echinoid egg that has been described", measuring about 0.26 mm in diameter. From the present researches it is seen that much larger eggs (ca. 0.5 mm.) are found in several other Echinoids, *Phyllacanthus parvispinus*, *Heliocidaris erythrogramma*, *Peronella Lesueuri*. Also *Holopneustes purpurascens*, *Brisaster latifrons*, *Br. fragilis*, several deep-sea forms and the viviparous forms have large eggs.



mented mucilaginous coat. The first developmental processes are passed very rapidly; after 6 hours the embryos were free swimming gastrulae, and already at the age of 24 hours they had assumed the shape of young plutei, the skeleton having already developed its characteristic structure; on the other hand the intestinal tract is somewhat behind in its development, the mouth having still only the form of a small round opening (Pl. XIII, Fig. 5). This young larva otherwise shows a characteristic concavity on its dorsal side, as seen in Pl. XIII, Fig. 6, which

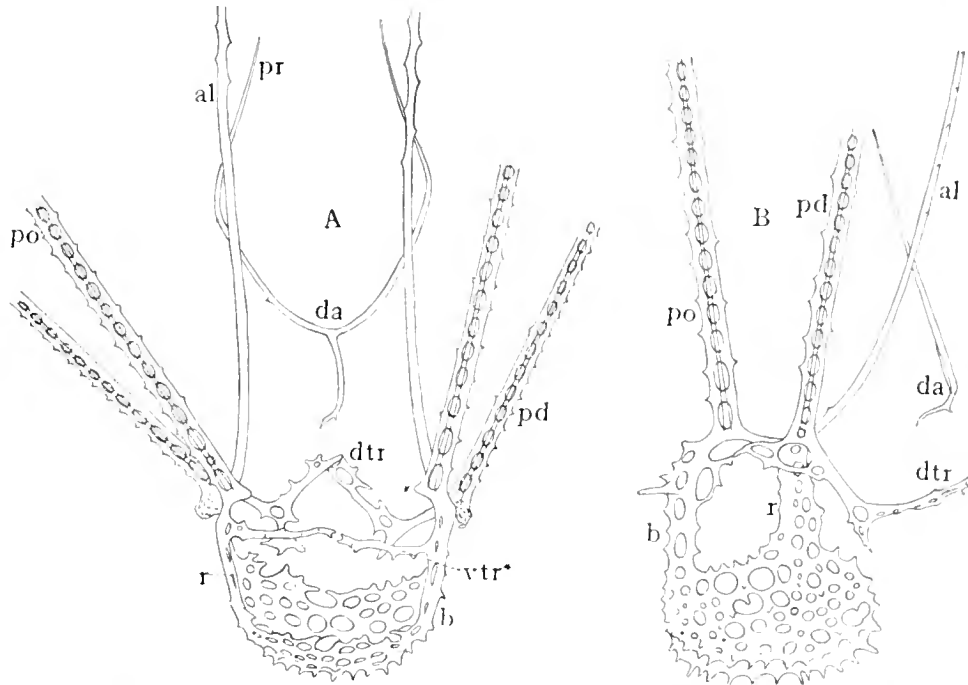


Fig. 42. Skeleton of the larva of *Mellita 6-perforata*. <sup>290</sup>1. A. From the ventral side; B. side view. Letters as in fig. 20. \* The rudiment of the upper ventral transverse rod; vtr\* lower transverse rod.

represents the young larva in side view. They are still rather opaque, and the vibratile band is not yet fully differentiated. Some red pigment has been formed. After 2½ days the larvae had assumed their full shape, with both posterodorsal and preoral arms developed. At the age of five days the metamorphosis was beginning, the body skeleton had been partly absorbed, the large fenestrated plate in the posterior end remaining, however, unaltered, evidently passing directly into the apical system of the sea-urchin. Muscles were distinctly seen to connect the bases of the postoral and posterodorsal rods, these four arms being thus actively movable, in the same way as in the larva of *Mellita 5-perforata* (or *testudinata*), as described by Grave. As the metamorphosis did not proceed

<sup>1)</sup> Caswell Grave. Some points in the structure and development of *Mellita testudinata*. Johns Hopkins Univ. Circ. No. 157. 1902.

further during the next days, I suspected that it was due to the lacking incitement of a natural bottom. Some of the larvæ were then transferred to a jar with sand on the bottom, and after a few days these larvæ had completed their metamorphosis, while those left in the jar without sand on the bottom showed hardly any further advance in the process of metamorphosis.

The shape of the fully formed larva is that typical of Clypeastroid larvæ (Pl. IV, Fig. 2). There are small vibratile lobes, as usual; that those of the dorsal side appear to be much larger than the ventral ones in the figure is due to the fact that the posterodorsal arms are directed nearly horizontally on account of the contraction of the muscle uniting the bases of their rods. The frontal area is remarkably small, the oral area being very large. The nervous system is not distinct in the preserved specimens, neither does the esophagus distinctly show the gizzard-like structure found f. i. in the *Arachnoides*-larva. There is a conspicuous coloration of red and yellow in the point of the arms, scattered red pigment cells occurring otherwise irregularly in the body, often in larger number along the preoral and postoral band and in the posterior end of the body. The stomach has a faint yellowish-green tint.

The skeleton (Fig. 12) is of the typical Clypeastroid-structure, the body skeleton forming a basket structure. The body rod and recurrent rod are thorny, often even fenestrated, and form in the posterior end a large, fenestrated, thorny plate. Even the transverse rods may develop into narrow, fenestrated plates. The upper ventral transverse rod is entirely absent or quite rudimentary. Postoral and posterodorsal rods of the usual fenestrated type; anterolateral rods thorny in the outer part. The small posterior prolongation from the dorsal arch appears to be constantly curved and more or less thorny or fenestrated.

The larva of the closely allied species *Mellita 5-perforata* (or *testudinata* Klein), which was reared by Caswell Grave, likewise through metamorphosis, has not been adequately described. From the outline figures given by Tennent in his paper on Echinoderm Hybridization Pl. I, Figs. 10—12, it appears to differ quite notably from the present species, especially through the much less developed fenestration of the posterior part of the body skeleton and through the presence of the upper and the absence of the lower ventral transverse rod. A more detailed description of this larva is, however, desirable

**Astriclypeus Manni** Verrill.<sup>1)</sup>

Pl. IV, Fig. 1.

This species, which occurs in quite shallow water, buried in the sand, near the Biological Station at Misaki, was found to have ripe sexual products in June (1914); fertilization was undertaken on the 2nd, but did not result in a good culture. After some more unsuccessful attempts I succeeded on the 27th of June in getting a good culture, the larvæ developing normally and metamorphosing.

The egg (Fig. 43) is surrounded by a strongly pigmented mucilaginous coat. About the first developmental processes I have no notices; at the age of 11 hours the embryos were in the process of gastrulation, the blastocoel being filled with mesenchyme cells; the ectoderm is thick, especially at the oral end. After three days the larvæ had already nearly reached the full shape, the posterodorsal arms having been formed. At the age of 6 days the metamorphosis was beginning, and after another week some of them had completed the metamorphosis, while other specimens were not yet so far

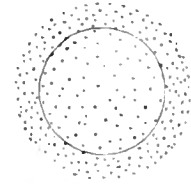


Fig. 43. Egg of *Astriclypeus Manni*. <sup>25</sup>/<sub>1</sub>.

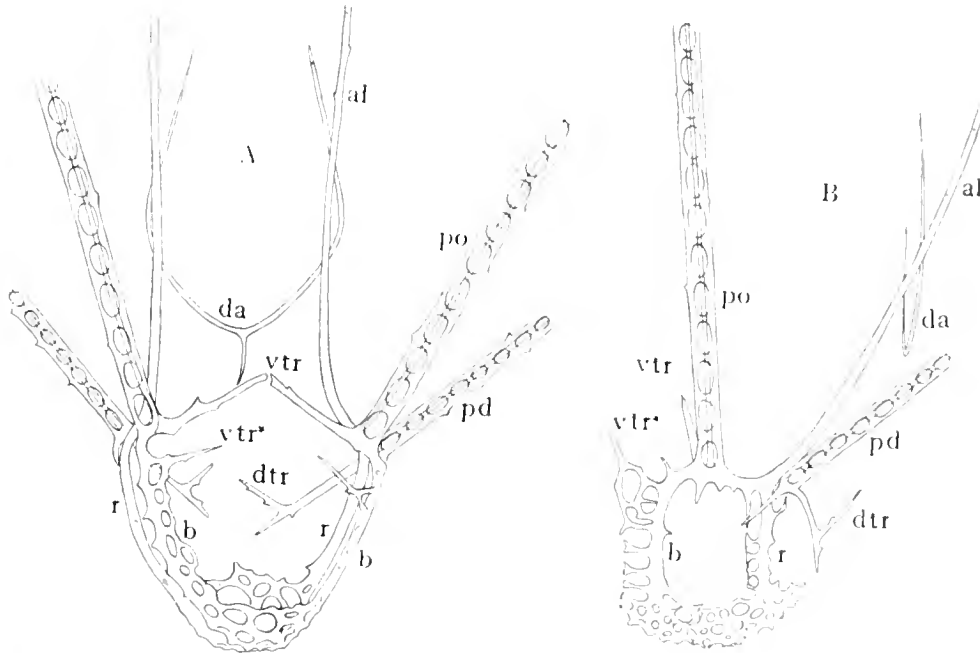


Fig. 14. Skeleton of the larva of *Astriclypeus Manni*. <sup>25</sup>/<sub>1</sub>. A. from the ventral side; B. side view. Letters as in fig. 20.

<sup>1)</sup> In the "Preliminary Notice on the Development of some Japanese Echinoderms" (Annot. Zool. Japon. VIII. 1914. p. 517) I designated this species as "*Mellita japonica*", having wrongly got it into my mind that there existed a *Mellita japonica*; that paper being written at sea, I had, of course, no access to literature so that I could not then correct the wrong idea.

advanced. Under natural conditions this species will then, evidently, complete its metamorphosis in less than two weeks.

The shape of the larva (Pl. IV, Fig. 1) is that typical of Clypeastroid larvæ. The arms are rather narrow, of the same width throughout. The vibratile lobes are small, as usual; between the postoral and posterodorsal arms the vibratile band forms a small, earshaped posterolateral process. There is some red pigment in the point of the arms and in the posterior end of the body.

The skeleton (Fig. 44) likewise is of typical Clypeastroid structure, body rod and recurrent rod forming in the posterior end a complicate, fenestrated plate, which is not distinctly thorny. Both the body rod and the recurrent rod may be more or less fenestrated (the thorns along their sides uniting with their ends so as to form holes). The lower ventral transverse rod is generally only slightly developed, often forming a small fenestrated plate at its base; sometimes it is not at all developed. The upper ventral transverse rod, on the other hand is well developed. Postoral and posterodorsal rods fenestrated, generally only slightly thorny. The holes in the postoral rod are somewhat unusually large, but diminish in size towards the end of the rod. Anterolateral rod slightly thorny in its outer part.

**Laganum diplopora** H. L. Clark.<sup>1)</sup>

Pl. XIV, Fig. 1.

On the 7th of July 1914, a few days before I left Japan, I got some specimens of this species, taken at the depth of ca. 800 meters in the Sagami Sea, which were found to contain ripe genital products. Fertilization was undertaken and proved to be perfectly successful. The small, very transparent eggs were apparently without a mucilaginous coat; in view of the fact that all other Clypeastroids, the development of which has been studied, have the eggs invested by a mucilaginous coat I would, however, not venture to state definitely that such coat is wanting in this species. It may be so transparent that it has been overlooked (the fertilization was undertaken rather late in the evening), or it may have been ruptured by shaking the eggs out of the ovary, as it happened also with *Clypeaster japonicus*. In the course of three days the embryos had developed into typical young plutei, differing in no way from other young Clypeastroid larvæ. It was noticed that the larvæ all kept swimming close to the bottom of the dish, never rising to the surface of the water, as do otherwise as a rule young Echinoderm larvæ.

<sup>1)</sup> In the preliminary notice on the development of some Japanese Echinoderms (p. 547) I designated this species as *Laganum judsiyama*. On my return I found it to belong to the closely related species *Laganum diplopora* H. L. Clark.

By this time I had to leave Misaki, so that there was no opportunity of rearing the larvæ beyond the first stage. This species being the first deep-water Echinoderm, the development of which has been studied — all other Echinoderms hitherto used for developmental studies being mainly littoral — this case is very interesting, as it proves that at least some deep-water Echinoderms may have typical pelagic larvæ. (The species is known to have a bathymetric range of ca. 100—800 meters).

The shape of the larvæ (Pl. XIV, Fig. 1) does not present any unusual features; it is, however, not old enough to show whether it will offer any marked special features in its full shape. No pigment was present at this stage.

The skeleton (Fig. 45) is in conformity with that of other Clypeastroid larvæ, the body skeleton forming a basket structure; there is as yet no large fenestrated plate developed in the posterior end of the body, which would seem to indicate that such is not formed in this larva, since in other larvæ it is found to develop already in the quite young stage. The body rod is strongly thorny, the recurrent rod smooth. The upper ventral transverse rod is well developed, smooth; there is no indication of a lower ventral transverse rod. The postoral rods are fenestrated, strongly thorny; the anterolateral rods are also rather strongly thorny.

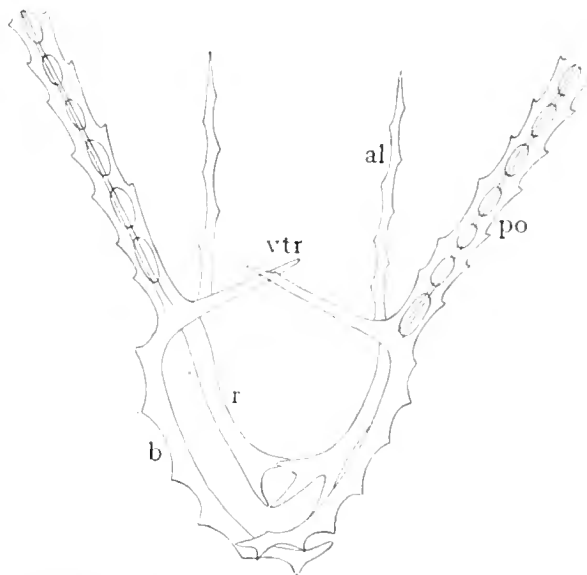


Fig. 45. Skeleton of the larva of *Laganum diplopora*. From the ventral side.  $\frac{300}{1}$ . Letters as in Fig. 20.

### **Peronella Lesueuri** (Val.).

Pls. XV—XVI.

In my paper "On the development of some Japanese Echinoderms" 1914 I gave a short summary of the development of this species under the name of *Laganum decagonale*; the wrong identification was due to lack of literature. In the following year Grace Medes published a paper on "The Pluteus of *Laganum* sp."<sup>1)</sup>, the identification of the species being omitted. As the larva described in that paper was very much like that of the Japanese species, I was, of course, very anxious to learn to which

<sup>1)</sup> Papers from the Department of Marine Biology of the Carnegie Inst. Washington. Vol. VIII. 1915.

species it belonged. Fortunately, H. Lyman Clark, who was a member of the Carnegie Expedition to Torres Strait, 1913, — on which Dr. D. H. Tennent reared the larvæ (at Badu Island), which made the object of Miss Medes' paper — was able to inform me that the species in question was *Peronella Lesueuri*; he, moreover, sent me a specimen from Badu Island, thus enabling me to compare it directly with my Japanese specimens and to convince myself of their identity.<sup>1)</sup>

The material studied by Miss Medes represented only two stages, of 29 and 55 hours respectively. The latter was used only for the study of the skeleton, especially the development of the spines being very carefully worked out. There was thus only the stage of 29 hours left for the study of the larval structure, and accordingly the results could only be very incomplete. The fuller report of the development of this species given here is thus by no means made superfluous by the said paper, the less so as the interpretations given in that paper are not all of them acceptable.

The material for the study of the development of this species, which I collected in Japan, is rather rich and well preserved and allows giving a fairly complete record of at least the younger stages. It has been possible to establish beyond doubt most of the remarkable facts revealed by the study of this form, so strongly deviating from the usual type of development in Echinoids, although less deviating than the other Echinoid with shortened development studied in the present work, *Heliocidaris erythrogramma*. The later stages of metamorphosis as well as the development of the adult skeleton and the postlarval development upon the whole have been rather disregarded, such monographic study being out of the plan of the present work.

The adult *Peronella Lesueuri* was found in considerable numbers in the sandy bottom of a shallow lagoon close to the Biological Station at Misaki; they were found lying buried in the sand, only a few centimeters down, a small elevation indicating their place. They were found to have ripe sexual products in the latter part of June and in July. Fertilization was undertaken on June 19th and repeatedly during the following three weeks. Metamorphosis was completed in the course of 3—4 days. The metamorphosed urchins very soon died, assuming the green colour so characteristic of dead Clypeastroid tissue. Wishing, if possible, to keep the young urchins alive and to follow their further growth changes I tried to keep them in dishes with a more natural bottom consisting of sand taken from

<sup>1)</sup> The specimen from Badu differs slightly in shape from the Japanese specimens. The species being known to be highly variable in regard to the outline of the test, the difference is not at all surprising. Perhaps, however, a closer study of the different forms, both in regard to their general characters and their development, may ultimately prove that what we now regard as one very variable species really is a group of closely allied but distinct species.

the locality where the adult specimens were found, the sand being, of course, first examined microscopically in order to ascertain that no young specimens from outside were contained in it. This proved to give an excellent result; the young sea-urchins now did not die, but lived and thrived well. On leaving Japan I carried a culture of the young *Peronellas* along with me to Australia; they stood the transport very well. On my arrival in Sydney the jar in which they were kept happened to be turned over, and I had to fill it up with water from Sydney Harbour. They stood that very well too. It was not until the 29th of October that the last specimens were preserved. Most of them had died already by that time — but a few were still in good condition, having reached a length of the test of 0.6 mm, while the newly metamorphosed urchin is only 0.2 mm long. The growth is not very considerable, it is true; but this is due, I do not doubt, to the lack of sufficient food supply. It seems beyond doubt that under good conditions it will prove very well possible to rear this sea-urchin to a much larger size, if not to full size — an experiment which would be of very considerable interest. — The rate of growth of this species under natural conditions most probably will be considerably faster. I regret being unable to give information about this matter in the same way as I did it for *Echinarachnius excentricus*, having found no young specimens in the place where the adult specimens were collected.

The eggs are ca. 0.3—0.4 mm in diameter, yolk-laden and opaque. They are surrounded by a thick mucilaginous coat, without pigment. The cleavage is total and regular. At the age of ca. 5 hours the embryo has reached the blastula-stage; it is much folded (Pl. XV, Fig. 1), the folds often being arranged in four meridians so that the embryo has the appearance of being in the four-cell stage. The folds then gradually disappear, the egg-membrane widening contemporaneously so as to give room for the now somewhat larger embryo. At the age of 8 hours the embryo has developed cilia and begins to rotate within the egg membrane, and at the age of about 10 hours it breaks through the membrane and is liberated; it has now the shape of a somewhat elongate gastrula.

Regarding the entoderm formation it is stated in the preliminary notice that it takes place "not as a real invagination, but more as a strong growth of cells at the oral end, and there is no gastrula mouth". The study of sections of the embryos has shown this statement to be wrong. At the age of 8—9 hours a rapid growth of mesenchyme cells from the truncated oral end of the embryo takes place (Pl. XV, Fig. 5), which may proceed so far as to fill out the blastocoel cavity almost completely. At the age of ca. 12 hours, sometimes earlier, the gastrula invagination begins (Pl. XV, Fig. 6), in the usual way.

In embryos 16—17 hours old the larval mouth is about to form (Pl. XV, Fig. 2, Fig. 14), in the usual place on the middle of the ventral side, the embryo now being distinctly flattened. The entoderm, into which most of the previously formed mesenchyme cells apparently merge, begins to assume a somewhat complicated structure (Pl. XV, Figs. 7—13). While at first a simple sac (Pl. XV, Fig. 14) its lumen now gradually is subdivided through a fold hanging down from the upper, thickened part of its wall. It is not easy to get a full understanding of the real shape of the archenteron. But it is clear that there are two main parts, which represent the hydrocoel and enterocoel pouches. There appears to be some variation in the time of appearance of these structures. Thus in the specimen from

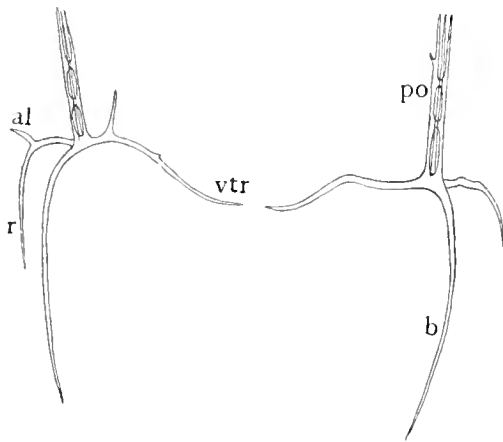


Fig. 46. Skeleton of the larva of *Peronella Lesueuri*, 20 hours old.  $\frac{300}{1}$ . al. anterolateral rod; b. body rod; po. postoral rod; r. recurrent rod; vtr. ventral transverse rod.

which the figures 7—10 were drawn the larval mouth had apparently not been formed, while in the specimen from which figures 11—13 were drawn the larval mouth had developed, the entoderm showing the same stage of development as in the other specimen. — As seen in Pl. XV, Fig. 13 there is a distinct apical thickening of the ectoderm at this stage.

At the age of 18—20 hours the postoral arms are beginning to develop (Pl. XV, Fig. 3). The skeleton has been formed (Fig. 46). It is seen in this stage to be essentially of the Clypeastroid type, but, as might be

expected from the rudimentary shape of the larva, it never develops into the typical Pluteus-skeleton. In the later stages it forms a very irregular network in the body, in which one can, with some difficulty, recognize the body rod, the recurrent rod and the ventral transverse rod. (Comp. fig. 2, p. 131, in Miss Medes' paper). It is noteworthy that an indication of an anterolateral rod may be found in the young larva, although the anterolateral arms are apparently never developed.

In the young larva with the beginning postoral arms (Pl. XV, Fig. 3) there is a fairly conspicuous preoral lobe, with a distinct ectodermal thickening at the point. This lobe, which is at first rather swollen, gradually diminishes in size and ultimately disappears completely, the mouth opening lying then at the anterior end of the body, in the situation between the postoral arms; in the later stages the mouth opening even is transplaced to the dorsal side (Pl. XVI, Fig. 10). The normal shape of



the fully formed larva is that shown in Pl. XV, Fig. 4, with only two arms, the postoral ones, which are fairly long, about body length. There is, however, a considerable variability in the larval shape; another pair of arms, the posterodorsal ones, may develop, but sometimes only one of these arms is formed. Also the arms may coalesce to a various extent.

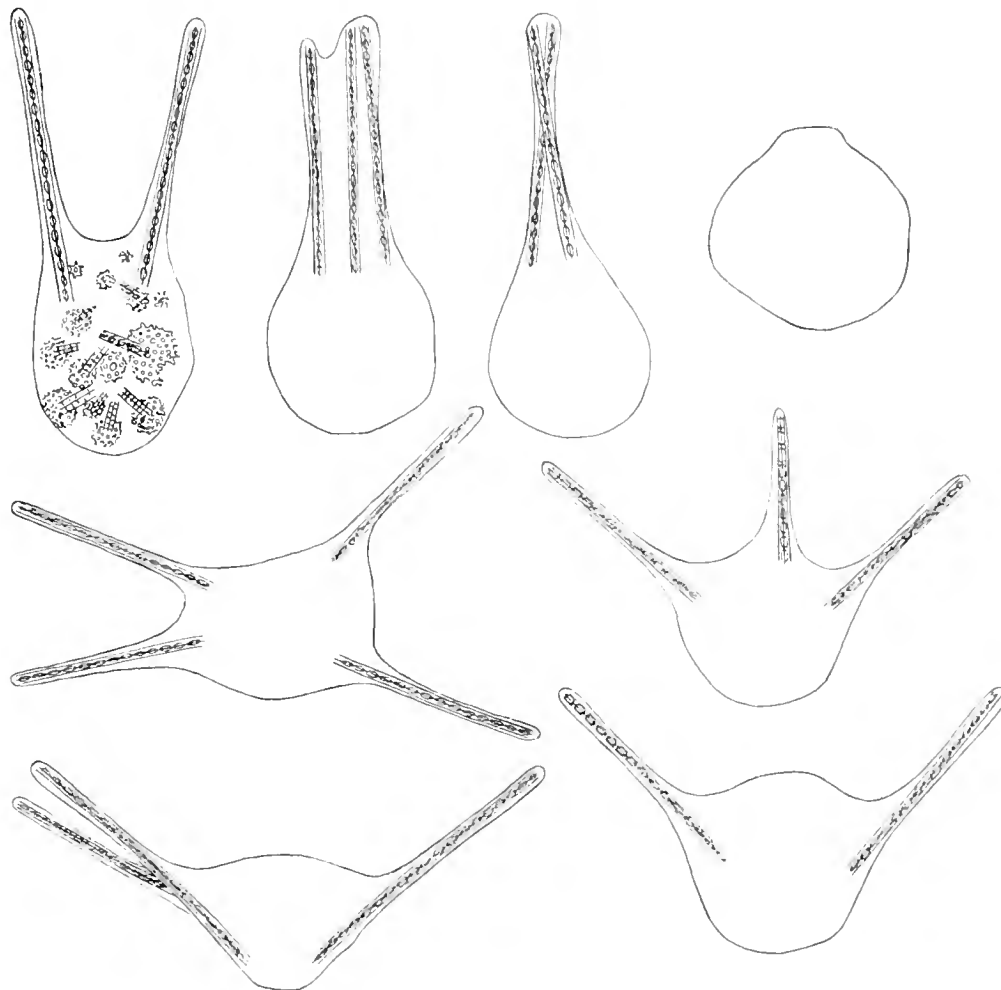


Fig. 47. Various forms of the larva of *Peronella Lesueurii*.  $\frac{100}{1}$ . Only in one of them the young spines are drawn; all the specimens figured were at about the same stage of development. Drawn from life.

Thus the variation as regards the larval shape is rather phantastic, as seen from the sketches represented in figure 47. And these larvæ could not be designated as abnormal, since the metamorphosis was completed by all of them, even by the one with no arms at all. Also among the larvæ reared by Tennent corresponding variations occurred, even a specimen with five arms, which I have not observed. On account of the rudimentary character of the larva these variations are not very surprising; possibly

they may be due partly to the influence of laboratory conditions. I have not found the larvæ in the free, so I cannot ascertain whether such variations occur also under natural conditions, but I should expect so. The main thing is, however, that the metamorphosis goes on quite normally in all the various forms, showing that the variations are of no real importance to the larvæ. All the arms are supported by a fenestrated skeletal rod. There is no vibratile band differentiated, only a general ciliation all over the body, by means of which the larva swims. Only in some exceptional cases a distinct ciliated band is formed (comp. p. 116). There is no pigment.

Turning now to the development of the internal organs the first thing to arouse attention is the larval esophagus. In Pl. XV, Figs. 19—22 a series of sagittal sections through an embryo 18—20 hours old are represented. There is no connection between the lumen of the pharynx and that of the entoderm, only their walls are closely apposed. From the base of the pharynx a sac-shaped prolongation proceeds along the dorsal side of the entoderm reaching about halfway backwards. In Pl. XVI, Fig. 5, representing a median sagittal section of an embryo 21—22 hours old, this prolongation is seen to reach to the posterior end of the body, thus covering the whole dorsal side of the entoderm. Corresponding series of frontal and transverse sections of embryos of the same age (Pl. XV, Figs. 15—18; Pl. XVI, Figs. 11—13) show both the pharynx and its posterior prolongation to be flattened; the latter is seen to be confined to the dorsal side of the larval body, the ventral side of the entoderm remaining uncovered. The ventral wall of the posterior prolongation is distinctly thickened, the dorsal wall remaining thin. In a slightly older stage, Pl. XVI, Figs. 14—16, representing transverse sections of an embryo 23—24 hours old, the ventral wall of the sac is considerably thickened and begins to fold, the underlying hydrocoel wall following the folds. The dorsal wall of the sac on the other hand becomes thinner and gradually assumes a perfectly endothelial character. Thus it is clear already at this stage, and is further definitely proved by the following stages (Pl. XVI), that this posterior prolongation from the pharynx is the amnion, which is accordingly formed here in a way quite unique among Echinoids, as far as hitherto known. The pharynx itself gradually shortens and soon completely disappears, as becomes evident from a comparison of Pl. XV, Figs. 15—18 and Pl. XVI, Figs. 1—4, or still more so on comparing the sagittal sections Pl. XV, Figs. 19—22 and Pl. XVI, Figs. 5—8 and 10. The larval mouth, which never assumes the normal functions of a mouth, since the pharynx never opens into the stomach, the larva being accordingly entirely unable to feed, thus directly becomes the open-

ing of the amniotic cavity, the median position of which, so different from the normal position of the amniotic opening in Echinoid larvæ, as emphasized by Miss Medes (Op. cit. p. 131), is thereby naturally explained. As Miss Medes had only one single stage for sectioning, the natural explanation of the median position of the amniotic opening could not possibly be found out by her, and the statement that there was "no indication of the formation of a mouth" was an equally unavoidable consequence of the lacking of the younger developmental stages. This also accounts for the fact that Miss Medes thinks the position of the amniotic opening to be ventral, "so that the dorsal surface of the pluteus forms the aboral surface of the adult" (Op. cit. p. 131). As shown definitely by the course of the development it is, on the contrary, the dorsal surface of the Pluteus which becomes the oral surface of the adult, the ventral surface of the larva becoming the aboral side of the sea-urchin.

Contemporaneously with the formation of the amniotic prolongation from the pharynx the blastoporus, or, as it might now be termed, the anal opening wanders upwards along the ventral side (Pl. XV, Figs. 20—21), where it may remain distinct for a little while yet; the last traces of it have disappeared at the age of about 25 hours. The posterior part of the entoderm is seen to lie in a transverse position on the ventral side, somewhat transplaced towards the left side. Its lumen remains distinct, and it appears to be somewhat curved (Pl. XVI, Figs. 4, 8). This part of the entoderm, which develops directly into the intestine of the sea-urchin, soon separates completely from the larger, originally anterior, part of the entoderm, from which the hydrocoel and enterocoel develop.

The lumen of the hydrocoel begins to differentiate at the age of 23—24 hours; but I cannot enter on a detailed description of the complicate processes of the differentiation of the hydrocoel and the enterocoel. I would only emphasize that no subdivision of the enterocoel takes place. The part to the aboral side of the intestine may have the appearance of being separate; a careful examination of the series of sections shows, however, definitely that it is in connection with the rest of the body cavity, there being in fact only one, common space. Accordingly I cannot agree with Miss Medes in designating the different parts of the body cavity as anterior or posterior enterocoel. We have here only a general body cavity, and a special homology between its different parts and the anterior and posterior enterocoel of typical Echinoid larvæ cannot be carried through.

A very important point is the formation of the hydropore. Miss Medes in her figure 22 represents a double series of nuclei forming something like a canal, which appears to open on the dorsal side. This is taken to be the pore canal. I must doubt the correctness of this view. Such series of nuclei



I have observed in some sections but they appear to be merely a casual arrangement of the nuclei. On the other hand I have found in a series of transverse sections of a specimen, 11—13 hours old, a distinct canal proceeding from the enterocoel and opening on the left side, at the level of the amnion (Pl. XVI, Figs. 19—20). This canal, the existence of which is undisputable, would rather seem to represent the pore canal, in spite of its unusual position. But in order to ascertain the correctness of this interpretation it would be necessary to follow its further development and see the pore assume the normal position at the aboral pole of the urchin; this, however, could not be done on the material available. The question of the development of the hydropore (and stone canal) thus cannot be regarded as settled. On the other hand I must ascertain that no trace of a hydropore is observable in the young larva.

It is a noteworthy fact that the larvæ of 29 hours age studied by Miss Medes were in a considerably more advanced stage of development than those of the corresponding age in my material; the spines and tubefeet have not reached the same stage of development here until the age of ca. 50 hours. This may depend on the temperature, the developmental processes going faster in the tropical conditions of Badu Island than in the cooler climate of Japan. Possibly it may also indicate that the Japanese form is not really the same species as the tropical form. — By this time the tubefeet and spines begin to protrude from the amniotic cavity. This takes place partly through the natural opening, which has gradually been somewhat transplanted to the dorsal side of the larva (Pl. XVI, Fig. 10; comp. also figure 20 of Miss Medes' paper), the young sea-urchin thus in fact coming out of the mouth of the larva; partly also the dorsal wall of the amnion, together with the dorsal wall of the larva is broken through directly, both the dorsal wall of the amnion and the larval skin being by that time very thin.

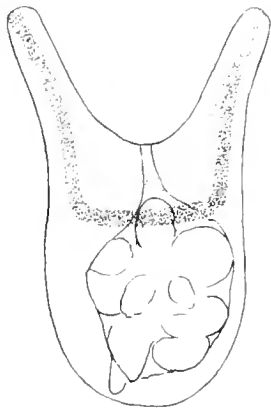


Fig. 48. Larva of *Peronella Lesueuri*, 5 days old. Abnormal; showing distinct vibratile band.  $106/1$ .

The development of the plates and other structures of the young sea-urchin cannot be considered here. I would only point out the presence of a pair of long spines at the posterior end of the body, much as it is represented in *Echinocyamus pusillus* in Pl. IX, Fig. 107 of Théel's monograph. Such a pair of long posterior spines were also found in the newly metamorphosed *Astriclypeus mauni*, and they may perhaps prove to be of general occurrence in young Clypeastroids (and Spatangoids); possibly they may have some phylogenetic meaning.

It should still be mentioned that in some of the young larvæ the entoderm was everted, turning inside out. Some of these abnormal larvæ were isolated in order to see what would become of them. They partly assumed the normal shape again, the entoderm being again invaginated, and afterwards developed normally, being only somewhat delayed in their development, so that at the age of five days they were at a stage of development corresponding to that of two days age in the normal larvæ. These belated larvæ otherwise showed the very interesting feature of having a distinct vibratile band (Fig. 48), which was never observed in any of the normal larvæ.

**Echinobrissus (Oligopodia) recens** (M. Edw.).

Pl. XI, Figs. 4—5.

On my visit to New Zealand I was, of course, very anxious to get an opportunity of studying the development of this interesting Echinoid, which is known with certainty to occur only in New Zealand waters. It was not met with on the trip with the "Hinemoa" (comp. above p. 62). On my return to Wellington I then made (on the 16th of February) a little dredging trip from there, the species being known to occur in the neighbourhood, as it is sometimes found washed up on the beach there. After some unsuccessful attempts in the Cooks Strait I had the pleasure of finding some few (9) adult specimens and also some young ones in the entrance to Wellington Harbour at a depth of ca. 10—12 meters on a fairly coarse gravelly bottom. They proved to be nearly empty all of them, but fortunately a few females still contained some eggs in good condition, and also a ripe male was found so that it was possible to undertake fertilization, which proved successful.

The eggs are surrounded by a very peculiar membrane, which appears concentrically stratified; the inner layers are following the outline of the cleavage cells, while the outer ones remain spherical (Fig. 19). I am not sure, whether this is the fertilization membrane or it is also found in the unfertilized egg, corresponding to the mucilaginous coat of the Clypeastroid eggs. (The fertilization was undertaken somewhat late in the evening, at the Zoological Laboratory of the Victoria College, where the material from the dredging was taken, Professor H. B. Kirk kindly lending me every assistance). On account of the late hour it was also impossible to follow the cleavage process, only the two-cell stage being observed. At the age of ca. 24 hours the embryos were in the gastrula stage, and on the second day they were beginning to assume the Pluteus-shape.

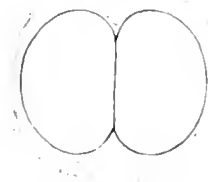


Fig. 19. Egg in cleavage of *Echinobrissus recens*, showing the peculiar membrane. After a free hand sketch.

On the 19th of February I left Wellington and then carried the culture onboard the steamer to Sydney. The young larvæ apparently not being in the very best condition, as they were mostly lying on the bottom of the dish I undertook to change the water of the culture onboard, which could not be done without some amount of trouble; but it proved to have good results; the larvæ now again appeared healthy, and they went on developing normally. On the 3rd of March, 15 days after fertilization, they had formed the dorsal arch and were evidently near metamorphosis. I now left Sydney for an excursion of some days and on my return I found the culture dead, evidently because of the excessive heat of those days. But, anyhow, valuable information about the larva of this Echinoid was obtained. There was no opportunity of making drawings of the living larvæ and, to my great disappointment, the skeleton had been dissolved in all the preserved specimens. Fortunately I had made a free hand sketch of the larval skeleton so that I am able to give information about the main features of the skeletal structure of this larva.

The shape of the larva (Pl. XI, Figs. 4—5) in general recalls that of the Clypeastroid larvæ. The body is short in accordance with the fact that the body rods are not especially elongated. The arms are all broad and flat, not very long; still they are in all probability normally somewhat longer than shown in Pl. XI, Fig. 5. One of the preserved specimens has one of the post-

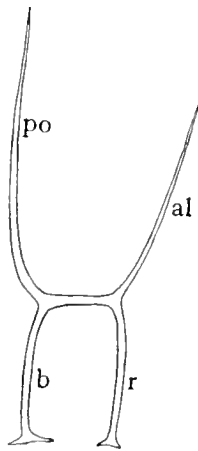


Fig. 50. Skeleton of larva of *Echino-brissus recens*; side view. After a free hand sketch from life.

Letters as in fig. 51.

oral and one of the anterolateral arms somewhat longer, which would tend to show that they have not attained their full length in the specimen figured. There is a pair of vibratile lobes on the ventral side, but none on the dorsal side, at least not in any of the preserved specimens, whereas there is a pair of small posterolateral lobes. The body is somewhat widened on the dorsal side at the level of the preoral band. The anterolateral arms are of unequal length in the preserved specimens, which may perhaps be a normal feature of the larva. The preoral arms are quite short in all the specimens. Some light yellow pigment was found in the point of the arms, the larva being otherwise unpigmented.

The skeleton (Fig. 50) recalls the Clypeastroid type; there is a well developed recurrent rod, slightly widened at the end, as is also the body rod; the processes from these rods, however, do not join so that no true basket structure is formed. The rods of the arms are simple.

It is a noteworthy fact that the larvæ on being preserved in alcohol turn green, as do the Clypeastroid larvæ. Also the adult specimens have

that peculiar property of turning green on being preserved in alcohol, so characteristic of the Clypeastroids. These facts, together with the characters of the larva, decidedly indicate that *Echinobrissus* is related to the Clypeastroids, not to the Spatangoids, which, of course, applies to the Cassidulids in general.

***Brissus Agassizi* Döderlein<sup>1)</sup>.**

Fertilization of this species was undertaken at the Biological Station, Misaki, on June 21st. The eggs are small and very clear, and the cleavage is stated in my notebook to be "ideally beautiful."

The gastrula stage was reached at the age of 1.4 hours. The larva is a typical Spatangoid larva, with an unpaired posterior process, not very long. At the age of 7 days the postero-dorsal arms had begun to develop and the dorsal arch had just appeared. There is a prominent cluster of red pigment in the point of the long and slender postoral arms, and also the posterior process is red pigmented in nearly its whole length. The larvæ were observed to swim horizontally just beneath the surface film.

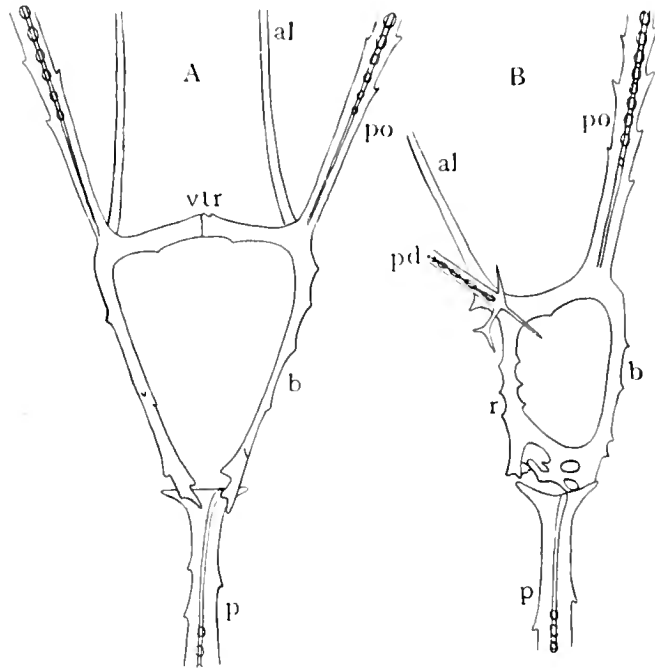


Fig. 51. Skeleton of larva of *Brissus Agassizi*. A. from the ventral side; B. side view. <sup>200</sup>/<sub>1</sub>. al, anterolateral rod; b, body rod; p, posterior rod; pd, postero-dorsal; po, post-oral; r, recurrent rod; vtr, ventral transverse rod.

Although the larvæ were kept alive until the 10th of July they did not develop beyond this stage. Thus the important question whether postero-lateral arms are present in this larva or not could not be settled, and the character of the posterolateral rod, if present, remains unknown. The fact that the basal prominences of the posterior rod do not show any sign of prolongating upwards in the latest stages would seem to indicate that

<sup>1)</sup> H. L. Clark (Hawaiian a. o. Pacific Echini. Echinoneidæ . . . Spatangidæ) regards all the Pacific forms of *Brissus*, including the Panamic *Brissus obesus* Verrill, as one single species, *Br. latecarinatus* (Leske). Not yet having had an opportunity of examining the question myself, I prefer to keep for the present both the Japanese and the Panamic forms under their separate names.

there are no posterolateral rods. The postoral, posterodorsal and posterior rods are fenestrated, excepting for a short distance in the basal part (Fig. 51). The ventral transverse rods are straight and rather broad, not crossing one another with their points.

### **Brissus obesus** Verrill.

This species was found in considerable numbers in the sand in shallow water, so shallow as to be quite dry at ebb tide, at the island of Taboguilla in the Gulf of Panama; they were generally lying buried about a decimeter down in the sand. A few ripe specimens were found,

fertilization being undertaken on the 7th January 1916. The culture was not very good and the larvæ did not develop so far as to form the posterior process. It was repeatedly tried to start new cultures, but the breeding season had apparently ceased already by the end of January, and I did not succeed any more in finding fully ripe specimens which could be used for fertili-

zation. Only little information can therefore be given about the larva of this species, the more so as the skeleton of the preserved larvæ has been dissolved. Although no posterior process had developed before the larvæ died, it is beyond doubt that it is present in this larva, since the body skeleton is otherwise of the typical Spatangoid structure. The postoral rods are fenestrated only in their outer part; the ventral transverse rods are broad as in the *Br. Agassizi*-larva. Concerning the colour I have only noticed that there is a dark-red pigment spot in the posterior end of the body.

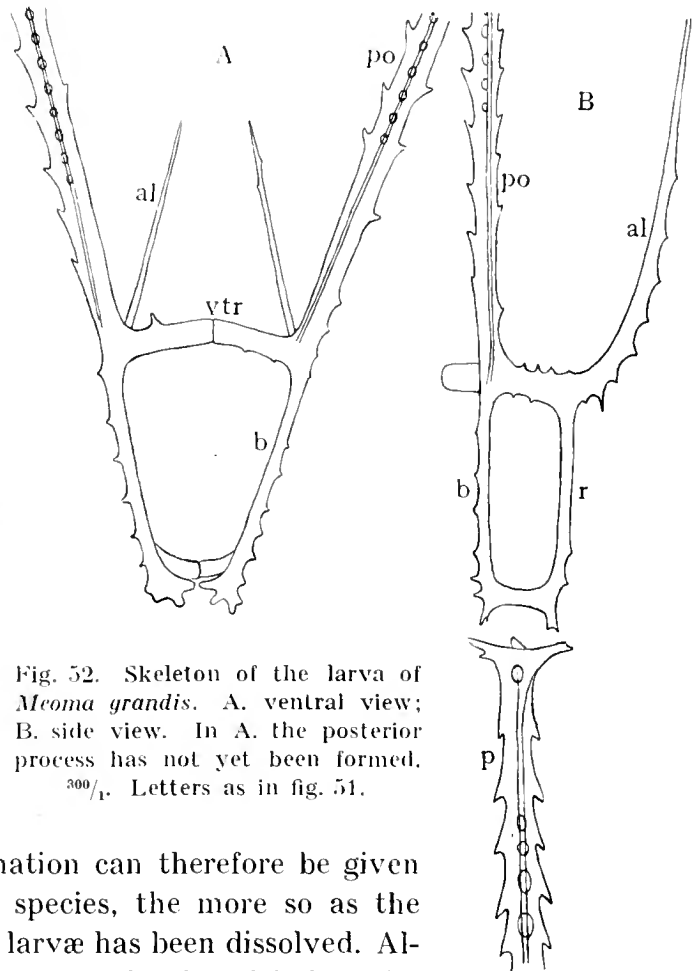


Fig. 52. Skeleton of the larva of *Meoma grandis*. A. ventral view; B. side view. In A. the posterior process has not yet been formed.  $\frac{300}{1}$ . Letters as in fig. 51.



### **Meoma grandis** Gray.

Younger specimens of this species were fairly common in quite shallow water along the sandy shore of Taboguilla in the Gulf of Panama, while larger specimens were found only in somewhat deeper water, ca. 8—10 meters; especially at the little island of Tortola they occurred in great numbers. Fertilization was undertaken on the 21st of December 1915. The cleavage had the appearance of being somewhat unusual, the cells not separating completely; but this could not be ascertained beyond doubt, the fertilization being made in the evening. The gastrula-stage was reached at the age of 14 hours; the embryos had an unusually thick ectoderm and small cleavage cavity. Already at the age of 20 hours they had assumed the shape of small Plutei, with distinct postoral arms. The posterior process did not appear until the 3rd day. I did not succeed in rearing the larvæ beyond the first stage.

The shape of the young larva is that typical of Spatangoid larvæ. There is a large patch of red pigment in the end of the postoral arms and of the posterior process. In the skeleton (Fig. 52) the broad ventral transverse rods are noticeable. The postoral rods are fenestrated, excepting the lower part; also the lower part of the posterior rod is unfenestrated.

### **Echinocardium australe** Gray.

Fertilization of this species was undertaken on December 28th 1914 onboard the "Hinemoa" off the northern coast of New Zealand. The larvæ developed normally until the formation of the posterodorsal arms, but not beyond that stage. Further material was, however, obtained from some plankton samples from Wellington Harbour. No other Spatangoids occurring there (— a species of *Brissopsis* was obtained farther North, off Bare Island, but this could hardly come into consideration on this occasion —), it is beyond doubt that these larvæ belong to *Echinocardium australe*.

Although none of the larvæ are in a very good state of preservation, it is evident enough that they agree very closely with those of *Echinocardium cordatum*, as might be expected on account of the fact that it is hardly possible to distinguish the adult specimens of these two "species". I have the impression that the larva of *Ech. australe* is somewhat smaller than that of *Ech. cordatum*, but it will be necessary to study the living larvæ of *E. australe* in order to ascertain whether a specific difference between the two forms can really be pointed out. I have made no notices about the coloration of the *Ech. australe*-larva.

A considerable number of Spatangoid larvæ has been found in plankton samples from various parts of the world. The study of these discloses a remarkable uniformity in shape and skeletal structure. The presence or absence of posterolateral arms appears to be an essential character, distinguishing two main groups. Among those with posterolateral arms the structure of the posterolateral rod may afford an important feature. In some of them this rod is widened, tri-carinate at the base (*Echinopluteus fusus* Mrtsn.), in others it is simple as in the larva of *Echinocardium cordatum*. The extent of fenestration of the postoral, posterodorsal and posterior rods also affords specific characters, and likewise the shape of the ventral transverse rods may be of importance. But, upon the whole, these differences are so small and so unimportant from a morphological point of view that I do not see any reason for describing the various species found in my material. I would only point out that I have specimens of the three said main groups both from the Atlantic, the Indo-Pacific and from the Gulf of Panama.

## II. Ophiuroidea.

While it is, with some very rare exceptions, a very easy thing to undertake artificial fertilization of the Echinoids and to rear the larvæ even through metamorphosis, the Ophiuroidea in general resist artificial fertilization. It appears next to impossible to find the eggs fully ripe and ready for fertilization on opening the female specimens and taking the eggs directly from the ovaries. Mostly they are found connected into clusters; those few eggs which may be found lying isolated on the bottom of the dish are not ready to accept the spermatozoa, and even being left some time free in the water will not induce them to ripen, as is often the case especially in Asteroids. Over and over again I have tried artificial fertilization of Ophiuroids in this usual way, but always in vain, and it appears that other investigators have had the same experience. Only with *Ophiothrix fragilis* (which I have not tried) it seems to be easier to obtain true artificial fertilization; at least some authors (Selenka, MacBride, Carlgren) state to have succeeded in fertilizing the eggs of this species; Selenka and Graeffe also have succeeded in doing it with *Ophiura texturata*.

By far the easiest way to obtain fertilization of the Ophiurids is this to put a number of ripe specimens, males and females, together in a dish. It may then happen that some of them will cast their sexual products; probably it will generally be some male which starts to emit its sperm, and then the sperm in the water acts as a stimulus inducing the female

to shed the eggs. The fertilization follows immediately, and the eggs develop normally. In this way I have succeeded in obtaining the larvæ of several species, and also other investigators have succeeded in the same way (Apostolidès, Fewkes, Grave).

But even if one succeeds in obtaining the young larvæ, the difficulties are not at an end. The Diatom cultures, which are used so successfully for feeding the Echinoid-, Asteroid- and Holothurioid-larvæ, are not readily accepted by the Ophiuroid-larvæ and apparently do not form a proper food for them. It is very probable that cultures of different Flagellates will prove to give good results, and this should of course be tried on future occasions. But this has not yet been done. The results obtained till now, those of my own researches included, are thus comparatively poor, and especially quite insufficient with regard to the main object of the present researches, the study of the interrelation between the larvæ and the adults and their bearing on a natural classification.

There is also another way in which it is possible to trace the larvæ to their parental origin, viz. to rear the Ophiurid from the larva. When taken from the plankton in so far advanced a stage of metamorphosis that feeding has ceased, the larvæ, if unhurt and carefully transported to separate dishes, will go on metamorphosing. If then suitable conditions are given the young Ophiurid, it is possible to rear it, till it has grown to a size which allows identification. This was done recently by the author with *Amphiura filiformis*<sup>1)</sup>. There is no doubt that we may obtain important results in this way owing to the fortunate circumstance that the main specific characters of the larvæ remain unaltered till metamorphosis is almost complete, so that it is very well possible to identify first the larvæ and then later on the Ophiurid developing from it and thus to establish their genetic relation.

Till now, however, both methods have yielded so few results that not much can be concluded therefrom, and the question whether definite types of larvæ corresponding to the larger groups of Ophiurids can be recognized does not get a definite solution from the knowledge thus acquired; indeed, the impression conveyed by the facts hitherto made known rather comes to this that there are no such natural groups among the Ophiurid-larvæ.

The Ophiurid larvæ are very easily preserved in a fairly good condition, in general far better than the Echinoid-larvæ; even in usual plankton samples, preserved simply in alcohol, Ophiuroid-larvæ may be found in very good, or at least in fully recognizable state. On account of this fortunate circumstance I have been able to collect a very large material of

<sup>1)</sup> Th. Mortensen. Notes on the development and the larval forms of some Scandinavian Echinoderms. Vid. Medd. Vol. 71. 1920. p. 138.

Ophiuroid-larvæ from many different parts of the world. It occurred to me that this material might, on a careful comparative study of all the larvæ, perhaps give some answer to the question, whether it is, upon the whole, possible to distinguish natural groups in the great variety of forms, or whether there is no system at all. The results of this study has fully borne out the expectations. It was found possible to distinguish several very well characterized groups, and there is good reason to expect that future researches will give no less satisfactory results than those obtained from the study of the Echinoid-larvæ.

Besides the finding of several new, interesting larval types the study of this material led to a most interesting observation. It is well known from the observations of Joh. Müller (V. Abhandl. Taf. VII—VIII) that the metamorphosing larva of *Ophiothrix* keeps its long posterolateral arms unaltered, the young Ophiurid remaining for some time attached to these arms, which thus serve as a floating apparatus. When ultimately the Ophiurid drops off, these two arms still remain in connection and may continue their pelagic life for some time, the vibratile band along the arms remaining quite intact. I have often found such "specimens" in considerable numbers in the plankton samples (Pl. XIX, Fig. 6). The same may occur in other larvæ, e. g. *Ophiopluteus opulentus* (Pl. XX, Fig. 3). In this latter case, however, it appears that the "larva" does not perish after a little while, as it must doubtless happen to the *Ophiothrix*-"larva". In the figure quoted a small swelling is to be noticed in the middle, where the two arms join. In other specimens this swelling is considerably larger and shows an indication of a mouth and a vibratile band and there are small postoral (or anterolateral) rods. This can only mean that a new larval body is about to regenerate from the posterolateral arms, after the young Ophiurid has been developed and dropped off. The fact that the posterolateral arms are perfectly developed proves that we have not simply with an abnormal larva to do; it would be impossible that such abnormal larva with the mouth and intestinal organs imperfectly developed and accordingly unable to feed, could have developed these long arms and their supporting rods perfectly normally. It must then, evidently, be accepted as an established fact that a regeneration of the larval body has taken place here. Whether it would ultimately proceed so far as to result in the formation of a normal new larval body and then a second metamorphosis, must be left an open question; this could probably be ascertained only from a study of living material. But the fact here established that a regeneration of the larval body begins after the completed metamorphosis and may be carried quite a long way is of considerable interest.

It is worth mentioning in this connection that such cases, where regeneration of an arm after some injury appears to have taken place, are not very rarely met with.

I may here point out the fact that the metamorphosis in the Ophiurid larvæ may proceed after two different types. One is that occurring e. g. in *Ophiothrix* and *Ophiopluteus opulentus*, where all the inner arms are absorbed, the posterolateral arms alone remaining unaltered, to be cast off on completion of the metamorphosis: in the other type, which appears to be of more usual occurrence, also the right anterolateral arm remains intact, together with the posterolateral arms, until in a more advanced stage of metamorphosis all these three arms are also absorbed (Pl. XXIV, Fig. 3; Pl. XXIX, Fig. 3; Pl. XXX, Fig. 2).

It must be left for future researches to find out, whether this remarkable difference has any deeper meaning. I would only here in general emphasize the fact that the metamorphosis of the *Ophiothrix*-larva cannot serve to typify that of all Ophiurids with a well formed Pluteus-larva. Thus e. g. the hydrocoel, in growing to form the hydrocoel-ring, will in some forms start growing from the upper end, in others from the lower end, which certainly makes a considerable difference, both from a morphological and from a biological point of view. Also some conspicuous peculiarities obtain with, at least, the initial stages of metamorphosis in the *Ophiopluteus bimaculatus-serratus* group.

The fact that in several forms, especially those which keep one of the anterolateral arms intact during metamorphosis, the ciliated band is broken up in pieces, so as to recall the ciliated rings in the Auricularian pupa, may merely be hinted at here. The discussion of its meaning must be left for another occasion.

### **Ophiopluteus of Ophiothrix.**

The *Ophiothrix*-larva is a characteristic, easily recognizable larval type, The posterolateral arms are generally much diverging, sometimes nearly horizontal; they are considerably longer than the inner arms. The body skeleton is simple, with a single small median process from the ventral and dorsal transverse rods. The body rods are mostly thick and robust. The posterolateral rods are slightly thorny along the inner side, the rods of the inner arms have few small thorns. The posterolateral arms are often conspicuously pigmented.

Characteristic of this larval type is furthermore the symmetrical position of the developing young Ophiurid, which latter is also peculiar through its ventrally incurved arms with the clawlike spines. The posterolateral arms remain intact during metamorphosis and serve as a floating apparatus

to the young Ophiurid, being cast off when metamorphosis is completed. (Comp. above, p. 124).

The study of the numerous larvæ of *Ophiothrix* (or of forms belonging at least to the family Ophiothrichidæ) which I have from different localities: Japan, the Philippines, Malacca Strait, the Gulf of Aden, the Gulf of Panama, California, the West Indies and the European Seas makes evident the interesting fact, that it is simply impossible to find reliable characters by which to distinguish with certainty the various species of these larvæ. There are some exceptions. The forms described here as species **c** and **d**, especially the latter, are fairly well characterized and easily distinguished: but the forms designated as species **a** and **b** certainly both comprise several species, as is evident from the fact that they are found in widely separated localities (Europe, West Indies, Panama, Japan), which have no species of Ophiothrichidæ in common. If specimens of these larvæ from the different localities were put together, it would be impossible to separate the different species again. Perhaps the pigmentation of the larvæ may prove to be somewhat different, so that it would be possible to distinguish the species on having the living specimens. But the pigmentation is liable to be more or less destroyed on preservation. In the skeleton no reliable distinguishing characters can be pointed out. There may be some slight differences in the length and thickness of the body rods and in the length of the median processes; but I have been unable to find any definite specific characters therein. In consequence of this fact I have thought it useless to give a description of each of these larval species, which can only from zoogeographical facts be recognized as separate species.

Species **a**. (Pl. XIX, Fig. 1). The posterolateral arms are about three times the length of the inner arms and generally have three large spots of black pigment: some smaller pigment spots are found in the posterior part of the body. The skeleton, see Fig. 53.

To this type belongs the larva of *Ophiothrix fragilis*. Specimens not distinguishable from this larva were found at Misaki, Japan (the species represented in Pl. XIX, Fig. 1); in the Malacca Strait (off Pulo Pisang, 1/XII, 1899); off the East end of Sokotra (XII, 1913); Taboga, Panama (XII, 1915); San Diego, California (7/IX, 1915); St. Cruz, West Indies (16/VI, 1915, H. Faye). Likewise the *Ophiopluteus robustus* (Echinodermen-Larven d. Plankton-Exped. p. 57. Taf. V. Fig. 3—4) from Fernando Noronha belongs to this type.<sup>1)</sup>

<sup>1)</sup> In the place quoted I stated that this larva is undoubtedly nearly related to the *Ophiothrix*-larva, then adding: "zu welcher Ophiure sie gehört kann man nicht erkennen"; the

To this same larval type further belongs the larva of **Ophiothrix angulata** Say (Var. **poicila** H. L. Clark), which I succeeded in rearing during my stay at Tobago, B. W. I. in April 1916. Ripe specimens of this species were secured on April 11th, which gave off sperm and eggs; the eggs were shed all at the same time, almost as by an explosion. The first development processes pass very much in accordance with what is known from *O. fragilis*. At the age of 18 hours the embryos were found to be lenticular in shape, but still without skeleton. At the age of 21 hours they were already small plutei with fairly long posterolateral arms, the other arms not yet having appeared (corresponding to the stage represented in Pl. 31, Fig. 6

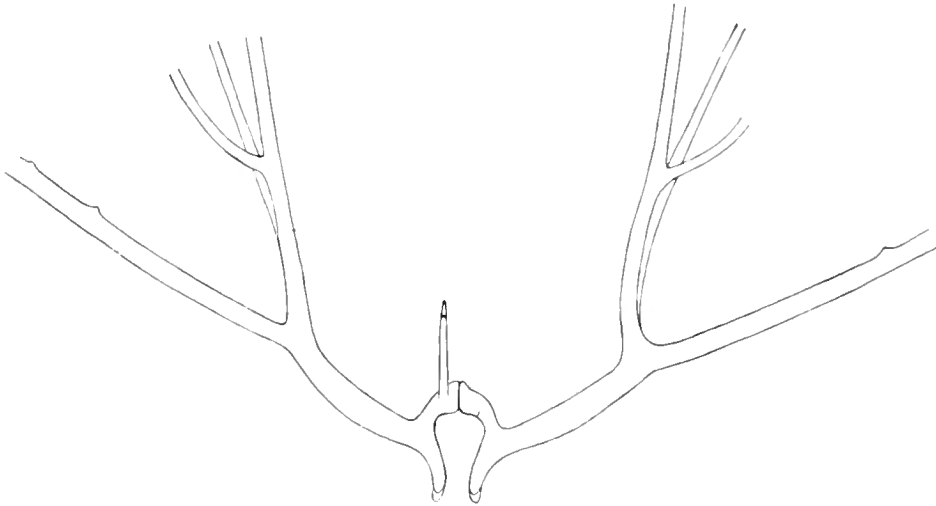


Fig. 53. Skeleton of *Ophiopluteus* of *Ophiothrix*, species **a.** <sup>290</sup>/<sub>1</sub>.

of MacBride's memoir on the development of *Ophiothrix fragilis*<sup>1)</sup>, which is, however, much older, 55 hours). At the age of 10 hours the postoral and anterolateral rods had begun to form, the corresponding arms being as yet merely indicated, while the posterolateral arms are already of considerable length; their rods are still without thorns. The larva in this stage is exceedingly characteristic, the preoral and postoral band continuing almost straight across the anterior edge of the body (Pl. XX, Fig. 1). At the age of 4<sup>1</sup>/<sub>2</sub> days the larvæ had reached nearly their full shape, only the inner arms not having attained their full length (Pl. XX, Fig. 2). Thorns had begun to appear on the posterolateral rods; the median process from the transverse rods had not yet been formed. A small group of red pigment grains is found near the base of the posterolateral arms, and there

meaning was, of course, that it is impossible to decide to which species it belongs, as it could hardly be doubted that it must belong to some species of the genus *Ophiothrix*.

In the "Echinodermlarven d. deutschen Südpolar-Expedition" (1913 p. 98) this larva was recorded from off Ascension.

<sup>1)</sup> Quart. Journ. Micr. Science, Vol. 51, 1907.

is a very faint indication of yellow color at the point of these arms. The stomach has assumed a faint yellowish tint. The red pigment at the base of the posterolateral arms is indicated already in the stage represented in Pl. XX, Fig. 1.

Beyond this stage I did not succeed in rearing this larva, the culture being only small. Still the result acquired is sufficient for showing the very close resemblance of this larva with that of *Ophiothrix fragilis*. Only in the pigmentation there appears to be a distinct difference between these two larva, that of the *O. fragilis*-larva being black. Also the time required for the development appears to be rather different in the two species; at least the earlier stages require much shorter time in *angulata* than in *fragilis*.

It would appear to be characteristic of this larval type (and perhaps of all larvæ of Ophiothrichidæ) that the oral lobe is late developing, the ciliated bands going in a nearly straight line along the anterior border of the body, whereas in other Ophiuroid larvæ the oral lobe develops much

earlier. (This characteristic young stage of the *Ophiothrix* larva was figured already by Joh. Müller in his V. Abhandl. Taf. VI. Fig. 8).

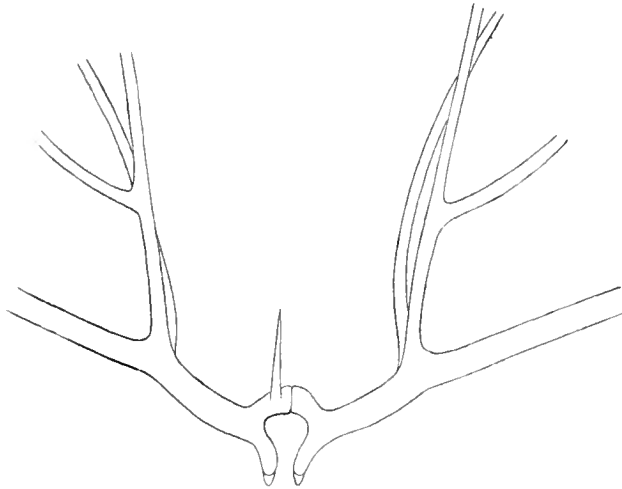


Fig. 54. Skeleton of *Ophiopluteus* of *Ophiothrix*, species **b.** <sup>290</sup>/<sub>1</sub>.

Species **b.** (Pl. XIX, Figs. 3—6). This larva is characterized by the great length of the posterolateral arms, which are generally about 6—7 times the length of the inner arms; these arms also form a more obtuse angle than in species **a**, in fact,

they may almost make a straight line. Otherwise there is no noteworthy difference from species **a**. Also the skeleton (Fig. 54) is alike, only the body rods being slightly shorter. The pigmentation appears to be as in species **a**, black spots on the posterolateral arms.

As seen by a comparison of the figures quoted, there is a rather considerable amount of variation among the larvæ referred to this "species", both with regard to the length and the outward direction of the posterolateral arms. Possibly they represent in reality two different species. The specimens figured are all from the Gulf of Panama. Now, so far as I can see, without going too deep into literature, only one species of *Ophiothrix*, *O. spiculata* Le Conte, has been recorded from there; but it can hardly



be doubted that *O. dumosa* Lym. and *O. rudis* Lym., both known from off Southern California, will be found there also. It is thus very well possible that the specimens from Panama comprised here under species **b** really represent two or three different species.

Specimens referable to the same type and hardly distinguishable from the specimens from Panama were found in the Malacca Strait (30/XI, 1899); in the Gulf of Aden (14/XI, 1899; 2—3/V, 1900); in the Red Sea, off Jebel Zukur (5/IV, 1900); in the Bay of Bengal (5° 50' N. 85° 30' E. 4/I, 1914).

To the same larval type the larva from the Adriatic Sea, figured by Joh. Müller in his V. Abhandl. Taf. VII. Fig. 1, must further be referred. In the "Echinodermenlarven d. Plankton-Exped." p. 56 I have referred this larva to *Ophiothrix fragilis*, as is also done by Joh. Müller. It is, however, more probable that it belongs to the other *Ophiothrix*-species found in the Adriatic, viz. *O. echinata* M. & Tr. The fact that in the Danish seas, where only *O. fragilis* occurs, only the larval type of species **a** has been found, is not in favour of the suggestion that we may have here only a variety of the *O. fragilis*-larva. If that should be proved ultimately to be the case, it would be impossible to distinguish the larval types of species **a** and **b**, and the larva of *O. fragilis* and other related species would turn out to have an extraordinary range of variation.

Species **c**. (Pl. XIX, Fig. 2). This species has the same shape as species **a**, but differs markedly from it in the pigmentation, the

postero-lateral arms being strongly pigmented (black?)

in their whole length, continuously, not in spots separated by unpigmented parts. In the skeleton no noticeable difference appears to exist (Fig. 55 to compare with Fig. 53). The small difference in the shape of the transverse rods seen in the two figures is hardly constant enough to represent a valid specific difference.

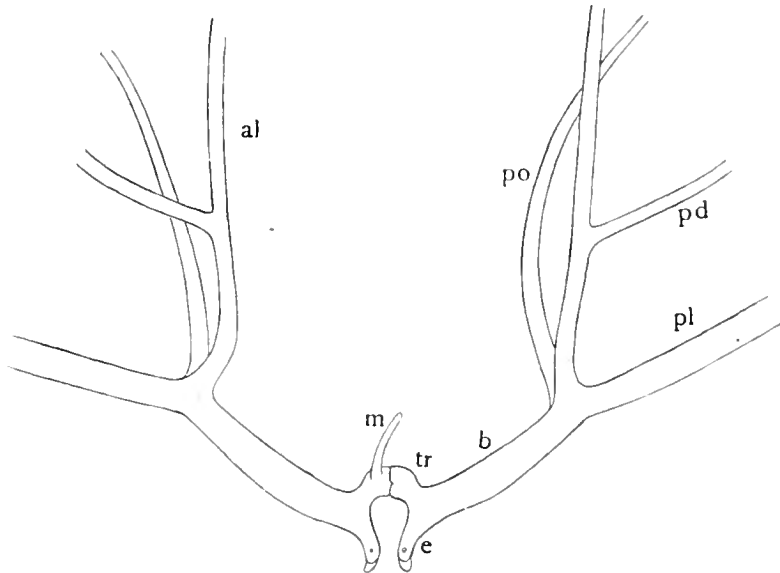


Fig. 55. Skeleton of the *Ophiopluteus* of *Ophiothrix*, species **c**. <sup>290/1</sup>. al. anterolateral rod; b. body rod; e. end rod; m. median process; pd. posterodorsal; pl. posterolateral; po. postoral rod; tr. transverse rod.

This species was met with only at Jolo in March 1914; there are 4 specimens. Unfortunately it was not observed alive, so that the color of the pigment is uncertain, but it looks in the preserved specimens very much like the black pigment of the *O. fragilis*-larva.

Species **d.** (Pl. XIX, Fig. 7). Although in its main characters in conformity with the general type of the *Ophiothrix*-larvæ this species is markedly distinguished from the other species of this type by several characters. The postoral and posterodorsal arms are not much more than half body

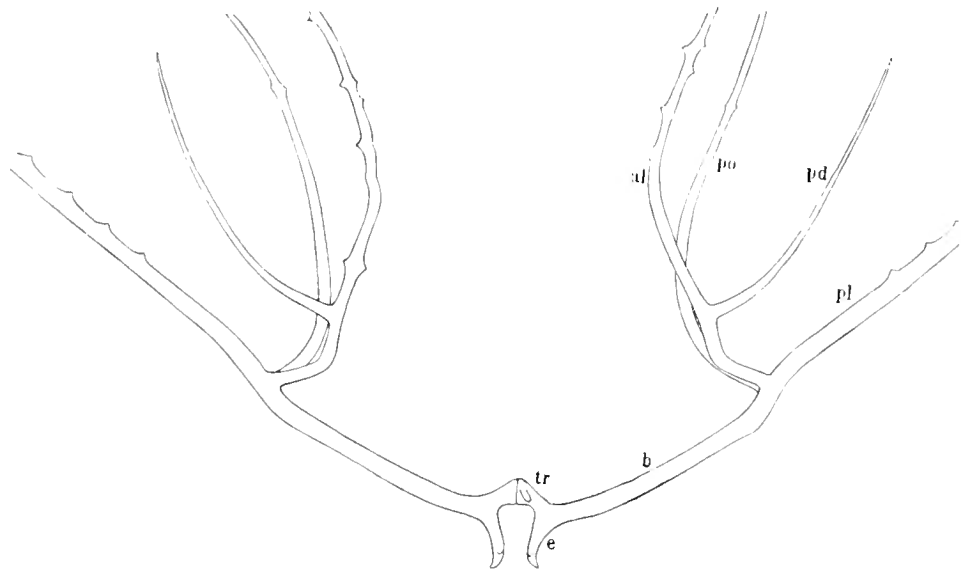


Fig. 56. Skeleton of *Ophiopluteus* of *Ophiothrix*, species **d.**  $\frac{220}{1}$ . Letters as in fig. 55.

length, the anterolateral arms even shorter, only about  $\frac{1}{3}$  of the body length; the posterolateral arms are three times the length of the body. All the arms have a distinct widening at the point. The body is wider than usual, corresponding to the unusual length of the body rods. The skeleton (Fig. 56) differs from that of the usual *Ophiothrix*-type, besides in the great length of the body rods, in the distinct curvature at the point where the rods of the arms issue. The postoral and the anterolateral rods have some rather coarse thorns, and also the posterolateral rods are more closely thorny along their innerside than is the rule in other *Ophiothrix*-larvæ. The anterolateral rods also show a characteristic angular curve below the point of issue of the posterodorsal rod, from there proceeding straight on to somewhat above that point, where it then once more fairly abruptly bends.

The inner structure was indiscernible in the single specimen in hand,

and has been reconstructed in free hand in the figure. It is then quite possible that the stomach really fills the whole space between the skeletal rods. Also the anterior vibratile band was indiscernible. — The pigmentation is characteristic, consisting of fairly large pigment cells, scattered along the body rods.

Only one specimen of this very interesting larva was found, off Jolo, 20/III, 1914. That it belongs to one of the Ophiothrichidæ seems fairly certain; in all probability it does, however, not belong to the genus *Ophiothrix* itself, but rather to one of the other genera within that family.

### Ophiopluteus of Ophiocoma.

*Ophiopluteus Henseni* Mrtsn.

In a note on the "Embryology of *Ophiocoma echinata*"<sup>1)</sup> Caswell Grave reports having reared the larva of this species, but gives no descrip-

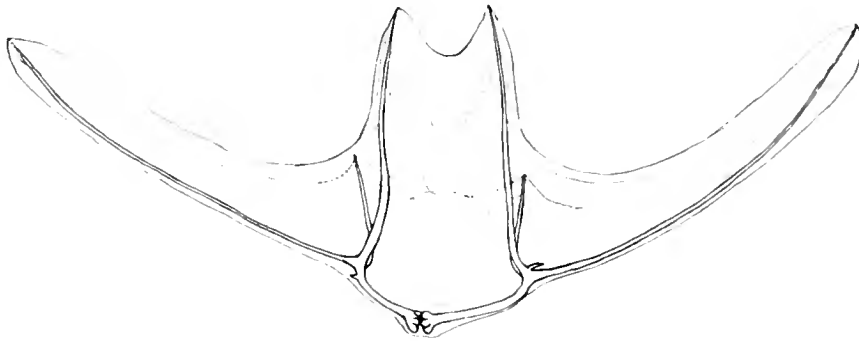


Fig. 57. Larva of *Ophiocoma echinata*, 11 $\frac{1}{2}$  days old. After a sketch from life by Caswell Grave, 10/VIII, 1897.

tion or figures of it, only the first embryonal stages being described. A full report was never published. On my applying to Professor Grave concerning this larva he most kindly sent me a sketch of the larva at the age of 11 $\frac{1}{2}$  days for free disposal. Also slides containing some young larvæ were sent me. The sketch proved especially valuable, making it possible to identify the *Ophiocoma*-larva with full certainty; it is reproduced in a reduced scale in Fig. 57. I beg to express my deep gratitude to Professor Grave for his kindness in supplying me with this important information.

In the said paper Grave mentions that the eggs "after being fertilized threw about themselves a tough prickly egg membrane", as is also shown in figs. 1—2 of that paper. I would suggest that this peculiar membrane, otherwise unknown in Ophiurids, is a special adaptation, serving as a

<sup>1)</sup> Johns Hopkins Univ. Circulars. Vol. 18. 1898. p. 6—7.

floating apparatus, as appears to be the case in the Crinoids *Tropiometra carinata* and *Antedon petasus*.<sup>1)</sup>

Eminently characteristic of this larva is the body skeleton. The body rods are simple, nearly horizontally directed; there is a deep sinuation at the point of issue of the rods of the arms. The end rods and the transverse rods are very short and broad, forming together, as it were, a link between the two parts of the skeleton. — The stage figured is too young to show the shape of the fully formed larva; it is only evident that the posterolateral arms are fairly broad. By means of the skeletal characters it is, however, possible with certainty to recognize some of the larvæ in my material as belonging to the genus *Ophiocoma*, and through these it is again proved that the larva described in my Echinodermen-Larven d. Plankton-Exped. (Taf. VII, Fig. 2) under the name of *Ophiopluteus Henseni* is the larva of *Ophiocoma* which is, accordingly, peculiar through having a kind of epaulets or rather vibratile lobes, otherwise unknown in Ophiurid-larvæ, excepting only the larva of *Ophiocomina nigra*.

The type specimen of *Ophiopluteus Henseni* had the skeleton dissolved. There is thus no possibility of ascertaining whether the latter is the fully developed larva of *Ophiocoma echinata*; I would rather be inclined to think that it could not be that species, the shape of the young larva differing not inconsiderably from the *O. Henseni*; especially the hind edge of the body is so different that it could hardly depend on age (or preservation) alone. In conformity with the nomenclature adopted in this work, I shall then designate the *Ophiopluteus Henseni* as *Ophiopluteus* of *Ophiocoma*, species **a**, referring to the description and figure given in the work quoted.

Species **b**. The shape of the body appears to agree very completely with that of species **a**; none of the specimens in hand are, however, sufficiently well preserved for being figured. The skeleton (Fig. 58) differs from that of the *O. echinata*-larva in the body rods being quite horizontal; also the basal part of the posterolateral rods is horizontal, the result being an extraordinary width of the skeleton, corresponding to the width of the posterior part of the larval body, as seen in the figure of species **a** (*Ophiopluteus Henseni*). The transverse rods are very short, pipe-shaped, thickened; the end rods are even shorter, also somewhat widened. All the rods

<sup>1)</sup> Th. Mortensen. Studies in the development of Crinoids. Papers from the Department of Marine Biology. Carnegie Inst. Washington. Vol. XVI. 1920.

Th. Mortensen. Notes on the development and the larval forms of some Scandinavian Echinoderms. Vid. Medd. Dansk Naturh. Foren. 71. 1920. p. 151.

Also the eggs of *Ophioderma brevispina* Say float, but in this case it is the large content of yolk which makes them float, no special structure of the egg membrane apparently serving as a floating apparatus. (Casw. Grave. Ophiura brevispina. Mem. Biol. Lab. Johns Hopkins Univ. IV. 5. 1900. — Ophiura brevispina. II. Journ. of Morphology. 27. 1916).

of the arms are perfectly smooth. The posterodorsal rods issue very near the base of the anterolateral rods; they are slightly widened at their base.

Five specimens of this larva were found in a plankton sample from off Taboga, the Gulf of Panama, taken in November 1915.

Among some larvæ presented to me many years ago by Prof. V. Hensen, Kiel, collected in January 1897 in the Bismarck Archipelago, there are a few specimens of this same larval type. Unfortunately the skeleton has been dissolved, and as the preservation is also otherwise poor, I shall give no description of these larvæ; but it is evident that we have here another

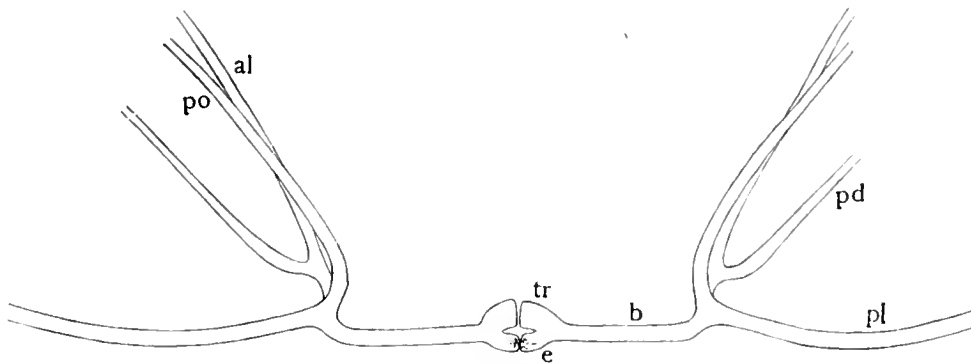


Fig. 58. Skeleton of *Ophiopluteus* of *Ophiocoma*, species **b**.  $\frac{290}{1}$ . Letters as in fig. 55.

species of *Ophiocoma*-larva, closely related to and very similar to species **a** and **b**, but different from both, of course, since there is no species of *Ophiocoma* common to these seas.

Species **c**. (Pl. XXX, Fig. 1). The shape of the body differs considerably from that of species **a** and **b**, the hind end of the body being not nearly so broad and flat as in those species; further the vibratile lobes are much less developed. (In the figure the two ventral ones are directed outwards and thus rather inconspicuous). The body is fairly elongated, the frontal area large. The preoral ciliated band forms a high arch, and the postoral band curves somewhat downwards in the middle, besides making a slight sinuation at each side. The arms are all short, the posterolateral ones only slightly exceeding the body length, the other arms merely about half the length of the body. They are all fairly broad and flat, but hardly widening at the point.

The skeleton (Fig. 59) is much more like that of *Ophiocoma echinata* than that of species **a** and **b**, the body rods being not horizontal, but rather more erect than in *O. echinata*. The posterolateral rods are slightly widened a little beyond the base (Fig. 60). The transverse rods are less widened than in species **b**, and the end rods are directed straight downwards, while in species **b** they are medially directed like the transverse rods. The rods

are smooth, excepting a pair of small thorns sometimes found in the lower part of the anterolateral rods.

There are some specimens of this larva from off Taboga, in the Gulf of Panama, taken in November 1915. None of them are so far developed

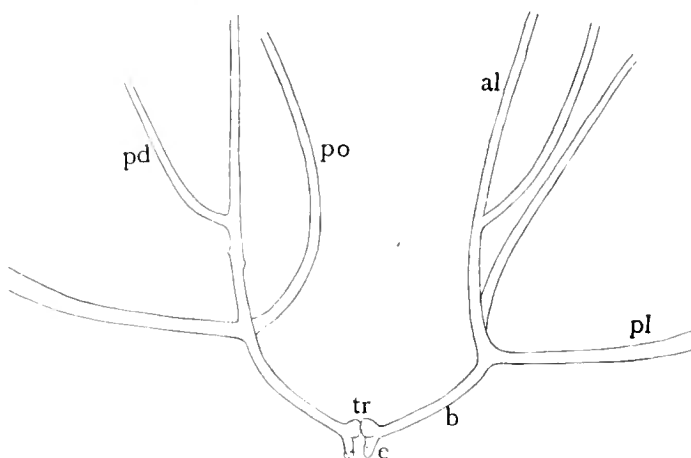


Fig. 59. Skeleton of *Ophiopluteus* of *Ophiocoma*, species c. <sup>290/1</sup>. Letters as in fig. 55.

that the hydrocoel has begun to form the primary lobes, and none of them are in a very good state of preservation, but it was possible to give a — slightly restored — figure of the larva, the comparison of the different specimens in hand making it easy to ascertain the correctness of the figure.



Fig. 60. Posterolateral rod of same larva. <sup>290/1</sup>.

It is a very noteworthy fact that the only other Ophiuroid-larva known to have vibratile lobes is the larva

of *Ophiocomina nigra*, which — although it has recently<sup>1)</sup> been removed from the genus *Ophiocoma* to which it was hitherto referred — is, evidently, related to the Ophiocomidæ and must probably be referred to that family. The skeleton of that larva differs, however, markedly from that of the *Ophiocoma*-larva, the transverse rods and end rods not forming a “link” as in the latter, but being of the type usual in Ophiurid larvæ. This difference in the skeleton from that of the *Ophiocoma*-larva is an additional proof of the necessity of removing the species *nigra* from the genus *Ophiocoma*.

### ***Ophiopluteus costatus* nova forma.**

This larval type is eminently characteristic through the unique feature of having a separate median skeletal rod supporting the high frontal area. The body skeleton is of the compound type, with a median ventral and dorsal process from the transverse rods. The posterolateral arms are

<sup>1)</sup> Th. Mortensen. Notes on some Scandinavian Echinoderms, with descriptions of two new species of Ophiurids. Vid. Medd. Dansk Naturh. Forening. Bd. 72. 1920, p. 50—54.

somewhat erect and very long, much longer than the inner arms; the posterolateral rods are strongly thorny along the inner side, more or less canaliculate.

Species a. (Pl. XXI, Fig. 1). The body length is 0.4 mm. The shape of the body is somewhat unusual through the frontal area being exceptionally high, the distance from the preoral ciliated band to the anterior edge being about half the distance from the postoral band to the preoral band is some- the middle. The postero- the body length, the than body length; the ly longer than the post-

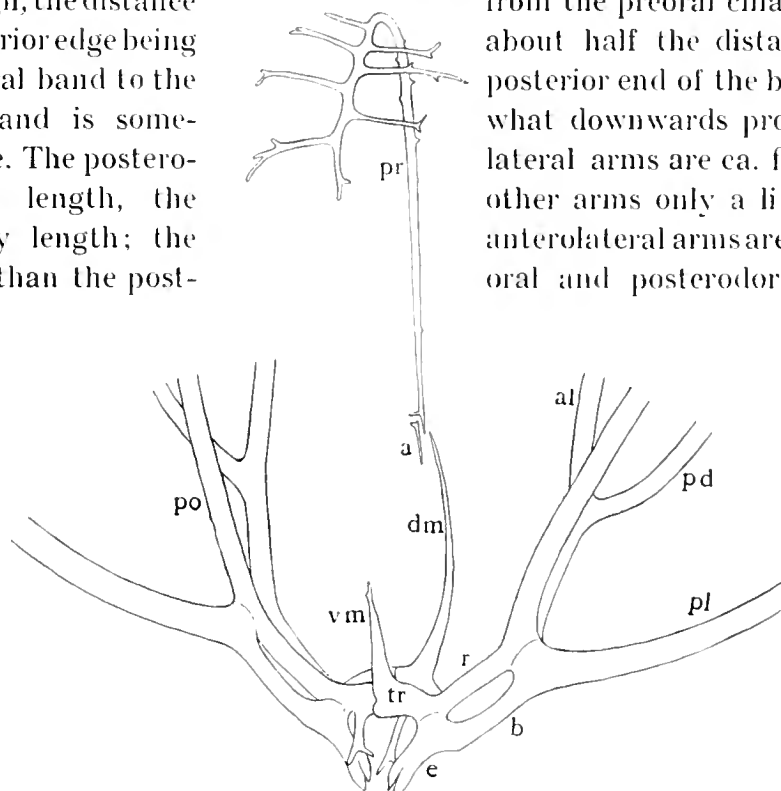


Fig. 61. Skeleton of *Ophiopluteus costatus*, a.  $\frac{290}{\mu}$ . a. accessory rod; al. anterolateral rod; b. body rod; dm. dorsal median process; e. end rod; pd. posterodorsal; pl. posterolateral; po. postoral; pr. preoral rod; r. recurrent rod; tr. transverse rod; vm. ventral median process.

There appears to be no swelling at the point of the arms. Pigmentation unknown.

Skeleton (Fig. 61). The body skeleton is fairly robust. The transverse rods are short and thick; from one of them proceed on the ventral side a short, pointed median process, and on the dorsal side a much longer, simple rod, the dorsal median process. A smaller process is directed backwards, with a small side branch near the end; there is one both on the ventral and on the dorsal side. The end rods are short, trifold. The posterolateral rods are set with thorns along their inner sides; they are peculiar in having what looks like a narrow canal in the lower part, reaching from the first thorn until about the middle, where it ends with a small swelling in one (the right) arm, while in the left arm it passes some way beyond this point

(Fig. 62). It appears to open in some places through small pores on the inside of the rod. The rods of the other arms are quite smooth.

While there is nothing remarkable in the structure of the skeleton thus far described, excepting the unusual feature of the canal in the postero-



Fig. 62. Part of postero-lateral rod of *Ophiopluteus costatus*, species a. <sup>500</sup>/<sub>1</sub>.

lateral rod, the separate rod developed on the dorsal side along the median line of the body represents quite a novel feature, otherwise entirely unknown in Ophiurid-larvæ. This extra rod, the preoral rod, as it may be termed, proceeds from the upper end of the dorsal median process upwards to the anterior end of the body, where it bends over to the ventral side and then proceeds downwards over the frontal area unto the preoral band. While the dorsal part of this rod is only slightly thorny, the part on the ventral side is provided with very long side branches, so that it has the appearance almost of a spinal column with its ribs. (The name *costatus* refers to this peculiarity). This remarkable skeletal rod supports the unusually large preoral part of the larval body, which forms like a large vault over the mouth of the larva. — The ends of the median process and the preoral rod nearly touch one another, but do not join and remain separately movable. In this place furthermore a quite small, styliform skeletal rod, the accessory rod, is found, which may perhaps have some function in connection with the movements of the oral lobe.

One specimen of this larva, fully developed, showing the five lobes on the hydrocoel, was taken in the Red Sea, 17° 40' N. 40° 10' E. 12/XI, 1899. Besides there are two younger specimens, taken at the same time, which may probably belong to the same species. The preoral rod has merely an indication of side branches, and there is no accessory rod. The backwards directed processes from the transverse rods have not yet developed. The posterolateral rods are canaliculate unto the very points in one specimen, not at all canaliculate in the other; but in this latter specimen they are, upon the whole, somewhat abnormal. — Both specimens being young and in a poor state of preservation, it is impossible to ascertain whether they belong to species a or to a separate species.

Also from 25 miles S.E. of Minikoi (1/I, 1914) there is a specimen of *O. costatus*, which probably belongs to species a; but it is in too bad a state of preservation for definitely ascertaining to which species it belongs.

Species b. (Pl. XXI, Fig. 2). The size and general shape of the body are as in species a. The arms are somewhat longer, the posterolateral ones six times, the other arms about twice the body length, the antero-



lateral arms being somewhat shorter than the postoral and posterodorsal arms.

Skeleton (Fig. 63). The body skeleton is somewhat more robust than in species *a*. The ventral median process is long, reaching to the anterior edge

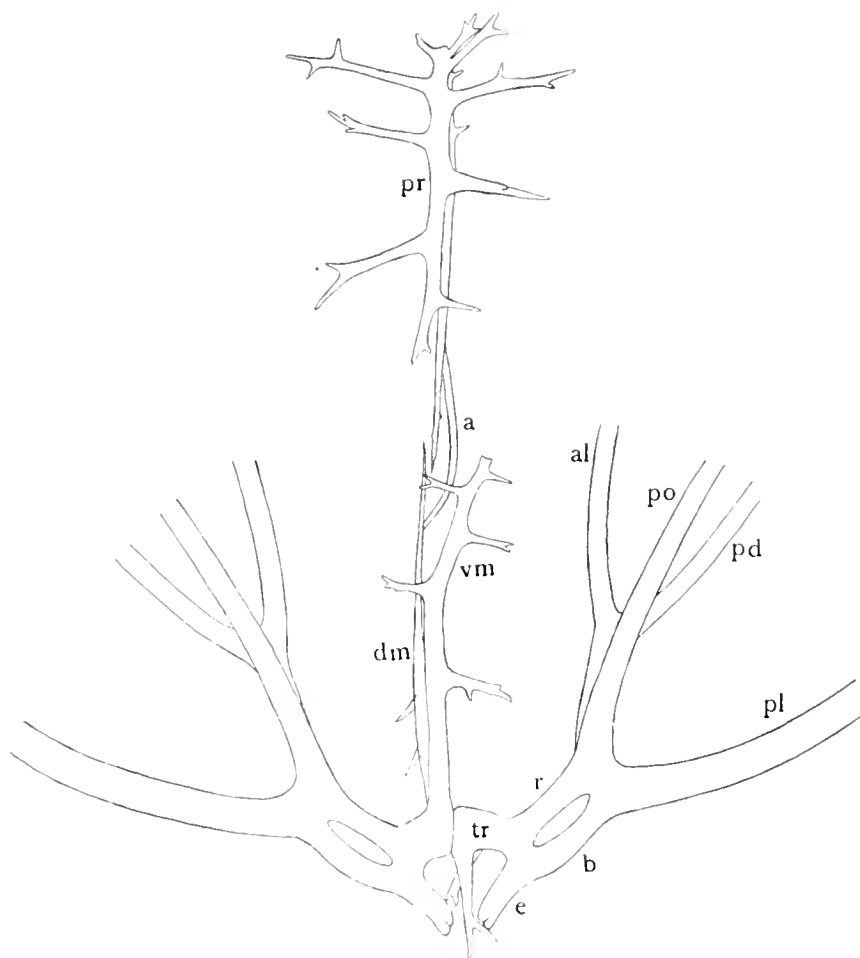


Fig. 63. Skeleton of *Ophiopluteus costatus*, species *b*.  $\frac{290}{1}$ .  
Letters as in fig. 61.



Fig. 64.  
Part of  
postero-  
lateral rod  
of *Ophiopl.*  
*costatus*,  
species *b*.  
 $\frac{400}{1}$ .

of the anal lobe; it has some conspicuous side branches, while the dorsal median process, which is of about the same length, is simple, pointed, only with a few backwards directed thorns in the lower part. The posterolateral rods are set with much larger thorns than in species *a*, and the "canal" is quite short, reaching only from the lowermost to the third spine (Fig. 64), and there is no widening at its upper end. The preoral rod reaches much farther down on the ventral side, beyond the preoral and even over the postoral band, so that a flap of the frontal area proceeds downwards over the oral area, covering the mouth. The exact shape of the accessory

rod could not be made out; but in any case it is somewhat curved and distinctly longer than in species **a**.

One specimen from the Malacca Strait, 7° 20' N. 98° 4' E. 7/IV, 1900.

Another specimen from the Malacca Strait (5° 53' N. 95° 43' E. 28/XI, 1899) is intermediate in its characters between the two above species. The ventral median process is as long as the dorsal, but very slightly spinous. The posterolateral rods are strongly thorny as in species **b**, but the canal

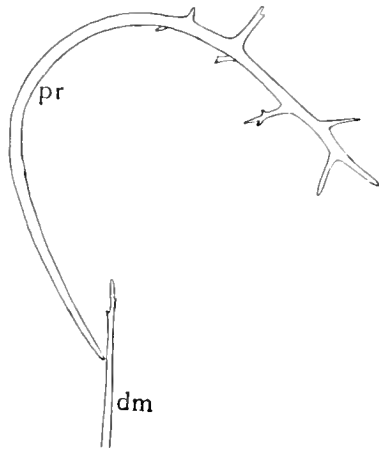


Fig. 65. Side view of preoral rod of *Ophiopluteus costatus*. <sup>290</sup>/<sub>1</sub>.  
dm. dorsal median process.

cannot be discerned. The preoral rod appears to be as in species **a**, but as it lies in a different position in the preparation, direct comparison with that of the two other species is impossible; on the other hand it affords an excellent view of this rod in side view (Fig. 65). The accessory rod appears to be lacking. The length of the arms is about as in species **a**. In this specimen, as well as in the type of species **b**, the primary lobes of the hydrocoel have not yet been formed.

On account of the insufficiency of the material available it is impossible at present to decide whether this latter specimen

belongs to species **a** or, perhaps, represents a third species. That, at least, the two forms described as species **a** and **b** are distinct species seems, however, beyond doubt.

It is quite impossible to give any reasonable suggestion as to which Ophiurid may be the adult form to which this very interesting larval type belongs.

### **Ophiopluteus undulatus** nova forma.

This larval form is especially characterized by its peculiar, undulated posterolateral rods. The body skeleton is of the compound type, very short and compact; the transverse rods are simple, without processes. The rods of the arms are very smooth; only on the posterolateral rods there may be an indication of thorns.

On account of the character of the body skeleton the posterior end of the body is rounded, the end rods forming only a very slight prominence or none at all. The frontal area apparently as a rule low, but wide. The stomach is very wide, the esophagus short. There appears to be a slight widening in the point of all the arms. Pigmentation unknown.

Species a. (Pl. XXIV, Fig. 3; Pl. XXV, Fig. 1). The posterolateral arms are fairly upright; they are about four times the body length, considerably longer than the three inner pairs of arms, which are scarcely twice the body length. The preoral ciliated band is straight, bending abruptly downwards at the sides. The frontal area is distinct.

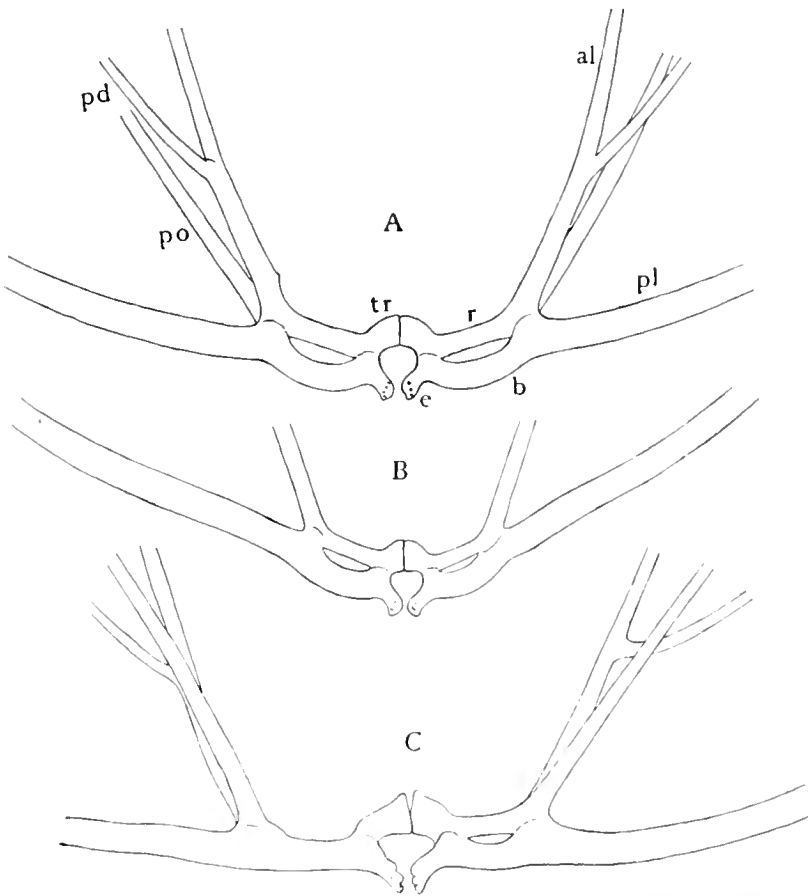


Fig. 66. Skeleton of *Ophiopluteus undulatus*. <sup>390</sup>/<sub>1</sub>. A. species a; B. species a. var. (off Pulo Pisang); C. species b. Letters as in fig. 61.

The skeleton (Fig. 66, A; Fig. 67, A, B). The body rods are rather strongly curved, the end rods very short, rounded, with three or four short prominences. The transverse rods are short and thick, forming together a small arch; the ends of the transverse rods abut on one another quite simply, without any sort of widening or indentations. The undulations of the posterolateral rods begin at about the level of the postoral ciliated band and continue unto the point; in the outer part the undulations are somewhat longer. A few short, straight thorns are found on the top of each undulation on the adoral side, sometimes also on the outer side.

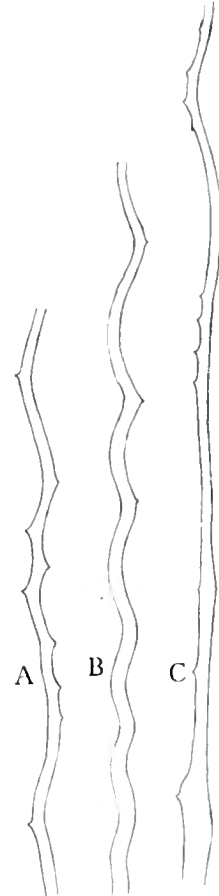


Fig. 67. Part of posterolateral rod of *Ophiopluteus undulatus*. <sup>390</sup>/<sub>1</sub>. A, B. from typical form of species a; C. from an abnormal (?) specimen.

Specimens of this species were found in plankton samples from the following localities: Off Koh Kong, Gulf of Siam, 25/I. 1900 (1 specimen); off Koh Chuen, Gulf of Siam, 3/III. 1900 (2 spec.); 7° 2' N. 75° 32' E. 22/XI. 1899 (1 spec.); 7° 37' N. 73° 34' E. 26/IV. 1900 (1 spec.); 8° 9' N. 71° 51' E. 27/IV. 1900 (1 specimen, peculiar through the outer fourth part of the posterolateral rods being straight); 6° 40' N. 77° 30' E. 2/I. 1914 (1 spec.); off the East end of Sokotra, 28/XII. 1913 (1 spec.); 12° 25' N. 46° E. 26/XII. 1913 (1 spec.). Also the larva in metamorphosis, figured in Pl. XXIV, Fig. 3, from the Malacca Strait, off Pulo Pisang (1/XII. 1899) must be referred to this species. Another specimen having very nearly completed its metamorphosis, only with the long beautiful posterolateral arms still intact, was found in a plankton sample taken by my brother, Mr. H. Mortensen, at Aden, in February 1898.

In a plankton sample from off Pulo Pisang, Malacca Strait, 1/XII. 1899, there is a young specimen differing from the typical form through the posterolateral rods being slightly concave at their base (Fig. 67, B); also the body skeleton is slightly different from that of the type. Perhaps this may represent another species.

One specimen from the Malacca Strait (5° 58' N. 95° 43' E. 28/XI. 1899) shows a characteristic feature in the postero-lateral rods, the lower part being distinctly thicker than the outer part, an abrupt narrowing being found a little beyond the beginning of the undulating part (Fig. 67, C). Whether this is only an individual abnormality or it represents a separate species, cannot be stated from the present material; the same, of course, holds good for the specimen mentioned above with the unusually formed lower part of the posterolateral rods.

As seen from Pl. XXIV, Fig. 3 this larva belongs to the type of Ophiuroid-larvæ, where the right anterolateral arm is preserved for some time after the other inner arms have disappeared during the process of metamorphosis. It also presents the very interesting feature that the vibratile band of the posterolateral arms continues directly across the body, below the developing Ophiuroid, so as to pass without interruption straight from one arm to the other. The same feature is seen in the metamorphosing *Ophiopluteus formosus*, species **a**, (Pl. XXX, Fig. 2) and *Ophiopluteus pusillus*, species **b** (Pl. XXIX, Fig. 3), indicating the existence of a sort of pupa-stage also in the Ophiuroid-larvæ. (Comp. p. 125).

A noteworthy fact is observed in the young Ophiuroid in the said figure, viz. the oral shields; they have appeared in four of the interradii but not in the fifth, and they are not quite of equal size. It should be emphasized that they make their first appearance on the ventral side, which proves that it is not a general rule that they are originally formed on the dorsal

side and then, during growth, transferred to the ventral side, as was stated by Ludwig.<sup>1)</sup>

Species **b.** (Pl. XXV, Fig. 2). This species is characteristic mainly by its remarkably short posterolateral arms, which are shorter than the anterolateral arms, and also broader, the vibratile band along them being distinctly broader than on the other arms. The posterior edge of the body is more rounded than in species **a**, quite semicircular, the body skeleton not at all projecting beyond the line formed by the posterolateral rods. The body is very short and broad, though perhaps hardly so low as shown in the figure; especially the frontal area may be somewhat higher in the living specimens. — The skeleton (Fig. 66, C) differs only very little from that of species **a**. The transverse rods are slightly widened at the end, and the end rods appear to differ somewhat in the shape of their thorny outgrowths.

Only two specimens, both in a poor state of preservation, are at hand, from the Gulf of Aden (12° 18' N. 50° 23' E. 27/XII. 13) and from off the East end of Sokotra (28/XII. 13). Both specimens agree in the characters pointed out, so that it seems beyond doubt that this is a separate species, not an individual abnormality. It should especially be emphasized that there is no doubt regarding the peculiar character of the posterolateral arms; the skeletal rod is complete, not broken, and although none of the two specimens are so far in their development as to have begun metamorphosis, there is no reason to expect that the posterolateral arms would ultimately reach the same length as in the other species.

The fact that the body skeleton (Fig. 66, C) has the recurrent rod developed only on one side is, of course, an individual abnormality; in the other specimen there is also a slight abnormality in the recurrent rod, but in this case it is on the right side.

Species **c.** (Pl. XXIV, Fig. 2). This third species has a considerable resemblance to species **a**. The posterolateral arms are long as in that species, but more divergent; the arms are, upon the whole, relatively shorter than in species **a**. Also the body is shorter and broader, and the frontal area is mainly confined to the edges. (The figure is drawn from a fairly well preserved specimen, so that it is not likely to be much different in the living specimens). In the skeleton (Fig. 68) only small differences from species **a** are to be noticed; the body rods and the transverse rods are more straight and the end rods have apparently only one small process on each side.

<sup>1)</sup> H. Ludwig, Jugendformen von Ophiuren. Sitzber. kgl. Preuss. Akad. d. Wiss. Berlin. 1899. p. 212.

One specimen of this species was found off Taboga, in the Gulf of Panama, in December 1915. Another specimen from the same locality very probably also belongs to this species; it is, however, abnormal, the right posterolateral arm being quite short, while the left is normally developed.

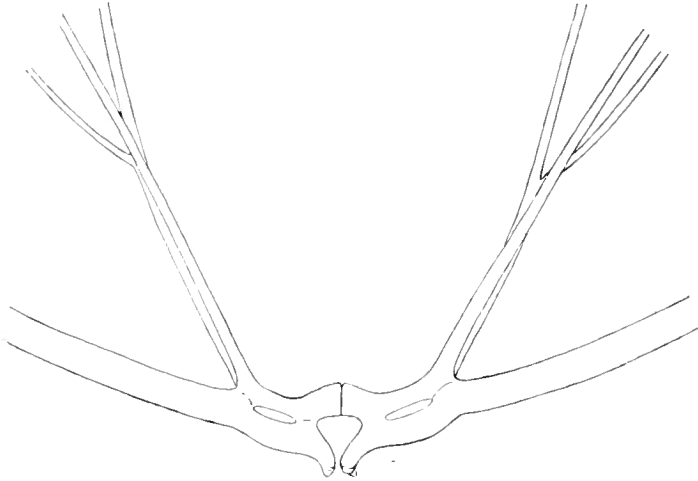


Fig. 68. Skeleton of *Ophiopluteus undulatus*, species c.  $\frac{290}{1}$ .

Also the postoral arms are quite short and rudimentary. The body is considerably smaller than in the normal specimen.

Besides this species there are two more larvæ from the Gulf of Panama (November and December 1915) which appear to represent two more species of the *undulatus*-type, related to species b.

As they are not in a good state of preservation, I do not think it worth while describing them, the main thing being the fact already sufficiently established that there are several distinct species within the *undulatus*-type.

The fact that this larval type occurs both at Panama and in the Indian Ocean affords an important indication for the determination of the Ophiurid to which it belongs. It may be concluded that it must be a type represented by more than one species both in the Indian Ocean and at the tropical west-coast of America. However, it would hardly be advisable to speculate more on this question at the present state of our knowledge.

### ***Ophiopluteus fulcitus* nova forma.**

The outstanding feature of this larval type is the branch proceeding obliquely upwards from the postoral rod towards the postoral vibratile band, giving thus a skeletal support to the anal area. There may be one or two more processes from this rod, situated farther down. The anterolateral rod is furnished with distinct, curved thorns along its outer side, from about the level of the frontal area. The posterolateral rods are provided with large, curved thorns along the inner edge. The postoral and the posterodorsal rods are smooth or finely thorny. Body skeleton compound; the transverse rods nearly straight, hardly widened towards the

point, but with a few short, irregular processes at the point. The end rods fairly long, with the point curved outwards, trifid, the median part being the largest. The anterolateral arms distinctly longer than the postoral and posterodorsal arms. Posterolateral arms fairly long, forming an obtuse angle. Arms slightly widened at the point.

Species **a**. (Pl. XXIII, Fig. 1; Pl. XXIV, Fig. 1). Anterolateral arms distinctly longer than the length of the body, the right one generally distinctly longer than the left. The frontal area is fairly large and distinct, the preoral band forming a beautiful curve. The postoral band makes a strong upward curve, on account of the supporting rods. Probably it will be found to reach even farther up in the living specimens; the fact that the supporting rods go beyond it is probably due to contraction on preservation.

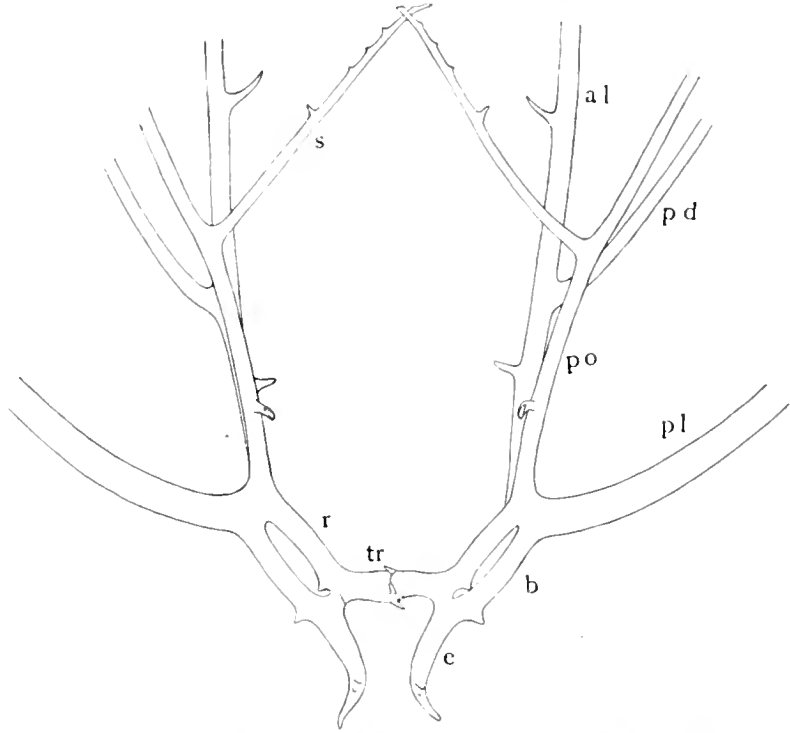


Fig. 69. Skeleton of *Ophiopluteus fulcitus*, species **a**. <sup>290</sup>/<sub>1</sub>.  
Letters as in fig. 61. s. supporting rod.

The skeleton (Fig. 69). The posterolateral rods are entirely smooth along the outer side. The supporting rods of the anal area are long, thorny in the outer part, their points generally crossing one another; another, shorter process issuing near the base of the postoral rod, directed ventrally. The anterolateral rods with one process near the base, somewhat below the point of issue of the posterodorsal rod; another somewhat higher up, both directed obliquely dorsally and inwards. Postoral and posterodorsal rods smooth. Body rod and recurrent rod with a prominence near the lower end. — The prominences on the anterolateral rod wanting in one young specimen, while in another specimen, also rather young, the upper one is wanting. One abnormal specimen (right postoral arm rudimentary) has only the upper one of these prominences developed.

This larva was taken in the Gulf of Panama, near the island of Taboga, in December 1915. 8 specimens.

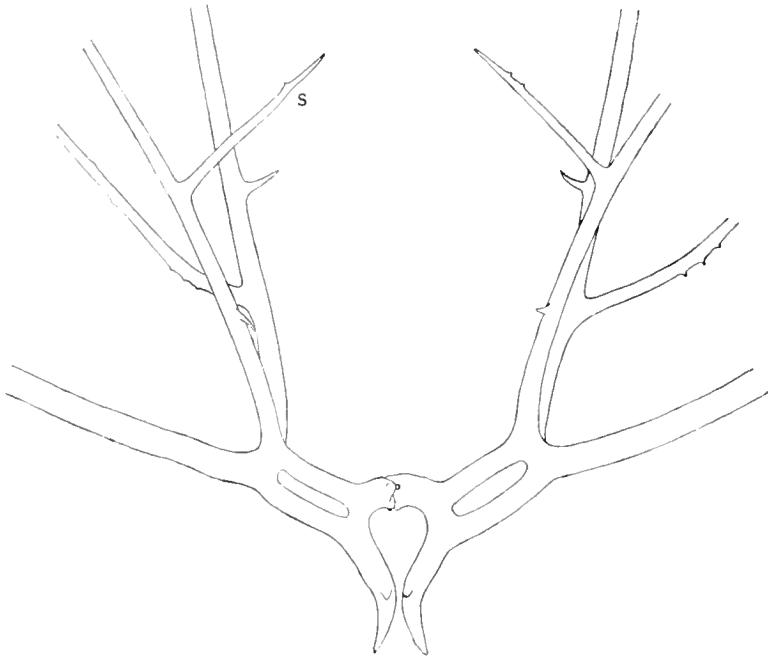


Fig. 70. Skeleton of *Ophiopluteus fulcitus*, species **b.** <sup>290</sup>/<sub>1</sub>.  
s. supporting rod.

anterolateral rods only with one process, corresponding to the upper one of the two found in species **a.** Postoral and posterodorsal rod slightly thorny, but to a variable degree. (Fig. 70).

This species was found, together with species **a.**, in the Gulf of Panama, near the island of Taboga, December 1915. 6 specimens.

**Species c.** (Pl. XXIII, Fig. 3). The main character distinguishing this species from the two preceding ones is the presence of three processes from the postoral rod, the median and the lower ones being directed ventrally (Fig. 71). The anterolateral rod with only one process, corresponding to the lower one of those in species **a.** The posterolateral rods thorny on the outer side, as are those of species **b.**; the postoral and posterodorsal rods slightly thorny. The shape of the body of this species is more like that of species **a.**

Gulf of Panama, near the island of Taboga; December 1915. 2 specimens.

Although there is some variation in the length of the supporting rods of the anal area, the three species are easily distinguished by the characters pointed out above, which are very constant, judging from the fairly large and well preserved material in hand. There can then hardly be any doubt that we have here three distinct species, not merely individual variations

**Species b.** (Pl. XXIII, Fig. 2). This species differs from the preceding one in the general shape of the body being shorter and broader, and the posterolateral arms somewhat more diverging. The supporting rods of the anal area are shorter and upon the whole more distant. The posterolateral rods are thorny on the outer side in the middle part. The



of one species, of the same eminently characteristic larval type, occurring together in the same locality and at the same time of the year.

It is useless to meditate over the problem to which genus of Ophiurids these larvæ belong. The fact that it is known only from the Gulf of Panama is not a sufficient indication for solving the problem.

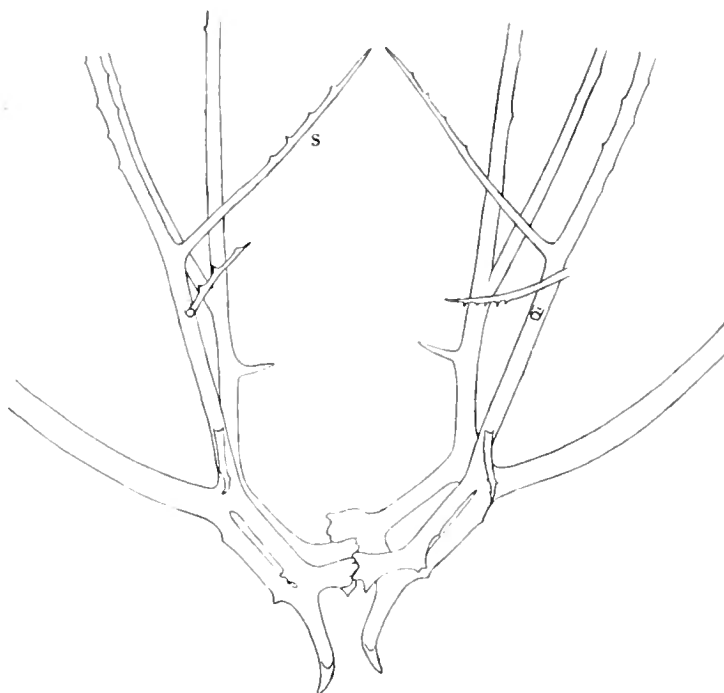


Fig. 71. Skeleton of *Ophiopluteus fulcitus*, species c. <sup>290</sup>/<sub>1</sub>.  
s. supporting rod.

### ***Ophiopluteus opulentus* nova forma.**

A very marked feature distinguishing this larval form from all the Ophiurid larvæ hitherto known is the presence of a pair of short extra arms on both the ventral and dorsal sides, proceeding from the lower part of the postoral and the anterolateral rods, below the point where the posterodorsal rod issues from the latter. These extra arms are very much shorter than the other arms and, upon the whole, hardly of the same morphological value as these; but their structure is the same, the ciliated band passing out along them in the same way as in the usual arms.

The body skeleton is of the compound type. There is a pair of small processes from the middle of each transverse rod. The posterolateral rods are canaliculate to a greater or lesser extent. The end rods are of medium length, straight, trifid at the point. The posterolateral arms are about 2—3 times as long as the inner arms.

Species a (Pl. XXI, Fig. 3). The posterolateral arms about twice the length of the inner pairs of arms, which are thin and round, ending in a small widening. It is uncertain whether there is any widening at the point of the posterolateral arms. The body is fairly large, the inner arms measuring about  $1\frac{1}{2}$  the length of the body. The frontal area is distinct, but not large.

The skeleton (Fig. 72). The posterolateral rods are canaliculate from about the middle unto the point. They are provided with small thorns, somewhat irregularly placed, along both the outer and inner sides (Fig. 73, A). The other rods are smooth or only here and there with a very small thorn. The transverse rods have a small thorn directed forwards and a somewhat larger one projecting backwards; the ends of the transverse rods are only slightly widened. The dorsal extra rods are a little thorny.

Only a single, not very well preserved specimen of this larva is at hand, taken off Koh Kam, in the Gulf of Siam, 4/II. 1900.

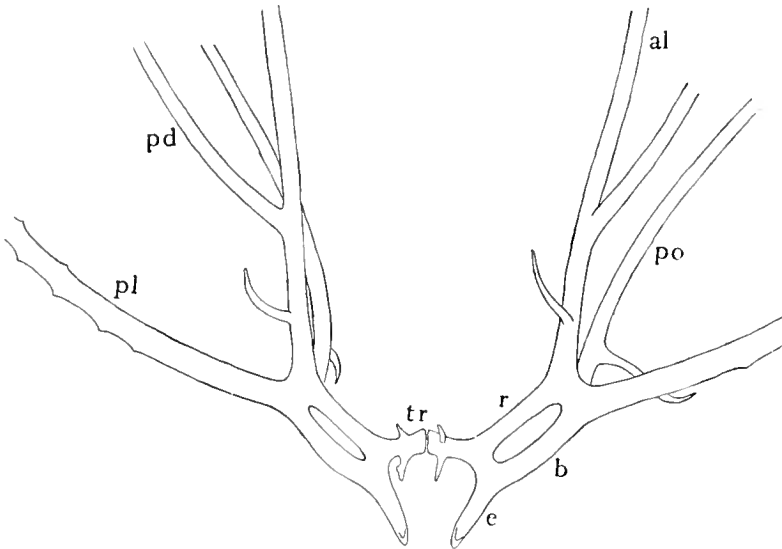


Fig. 72. Skeleton of *Ophiopluteus opulentus*, species **a**. <sup>290</sup>/<sub>1</sub>.  
Letters as in Fig. 61.

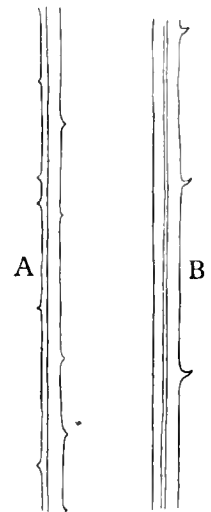


Fig. 73. Outer part of posterolateral rod of *Ophiopluteus opulentus*:  
A. species **a**;  
B. species **b**. <sup>290</sup>/<sub>1</sub>.

Species **b**. There are two specimens from off the East end of Sokotra (28/XII. 1913), both in so poor a condition that no whole figure can be given of this larval species. It can only be stated that the general form appears to correspond to that of species **a**. The skeleton (Fig. 74) affords some very good characters distinguishing it from the former species. The posterolateral rods are entirely smooth along the outer side (Fig. 73, B) and the canal goes almost from the base to the point of the rod. The processes from the transverse rods are directed more outwards in one of the specimens.

Species **c**. (Pl. XXII, Fig. 3). The relative length of the body and the interior pairs of arms about as in species **a**, but the posterolateral arms are conspicuously longer, about three times the length of the interior arms. The frontal area appears to be rather larger than in species **a**. The preoral vibratile band is somewhat upwards curving, while in species **a** it is nearly

straight. However, much stress cannot be laid on this character, which may to some extent depend on preservation. It appears that the small extra arms are less developed than in species **a**. In the specimen figured the ventral ones are distinct, but quite small; the dorsal ones are not distinct. In another specimen one of the dorsal arms is very distinct. That they will be developed, both pairs, in the fully formed larvæ (— the hydrocoel has not begun to form lobes in any of the specimens —) I have no doubt.

The skeleton (Fig. 75). The posterolateral rods are canaliculate almost from the base to near the tip. They are naked along the outer side, excepting one or a very few small prominences so placed off the thorns on

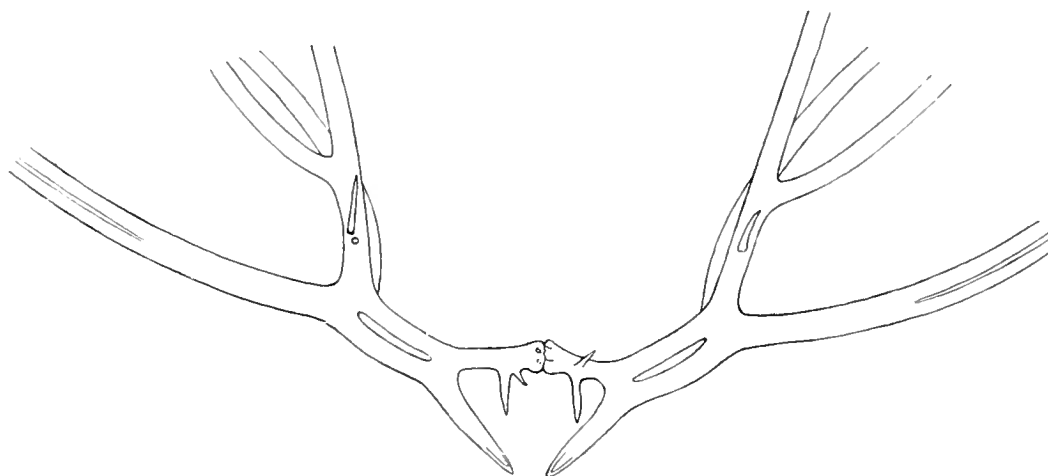


Fig. 74. Skeleton of *Ophiopluteus opulentus*, species **b**. <sup>390</sup>/<sub>1</sub>.

the inner side, that a slight thickening is formed (Fig. 76); there is generally such a thickening in the lower part, sometimes also a few farther out, and in that case the rod gets a peculiar, somewhat nodulose appearance. The dorsal extra rods are smaller than the ventral ones. The processes from the transverse rods are well developed; the ends of the transverse rods are distinctly widened.

Of this species there are three specimens from Christiansted, St. Cruz, West Indies, taken by Mr. H. Faye, 16/VI. 1915. There are also some younger specimens, which may possibly belong to the same species, but the distinguishing characters not yet being fully developed (— the extra rods have not appeared —) I cannot state definitely whether they do really do so.

To this species, however, some curious "specimens" (Pl. XX, Figs. 3—5) undoubtedly belong, which consist only of the body skeleton and the posterolateral arms, these arms still having their vibratile band intact. All the rest of the larva has disappeared. This is a case analogous to what obtains in the *Ophiothrix*-larva, viz. that the posterolateral rods are not

absorbed during metamorphosis, but are kept intact as a floating apparatus and then dropped, when the young Ophiurid has completed metamorphosis and is ready to give up pelagic life. The long posterolateral arms remain in connection, after the Ophiurid has gone, their ciliated band being intact and in the present case, moreover, joining in the middle, below the Ophiurid (this takes place before the Ophiurid leaves the "larva").

While in the case of *Ophiothrix* the abandoned posterolateral arms must evidently soon perish, this appears not to be the case with the present

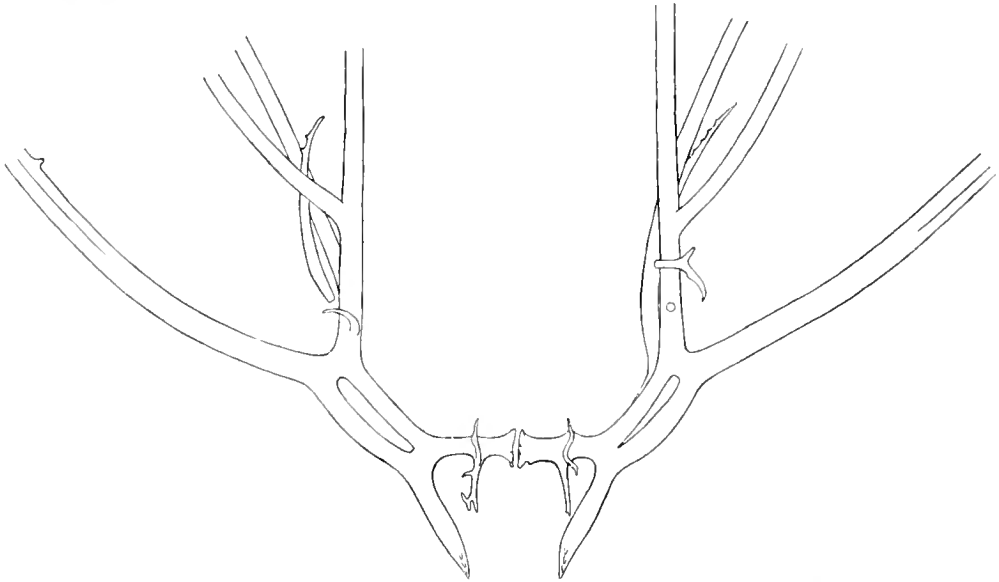


Fig. 75. Skeleton of *Ophiopluteus opulentus*, species c. <sup>290</sup>/<sub>1</sub>.

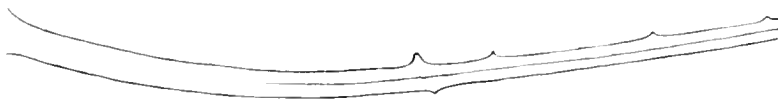


Fig. 76. Basal part of posterolateral rod of the same species. <sup>290</sup>/<sub>1</sub>.

larva. As stated above (p. 124) it seems fairly certain that a new larval body regenerates in the place of the former larval body. How far the process of regeneration goes cannot be ascertained; but in any case Pl. XX, Fig. 5 shows that it may go on so far as till the formation of a new mouth and esophagus: it is also evident from the numerous nuclei seen in the anterior part of the new body that a vigorous growth is going on here, so that it would seem most probable that the process may continue the short while, until the new digestive organs are able to assume normal function — and then there seems to be no reason to doubt that a new complete and ultimately metamorphosing larva may be the result. Thus we would here have a true case of metagenesis, otherwise totally unknown in Echinoderms. — As explained above (p. 124) the suggestion that

we might have to do here only with abnormal larvæ is quite unacceptable; it would be impossible for a larva with such incomplete digestive organs, and accordingly unable to feed, to form the long postoral arms and the whole body skeleton in a perfectly normal way. (That the transverse rods are somewhat different from those of the fully formed larvæ is evidently due to the absorption during metamorphosis). This, however, leads to another important problem. It is evident that the considerable growth of the regenerating larval body could not take place without some food supply. The "larva" itself being unable to feed until the new digestive organs are ready to function, there must be some nourishment stored somewhere. This also appears to be the case. In the vibratile band of the posterolateral arms there is generally seen a great number of very fine refractile grains. These might well represent the food supply; in fact, it is hard to see, where it could otherwise be found.

Of course, I do not mean to maintain that definite proof of this astonishing regeneration has been given. But the available material certainly indicates that it does take place. The problem most urgently invites closer investigation.

The fact that this larval type is found both in the West Indies and in the Indian Ocean gives a valuable hint as to the question to which Ophiurid type it belongs. Still it is not sufficient for solving the problem, and an attempt to find out the parental forms on the base of our present knowledge would be essentially guess work of very doubtful value.

### **Ophiopluteus similis** Mrtsn.

Pl. XXVII, Fig. 3.

Th. Mortensen. Die Echinodermen-Larven d. Plankton Exped. p. 60. Taf. V. 8; VI. 1.

The specimen figured, which was taken at Misaki, Japan, 29/VI. 1911, I am unable to distinguish by any noticeable character from the *O. similis* from off the Cape of Good Hope described in the work quoted. The more upright position of the posterolateral arms is hardly a reliable character but probably due to preservation, as, in fact, the arms of many Ophiurid larvæ are apt to bend and curve when the larvæ are mounted in Canada-balsam, especially such forms as have long arms with slender supporting rods. (In the present specimen all the arms are much curved, but have been restored to their natural shape in the figure). There is a distinct sub-oral cavity.

The skeleton (Figs. 77, 78) presents some minor differences in the shape of the transverse rods, which may perhaps indicate that the specimen from

Japan represents another species than that from Cape, but the differences are too insignificant for making it necessary to designate it as a separate species at present. In any case the two forms must be very closely related.

Another, younger specimen, from the same locality and the same day, probably also belongs to this species, although it differs in the anterolateral arms being longer than the postoral ones and in the suboral cavity being indistinct. In this specimen the posterolateral arms have the same

outward direction as in the type.

The suggestion made in the work quoted that this larva may belong to some *Amphiura*-species is without real support. It was made on account of the similarity between this larva and *Ophiopluteus bimaculatus* (Joh. Müll.), which latter was referred to the genus *Amphiura* on account of the fact that the young Ophiurid, as

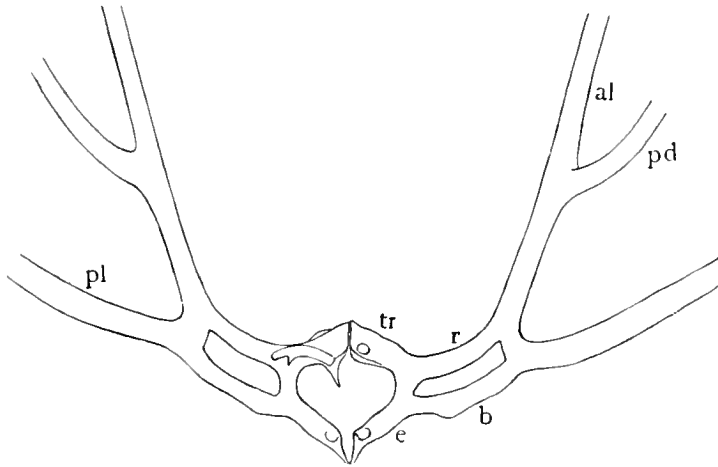


Fig. 77. Skeleton of *Ophiopluteus similis*. <sup>290</sup>/<sub>1</sub>.  
Letters as in fig. 61.

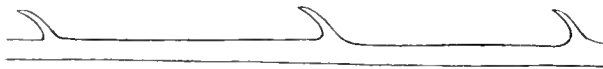


Fig. 78. Part of posterolateral rod of *Ophiopluteus similis*. <sup>290</sup>/<sub>1</sub>.

shown in the figures of Joh. Müller (V. Abhandl. Taf. V, Fig. 6) has two papillæ on each mouth angle, a feature mainly characteristic of *Amphiura*. However, as I have shown recently <sup>1)</sup> that *Ophiopluteus mancus* is the larva of *Amphiura filiformis*, the suggestion that *O. bimaculatus* might belong to an *Amphiura* becomes improbable. The two papillæ of the young Ophiurid are hardly the typical infradental papillæ of the Amphiurid type, but more probably tooth papillæ situated in the inner part of the mouth; in *Amphiura filiformis* I have found the infradental papillæ to appear only at a much later stage of development. The fact of the occurrence of this larval type both at Cape and Japan is not of sufficient zoogeographical importance for indicating to which species of Ophiurids it belongs. Whether it is more nearly related to *Ophiopluteus bimaculatus* must also remain uncertain for the present.

<sup>1)</sup> On the development and the larval forms of some Scandinavian Echinoderms. p. 138.

**Ophiopluteus formosus** nova forma.

Body skeleton compound; no processes from the transverse rods. The posterodorsal rod issues near the base of the anterolateral rod; posterolateral rods simple, with numerous, fairly large, curved thorns along the inner side; the other rods smooth.

This larval type is not distinguished by any specially marked characters, the low point of issue of the posterodorsal rods being the most conspicuous feature. The larva is a very typical, regular form, of a beautiful, graceful shape.

Species a. (Pl. XXVII, Fig. 1; Pl. XXX, Fig. 2). The body is fairly large; the inner arms hardly as long as the body, the posterolateral ones

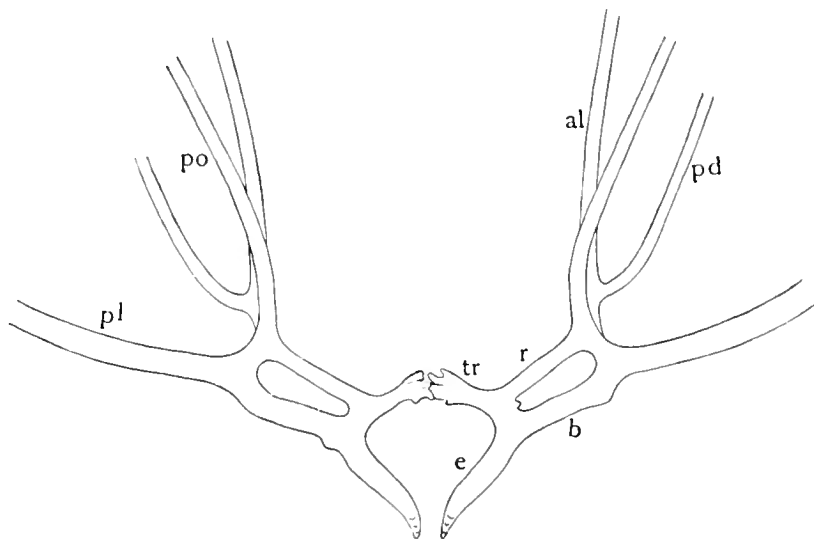


Fig. 79. Skeleton of *Ophiopluteus formosus*, species a. <sup>290</sup>/<sub>1</sub>. Letters as in fig. 61.

about twice that length, gracefully bent. The preoral band is straight in the middle, turning rather sharply downwards at the sides; the postoral band with a slight sinuation at each side. At the base of the posterolateral arms the band makes a deep downward curve, forming an incipient vibratile lobe. The frontal area is not very large. Arms fairly broad and flat.

In the skeleton (Fig. 79) the somewhat widened, lobate ends of the transverse rods are noticeable; otherwise there are no very prominent features.

5 specimens from the Gulf of Panama, near the island of Taboga, in December 1915.

One specimen is in the metamorphosis stage (Pl. XXX, Fig. 2) the inner arms, except the right postoral one, having been absorbed; also the left posterolateral arm has begun to undergo absorption. The outstanding feature of this stage is the arrangement of the vibratile bands. The two bands

of the posterolateral arms are continuing across the body, below the developing Ophiurid. At the anterior end there is another transverse band, apparently derived directly from the preoral band. Thus a remarkable rearrangement of the vibratile bands takes place in this form, something corresponding to what takes place in the transformation of the Auricularia into the pupa-stage (Cf. p.125). A similar case was observed in *Ophiopluteus pusillus*, species **b** (Pl. XXIX, Fig. 3) and *O. undulatus*, species **a** (Pl. XXIV, Fig. 3).

Species **b**. (Pl. XXVII, Fig. 2). This species differs so conspicuously from species **a** as regards its shape that it may seem doubtful, whether it

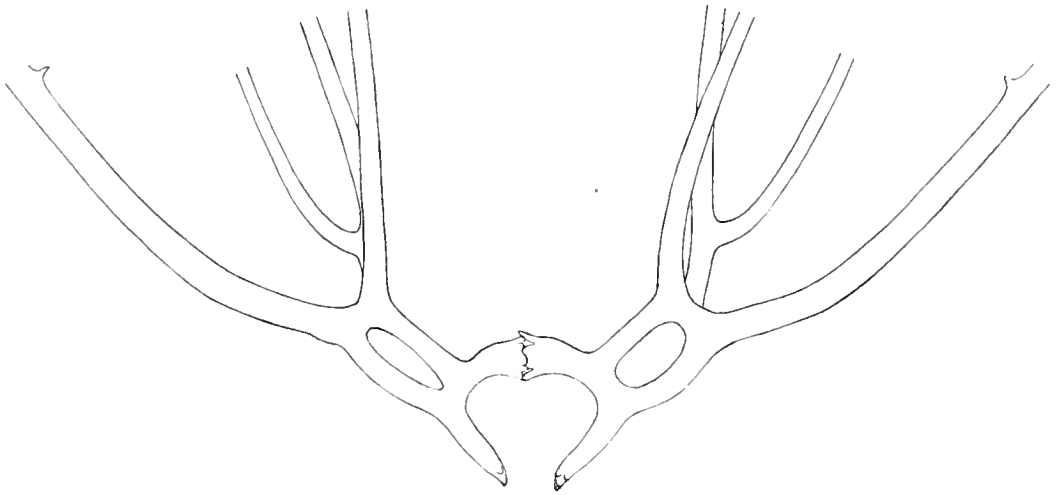


Fig. 80. Skeleton of *Ophiopluteus formosus*, species **b**. <sup>290</sup>/<sub>1</sub>.

really belongs to the same type. The inner arms are one and a half to two times, the posterolateral ones more than four times the body length. The arms are narrow, rounded, not broad and flattened as in species **a**. On the other hand the skeleton (Fig. 80) so closely resembles that of species **a** that only very small differences can be pointed out, the main thing being that the transverse rods are somewhat more robust, the indentations at the ends being less deep. Perhaps the shape of the meshes of the body skeleton will prove a little different. In species **a** the meshes are somewhat narrower at the lower end, which does not appear to be the case in the present species; but as there is only one specimen, and that one even showing a slight difference in the shape of the two sides of the body skeleton, this feature is not to be relied upon as a specific difference. The thorns on the posterolateral rods are blunt and more distant than in species **a**. (Fig. 82, B).

One single specimen, fairly well preserved, from the Red Sea, 24°43' N. 35° 15' E. 10/XI. 1899.



Species *c*. In a plankton sample taken by Mr. Gruelund in the neighbourhood of the Cape Verde Islands at 16°11' N. 21°57' W. 11/VI. 1920, a single specimen of a larva of the *O. formosus*-type was found. It is in a very poor state of preservation, only the body skeleton and the posterolateral arms being intact. These parts, however, clearly show that we have here another, distinct species of the *formosus*-type, which may be easily recognized by the characters of its skeleton, even though the shape of its body is unknown.

The skeleton (Fig. 81) differs from that of species *a* and *b* mainly in the peculiar shape of the end rods, the points of which are bent nearly at a right angle; they are longer than in the two other species and also provided with longer side-branches. One of the transverse rods carries a short process, which is, however, broken, so that its total length and the shape of its point cannot be ascertained; but it is evidently very nearly as shown in the figure. The point of issue of the posterodorsal rod is not so close to the base of the anterolateral rod as in the other species. (Apparently the distance is not the same on both sides; this, however, is due to the fact that the right one is broken and lies in a somewhat different position). The thorns on the posterolateral rods are finer and more distant than in species *a* and *b*. (Fig. 82). The posterolateral arms are very long and much diverging.

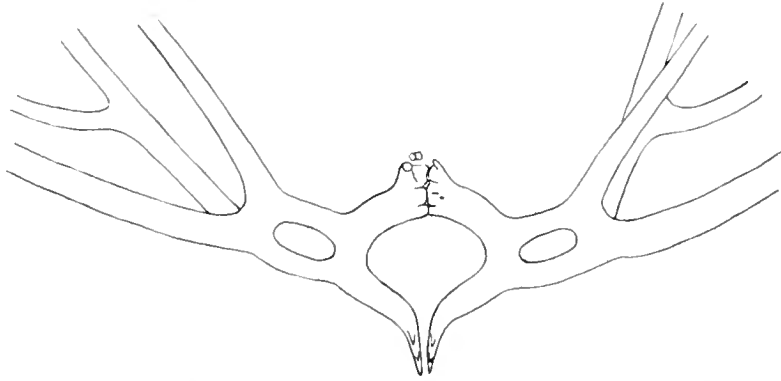


Fig. 81. Skeleton of *Ophiopluteus formosus*, species *c*. <sup>290</sup>/<sub>1</sub>.

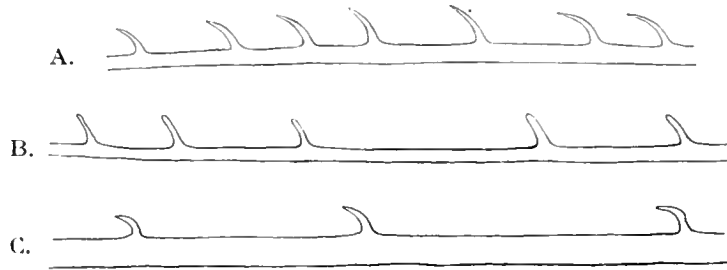


Fig. 82. Part of posterolateral rod of *Ophiopluteus formosus*, <sup>290</sup>/<sub>1</sub>.  
A. of species *a*; B. of species *b*; C. of species *c*.

The occurrence of this larval type in the Red Sea, at Panama and in the Atlantic Ocean is, of course, of importance, but it is not sufficient for venturing on a suggestion as to the Ophiurid to which it belongs. That *Ophiopluteus formosus* and *similis* are nearly related is fairly evident, the

characters distinguishing them from one another being very slight and unimportant.

Upon the whole the larval types *O. similis* and *formosus* are among the less interesting on account of their more generalized features. But I have thought it desirable to include them in this report in order not to exaggerate the impression that the Ophiurid larvæ are easily arranged into natural groups. That is the case with some forms, like e. g. *undulatus*, *costatus*; but the present forms are equally important as representing types which do not lend any special support to a natural classification.

### **Ophiopluteus fusus** nova forma.

Although there is only one specimen in hand, and that even in a very far advanced stage of metamorphosis, as seen from the figure 83, A, I have deemed it advisable to give a description of it, partly because the characters to be seen on the remnants of the larva still attached to the young Ophiurid are sufficiently marked for recognizing the species, partly because it seems to show affinities to another Ophiurid-larva which stood hitherto remarkably alone, viz. *Ophiopluteus paradoxus*.

The main character of this larva is the peculiar thickening of the posterolateral rods a little above their basis. While the thickening increases very gently from the base upwards, it ends rather abruptly outwards, the outer part of the rod being very thin, with fairly long, thin, straight thorns on either side (Fig. 83, C); the basal and thickened part is smooth. Also the postoral rod has the same shape, although the thickening is less pronounced. The other rods have already been absorbed, so that nothing can be said about their structure. The body skeleton is simple, the end rods moderately long, slightly bent in their outer parts. The transverse rods are irregularly widened at the point; there is no median process.

The shape of the posterolateral arms appears to be rather broad and flat, as in *O. paradoxus*. There is a distinct vibratile tuft at the posterior end, as in the latter species.

The single specimen in hand was taken at the Azores (38°14' N., 24°35' W. 19/III. 1911. H. Blegvad).

As stated above this species would appear to be nearly related to *Ophiopluteus paradoxus*, the larva of *Ophiura albida* Forb. They agree in the characters of the body skeleton, the presence of a posterior vibratile tuft, as in the general structure of the young Ophiurid, and probably also the larval arms have the same shape in both; the only essential difference is the swelling of the basal part of the posterolateral and postoral (a. o.?)

rods in *O. fusus*. If it should ultimately be proved that these two larvæ are really nearly related, it will be a fact of considerable importance, showing that also within the genus *Ophiura*, even as recently restricted

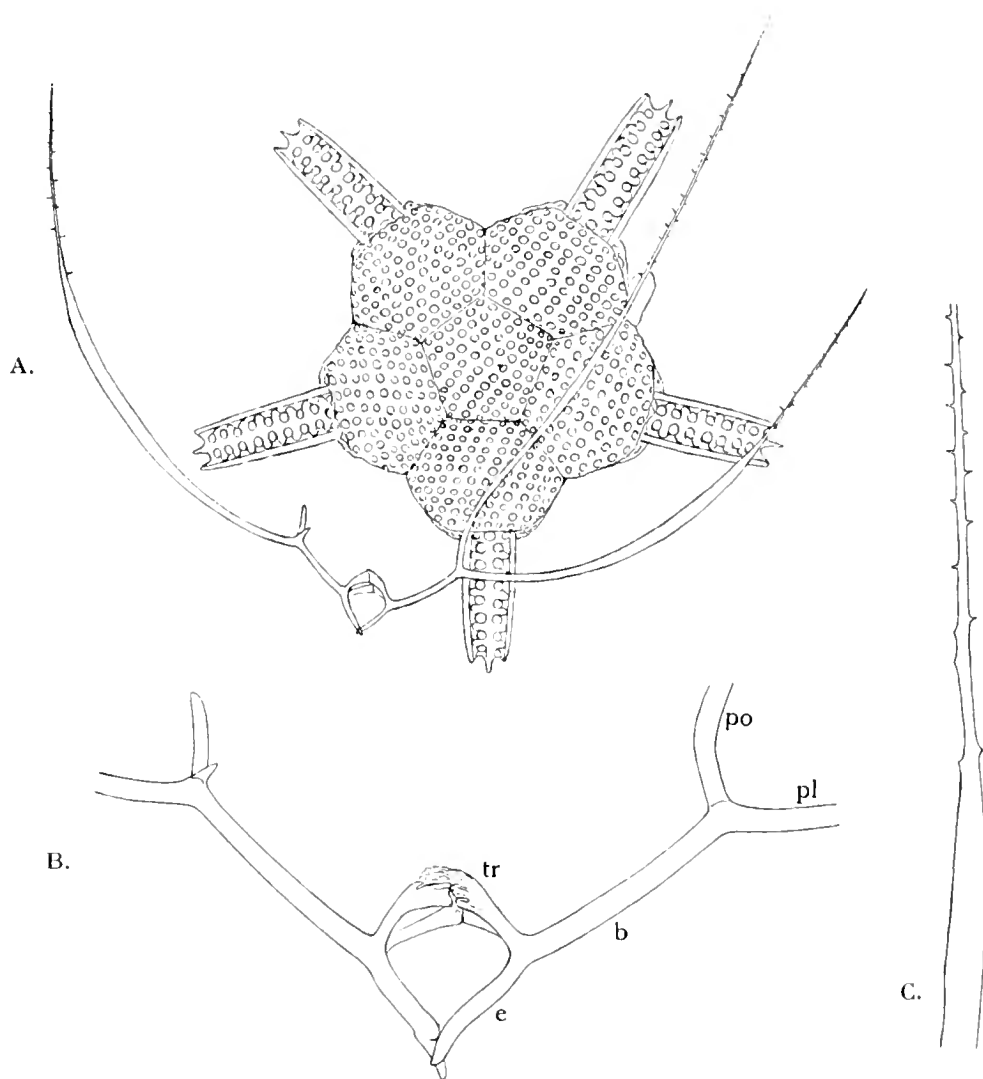


Fig. 83. *Ophiopluteus fusus*. A. specimen in metamorphosis;  $110/1$ . B. body skeleton of the same; C. outer part of posterolateral rod.  $380/1$ . Letters as in fig. 61.

by Matsumoto and H. L. Clark, different groups of larvæ may occur. The fact that the larvæ of the two species *O. albida* and *texturata* are so different would then prove that these species are not so nearly related as hitherto supposed; the other conclusion that might be drawn, viz. that the larvæ cannot show anything regarding the natural affinities, is much less probable, considering the facts brought to light in the present work.

**Ophiopluteus serratus** Mrtsn.

Pl. XXVIII, Figs. 1—2.

In the memoir "Die Echinodermlarven der deutschen Südpolar Expedition 1901—3" p. 96 (Taf. XIII, Fig. 1) an Ophiurid larva was described under this name, characterized especially by its very large median process with a series of more or less branched prominences along its outer side. In the material collected during my expeditions to Siam 1899—1900 and to the Pacific in 1914—16 there is a considerable number of Ophiurid larvæ which belong, evidently, to the same type. They may possibly represent two different species or even more; but as they show considerable variation, especially in regard to the size of the median processes, it is hardly possible to come to a definite result as to their specific limits. I have therefore preferred to designate them all simply as *Ophiopluteus serratus*. Only the study of living material and tracing their origin to the parental forms will give the clue to the question of the specific limits within this, evidently, very variable larval type.

This larva is characteristic through the great length of the inner arms and the nearly upright position of the posterolateral arms. These latter arms are ca. 5 times, the inner arms about 3 times the body length. There appears to be a very slight widening at the tip of the arms. The preoral area is very low; it may be distinct in its whole width or only at the corners. This is possibly a specific difference, which cannot, however, be decided from the preserved material. The preoral band is more or less covered by the postoral band, the whole oral area being almost totally covered up by the postoral or anal lobe<sup>1</sup>). A conspicuous feature in some of the specimens is the very large size of the stomach (Pl. XXVIII, Fig. 1), which fills the whole space inside the posterolateral rods. In other specimens it is much smaller, occupying only the space inside the rods of the inner arms (Pl. XXVIII, Fig. 2). It is very well possible that this is really a specific character, but in the preserved material it is too often impossible to decide, what is due to preservation and what not, so that, although there would seem to be no doubt in some cases that we really have to do with two different species, it is better to leave the species question undecided at present.

In the skeleton (Fig. 84) there appears to be no distinct characters eventually corresponding to the mentioned differences in the size of the stomach and the preoral area. A noteworthy fact is the very great variation in the size of the median processes from the transverse rods. In some specimens they are quite small and inconspicuous, in others as large as

<sup>1</sup>) The suggestion given in the original description that the peculiar feature of the oral region of the type specimen was due to compression is certainly correct.

in the type. The spinulation, of course, varies with the size of the processes. Some specimens observed alive at Misaki, Japan, in June 1911, were found to have the stomach green, while some tiny red pigment grains were scattered along the body skeleton. No pigment spots in the tip of the arms.

Numerous specimens were found from Japan to the Red Sea: Misaki, Japan, 29/IV, 2-17/VI. 1914; Zamboanga, 1/III. 1914; Malacca Strait,

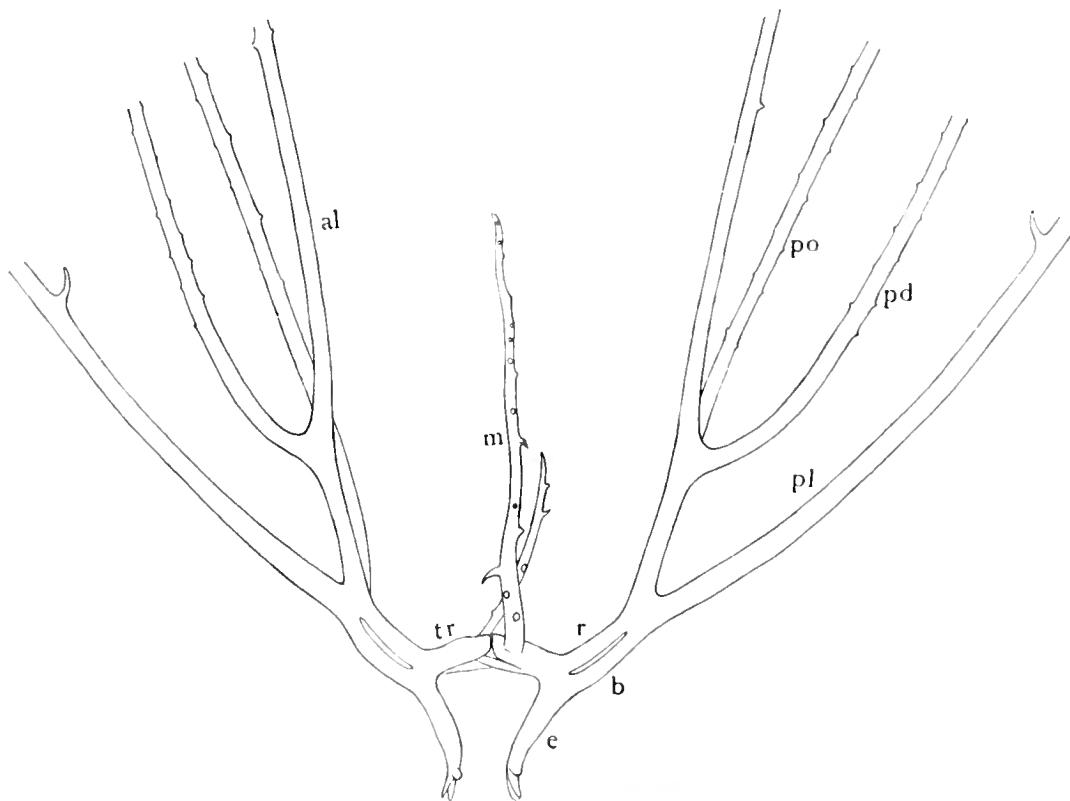


Fig. 84. Skeleton of *Ophiopluteus serratus*.  $\frac{200}{1}$ . Letters as in fig. 61.

30/XI. 1899; S. of Koh Chuen, Gulf of Siam, 3/III. 1900;  $89^{\circ}15' E. 5^{\circ}55' N.$  (Bay of Bengal), 5/I. 1914 (1 specimen);  $73^{\circ}34' E. 7^{\circ}37' N.$  26/IV. 1900 (1 specimen); Gulf of Aden, 11/XI. 1899; Strait of Bab-el-Mandeb, 5/V. 1900 (1 specimen); off Jebel Zukur, Red Sea, 5/V. 1900; Suez, 31/I. 1898 (Mr. H. Mortensen).

A very interesting feature is connected with the metamorphosis of this larval type. The suboral cavity continues some way down in the body, as a pouch on each side of the stomach. In the wall along the bottom of this pouch a thickening appears at the time, when the hydrocoel begins to form lobes (Pl. XXVIII, Fig. 2); this thickening grows very considerably and forms lobes, which ultimately combine with the lobes of the hydrocoel.



The process having been described in details by Joh. Müller in his Memoir "Die Ophiuridenlarven des Adriatischen Meeres" in the case of the larva, which he names *Pluteus bimaculatus*, there is no reason for me to give a detailed description of the process here again, the less so since the partly poor state of preservation of the material available would prevent the completeness of the description. But it is an exceedingly interesting fact that we have in this larva a type of development rather different from that found in the *Ophiothrix*-larva, the only larval type the development of which has been studied in detail as yet. A careful study by means of sections of the developmental processes of the present larval type would be very desirable and would be sure to yield most interesting results. — This is another instance serving to show that it is not justifiable to conclude from the study of the development of one single form that the whole of the group follows exactly the same type. (Cf. *Antedon*).

As stated above the mediterranean *Ophiopluteus bimaculatus* agrees with the present larva in the type of its development, and there is certainly no doubt that these larvæ are very nearly related. They are alike in structure and shape, and only in minor features specific differences can be pointed out. It might be suggested that perhaps also *Ophiopluteus affinis* (Echinodermenlarven d. Plankton-Expedition, p. 61, Taf. VI, 1—3) will prove to belong to this group. Its general appearance is very much like that of *O. serratus*, but its oral structure is incompletely known. The skeleton affords the same general structure, the only essential difference being that the posterolateral rod has a longitudinal ridge, dividing it into two parallel rods. But this would hardly be sufficient to disprove its relationship to the *serratus-bimaculatus* group. —

No suggestion can be given as to which Ophiurid is the parental form of these larvæ. As stated above, under *O. similis* (p. 150) the suggestion that *O. bimaculatus* might belong to an *Amphiura* is untenable, since it was found that the larva of *Amphiura filiformis* is of quite another type (*Ophiopluteus mancus*). The presence of the larval type both in the Indo-Pacific Ocean and in the Mediterranean and the Atlantic (— it was taken by Mr. Gruelund, VI. 1920, off Cape Blanco and at the Cape Verde Islands —) will, of course, be a fact of importance for judging of its parental origin, but it is not sufficient for making a definite suggestion as to that problem.

#### ***Ophiopluteus arcifer* nova forma.**

This larval type is distinguished by the very long median processes from the transverse rods, which in their highest development, in species **a**, when seen in side view, recall the shape of an old-fashioned cross bow (Fig. 85).

They cause a very prominent elevation of the body-wall, like a hump, on both the ventral and the dorsal side of the body.

The body is comparatively low, with a low frontal area. The preoral band is generally almost straight. A noteworthy feature is the more or less conical shape of the esophagus (especially so in species a). The arms

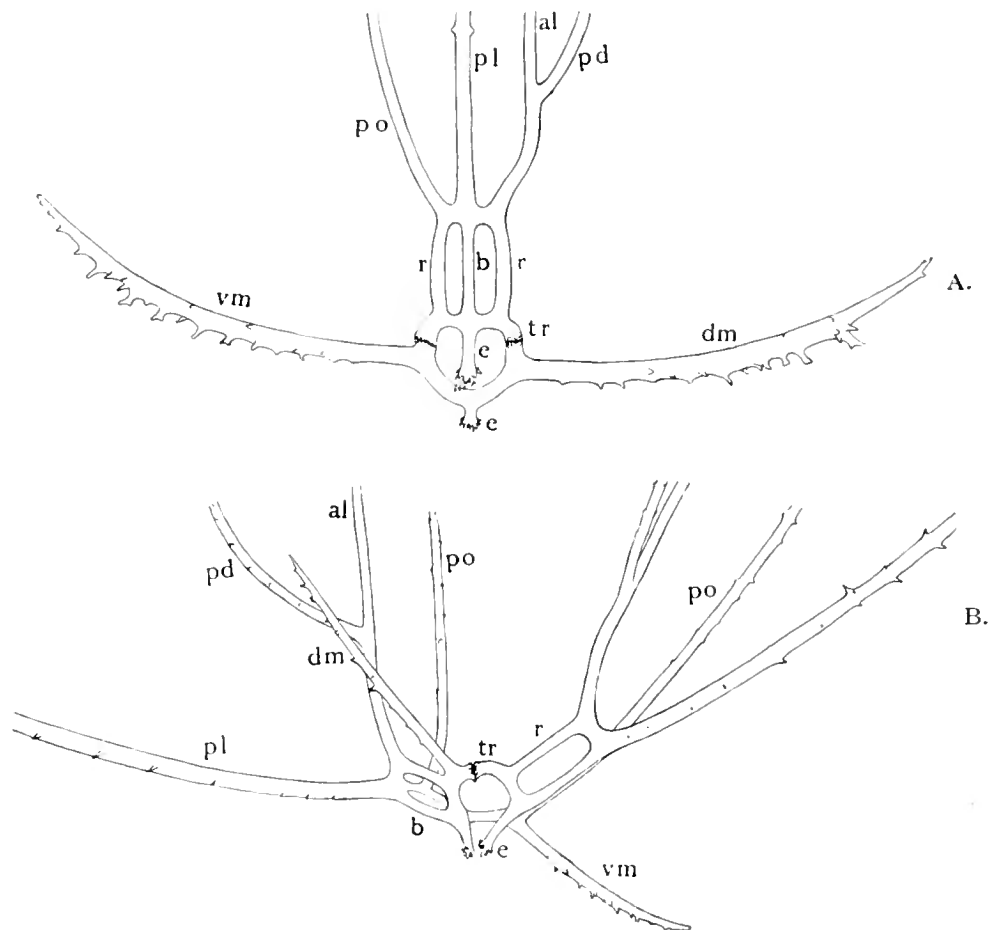


Fig. 85. Body skeleton of *Ophiopluteus arcifer*, species a. A. in side view.  $\frac{290}{1}$ ; B. oblique dorsal view. al. anterolateral rod; b. body rod; dm. dorsal median process; e. end rod; pd. posterodorsal; pl. posterolateral; po. postoral rod; r. recurrent rod; tr. transverse rod; vm. ventral median process.

are slightly widened at the point. The posterolateral arms are 3—5 times the body length, rather obliquely outwards directed. The other arms are not much more than body length, their point being at about a level with the point of the posterolateral arms. The body skeleton is of the compound type.

Species a. (Pl. XXVI, Fig. 1). The posterolateral rods are set with bilaterally arranged small thorns, which give the rod a peculiar, almost

banded appearance, when seen from the ventral or the dorsal side. Near their base they have a few small thorns along the outer side, and also the body rod generally has a few small thorns. The end rods are provided with several small branches at the point. The transverse rods are hardly widened at the point, but end in a number of very short thorns. The median processes, which proceed from the transverse rods of the same side, sometimes the left, sometimes the right, are very long, slightly curved and irregularly thorny along the outer side (Figs. 85, 86). The postoral and postero-

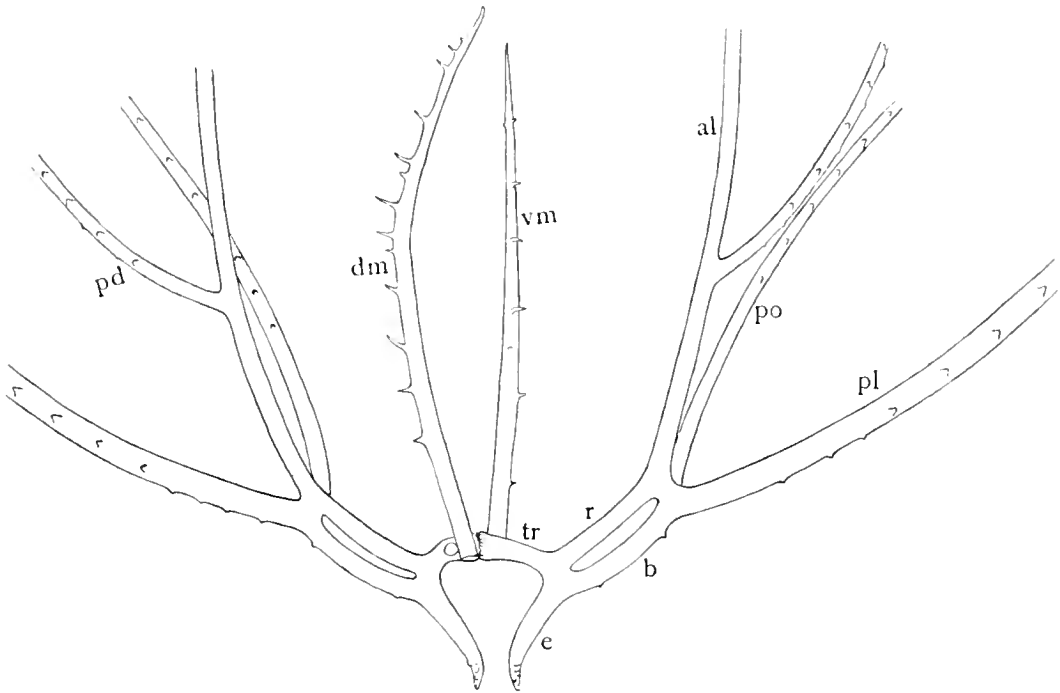


Fig. 86. Skeleton of *Ophiopluteus arcifer*, species **a**.  $\frac{290}{1}$ . Letters as in fig. 85.

dorsal rods have small, bilaterally arranged thorns, the anterolateral rods have thorns only along the outer side in their outer part. — The posterolateral arms are about 4 times the body length.

This species was found S. of Koh Chuen, in the Gulf of Siam, 3/III. 1900 (1 specimen), in the Malacca Strait (101° 12' E. 2° 45' N. 30/XI. 1899 (3 specimens) and off Jolo, 20/III. 1914 (5 specimens).

**Species b.** (Pl. XXVI, Fig. 2). The main difference between this species and the preceding one consists in the posterolateral rods being here provided with thorns along their outer and their inner side, not along the ventral and dorsal sides. The thorns on the outer side are irregular, slightly branched, those along the inner side simple, with the point bent a little forward. The end rods have only one side branch at the point, and the transverse rods are provided with only few, short prominences at the point.



The median processes are not so large as in species **a**, and set with only few thorns along their outer sides. The anterolateral rods are much more thorny than in species **a** (Fig. 87); the postoral and posterodorsal rods as in the preceding species. The length of the posterolateral arms is only about 3 times the body length, the other arms as in the preceding species.

Only two specimens of this species were found, in the Gulf of Panama, off the island of Taboga, in December 1915.

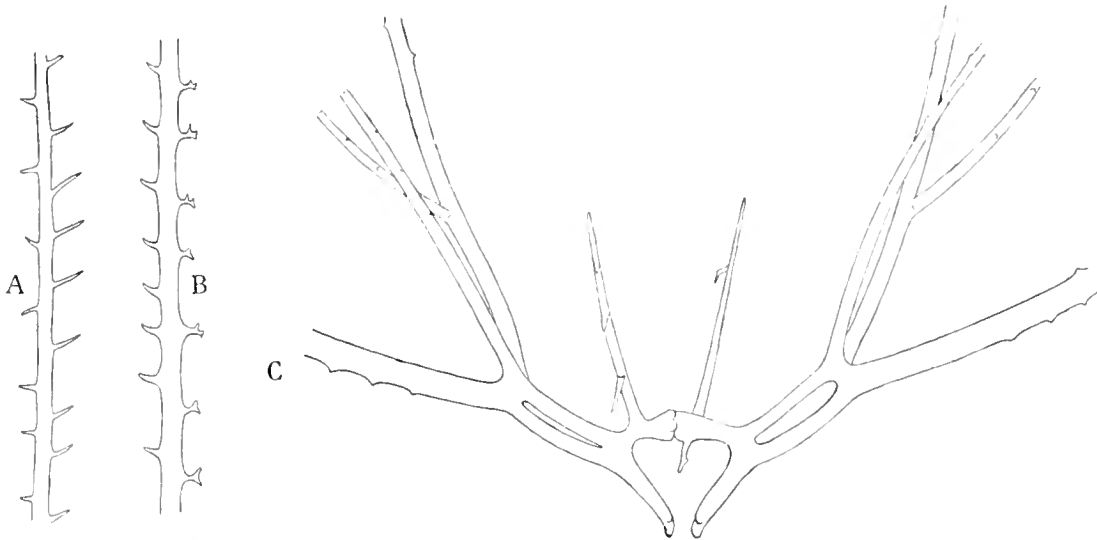


Fig. 87. Skeleton of *Ophiopluteus arcifer*, species **b**. <sup>290</sup>/<sub>1</sub>. A. Part of anterolateral rod. B. part of posterolateral rod; the adoral side of both is to the left. C. Body skeleton. The processes from the transverse rods are restored, being broken in the specimen, and are represented in a more upright position than normal.

Species **c**. (Pl. XXVI, Fig. 3). This species is nearest to species **b**, but differs from it in the character of the posterolateral rods, which have fewer, small thorns along their outer side, and not in their whole length, while those along the inner side are larger and continue until the point; they are partly (mainly in the lower part of the arm) somewhat spinulose. The rods of the other arms are almost as in species **b**. The median processes from the transverse rods are shorter than in that species (Fig. 88). The posterolateral arms are about five times the body length.

One specimen was taken at 17° 47' N. 70° 51' W., 1/II. 1911. (H. Blegvad).

This species recalls to some degree *O. bimaculatus* (Joh. Müller), but differs conspicuously from it in the presence of thorns along the outer side of the posterolateral rods and in the much greater length of the median processes from the transverse rods. Unfortunately, the only specimen in hand does not give any evidence, whether the development of the Ophi-

urid proceeds in the same way as in *O. bimaculatus* and *O. serratus* (see under the latter species). Neither are any of the specimens of the species **a** and **b** in the metamorphosis stage. In any case it should be kept in mind for future investigation, that these larvæ possibly have some nearer affinity to one another.

At our present stage of knowledge it is impossible to form an opinion of any value as to which forms of Ophiurids the larval type of *Ophiopluteus arcifer* belongs. The existence of species of this larval type in the East Indian Seas, in the Gulf of Panama and in the West Indies is, of

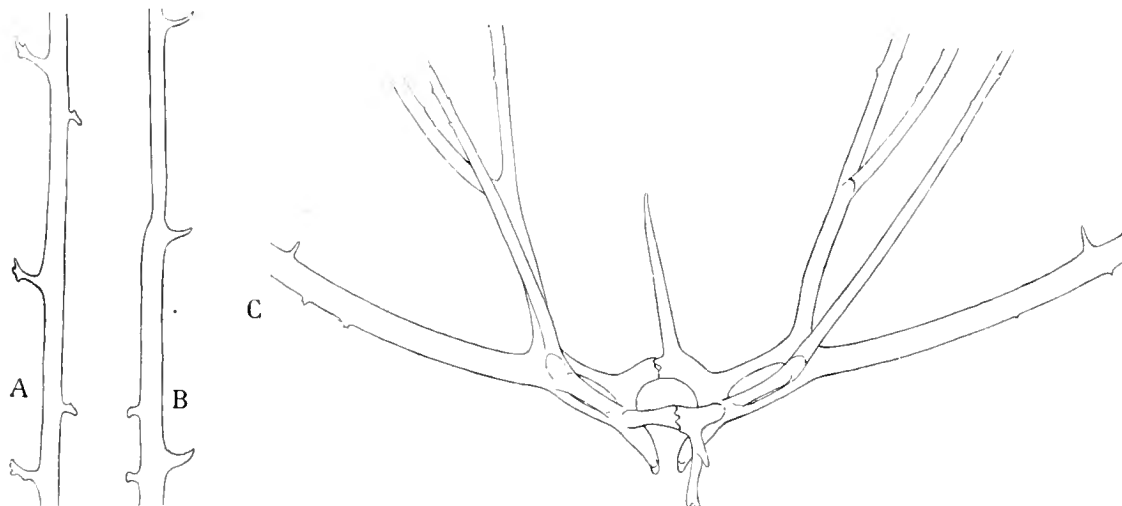


Fig. 88. Skeleton of *Ophiopluteus arcifer*, species c.  $\frac{290}{3}$ . A. Part of posterolateral rod; B. the same rod, probably showing regeneration. C. body skeleton, seen slightly from above.

course, a fact of importance, but not in itself sufficient foundation for a reasonable suggestion as to the solution of this problem.

### ***Ophiopluteus monacanthus* nova forma.**

Pl. XXX, Figs. 3—4.

From off Jolo (21/III. 1914) there are two specimens of a very peculiar Ophiurid larva, which seems to me well worth describing, although the fact that the skeleton has been dissolved prevents giving a complete description of it. The outstanding feature of this species is the presence of a very strong median process on the ventral side alone; it projects at a right angle to the body, forming a large hump on the ventral side, while the dorsal side of the body remains flat, there being evidently no median process from the dorsal transverse rods. There is a widening on the rectum, filling out the hump. In its general appearance the larva otherwise recalls *Ophiopluteus arcifer*. The postoral band makes a small, but very distinct backwards curve at each side. The posterolateral arms are somewhat more

than three times, the other arms about twice the body length. They have a slight widening at the point. Although the skeleton is dissolved, it can be definitely ascertained that the posterolateral rods are thorny along their outer sides.

There seems to be reason to think that this species is related to *O. arcifer*, but, of course, this cannot be definitely ascertained until its skeletal structure is made known. By the unique character of the ventral hump this species is easily recognizable.

***Ophiopluteus retrospinus* nova forma.**

The main distinguishing feature of this larval type is afforded by the peculiar backward projecting processes from the lower part of the postero-

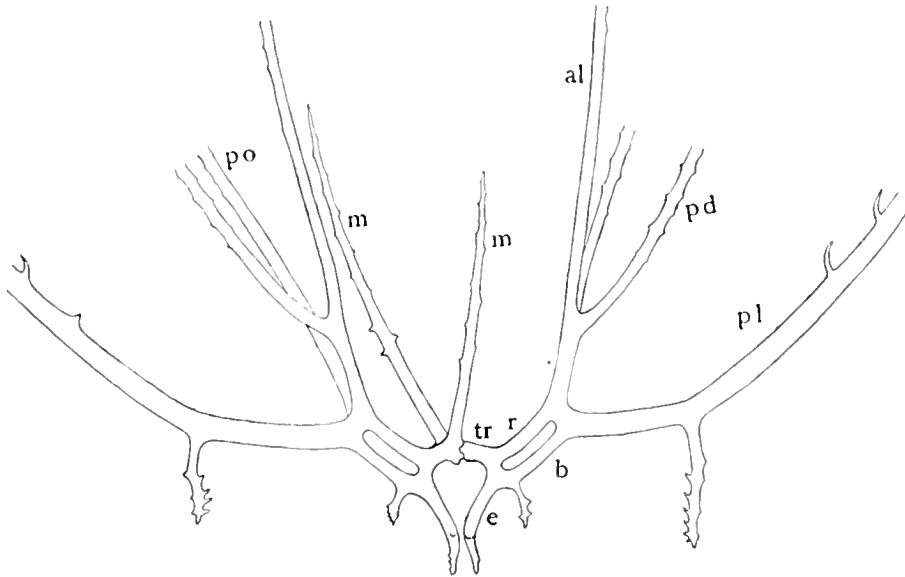


Fig. 89. Skeleton of *Ophiopluteus retrospinus*, species a.  $\frac{220}{1}$ . Letters as in fig. 85.  
m. median process.

lateral rods. — The arms are fairly long; the posterolateral arms are about three times, the anterolateral arms only a little more than body length, their point being at a level with the point of the posterolateral arms. The two other pairs of arms are somewhat shorter, their points not reaching the same level as that of the other arms. There is a very slight widening at the point of the arms. They are all gracefully curved, especially the posterolateral ones, which gives a touch of elegance to the shape of the larva. The frontal area is well developed. The preoral band is somewhat upwards curved, more or less straight in the middle. The postoral band makes a little downward curve at each side (more distinct in species **b**), and from here the nervous system is seen to proceed. (In species **b** only

the ventral part of it could be discerned). There is a distinct suboral cavity, as in *O. similis*. It is not represented in species **b**, owing to the less satisfactory preservation; but it is distinctly discernible also in that species.

The body skeleton is of the compound type; there is a more or less developed median process from the transverse rods. The posterolateral rods are provided with strong thorns along their inner side, the other rods have fine thorns.

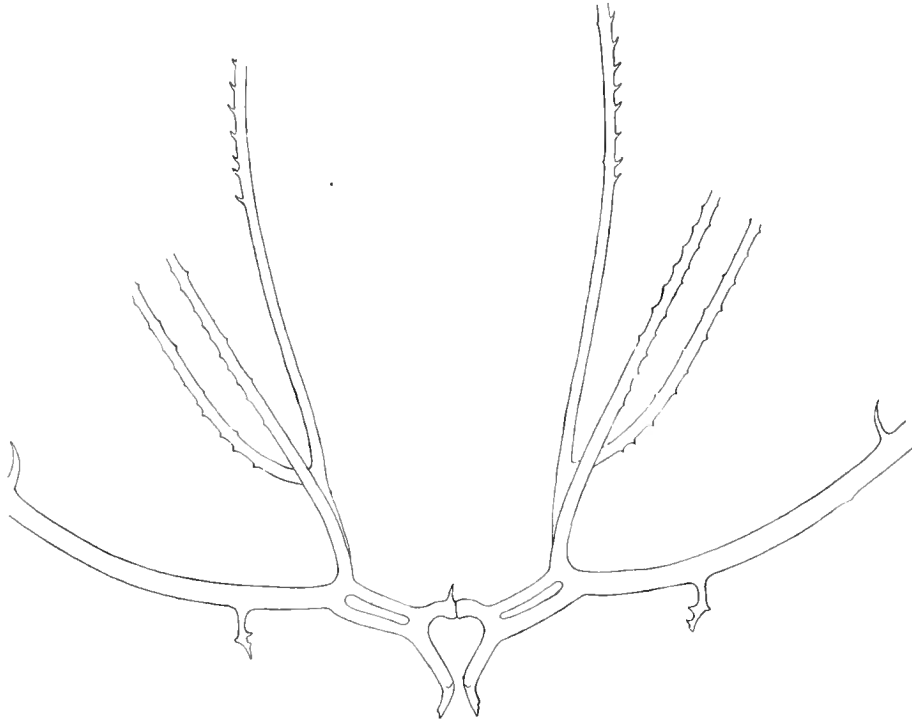


Fig. 90. Skeleton of *Ophiopluteus retrospinus*, species **b**.  $\times 20/1$ .

Species **a**. (Pl. XXII, Fig. 1). The anterolateral, the postoral and the posterodorsal arms are about  $1\frac{1}{2}$  the body length. The backward processes from the posterolateral rods are very prominent and conspicuously serrated, especially along their inner side (Fig. 89). Besides these there is a smaller process (more rarely two, or none at all) from the lower end of the body rod, also a little serrate. The end rods are of moderate length, curving outwards in the lower part; the small side branch is at some distance from the point. The transverse rods are hardly swollen at the point, with merely an indication of interlacing branches. The median rod is long, slightly thorny, the ventral rod somewhat longer than the dorsal one. The rods of the inner arms are only faintly thorny, also the anterolateral rod carries only small thorns along its outer side.

This larva was found in the Gulf of Siam, S. of the island Koh Chuen, 3/III. 1900 (2 specimens), W. of Koh Kong, 25/I. 1900 (1 specimen),

Malacca Strait, off Pulo Pisang, 1/XII. 1899 (1 specimen) and 101°12' E. 2°45' N., Malacca Strait, 30/XI. 1899 (6 specimens).

Species **b.** (Pl. XXII, Fig. 2). The inner arms are distinctly shorter than in species **a**, only of about body length, and especially the postoral and posterodorsal arms are conspicuously shorter than in species **a**. The backward process from the posterolateral rods is much shorter than in the former species and has only very few serrations; sometimes it is quite rudimentary; there is no process from the body rod, and the median process from the transverse rods is quite short. The anterolateral rod is provided with rather large thorns along the outer side (Fig. 90). The specimen figured presents a series of well defined spots in the vibratile bands along the arms, especially the posterolateral ones. Most probably these are pigment spots; but this can only be definitely ascertained by the study of living specimens.

This species was found off Jolo, 20/III. 1914 (1 specimen) and off Colombo, 13/II. 1898 (6 specimens) (Mr. H. Mortensen).

It is not quite easy to distinguish this species from *O. pusillus* species **c**, and the possibility cannot be denied that both are really the same, very variable species; the fact that they were taken together (Colombo, 13/II. 1898) would also point in this direction; but no definite conclusion can be reached from the preserved material, and I have thought it preferable to keep them as two separate species in view of the marked difference between typical specimens.

A suggestion as to the Ophiurid genus to which these larvæ belong, cannot be made for the present.

### **Ophiopluteus pusillus** nova forma.

The characters which distinguish this larval type are the following. The body skeleton is of the compound type, often with a process from the recurrent rod; the transverse rods are slightly widened at the point, with some short obtuse prominences, fitting into one another; no median process. The anterolateral rod is set with rather coarse thorns along the outer side in the outer part. The posterolateral arms are rather short, only about twice the body length, not much outwardly directed; the anterolateral arms are somewhat less than body length; their points are at about the level of the points of the posterolateral arms. The postoral and the posterodorsal arms are much shorter than the other arms and hardly reach beyond the frontal edge. Characteristic of this larval type is also its small size, which, in the fully formed larva, is only ca. 0.5—0.7 mm in total length,

from the posterior end of the body to the point of the anterolateral arms. Several species of this larval type are at hand.

Species a. (Pl. XXIX, Fig. 1). The length of the body from the posterior end to the frontal edge is ca. 0.34 mm. The frontal area is rather large. The postoral band may curve much downwards, as seen in the figure; this is, however, no constant feature and, evidently, to some degree at least, depends on preservation. The preoral band curves upwards,

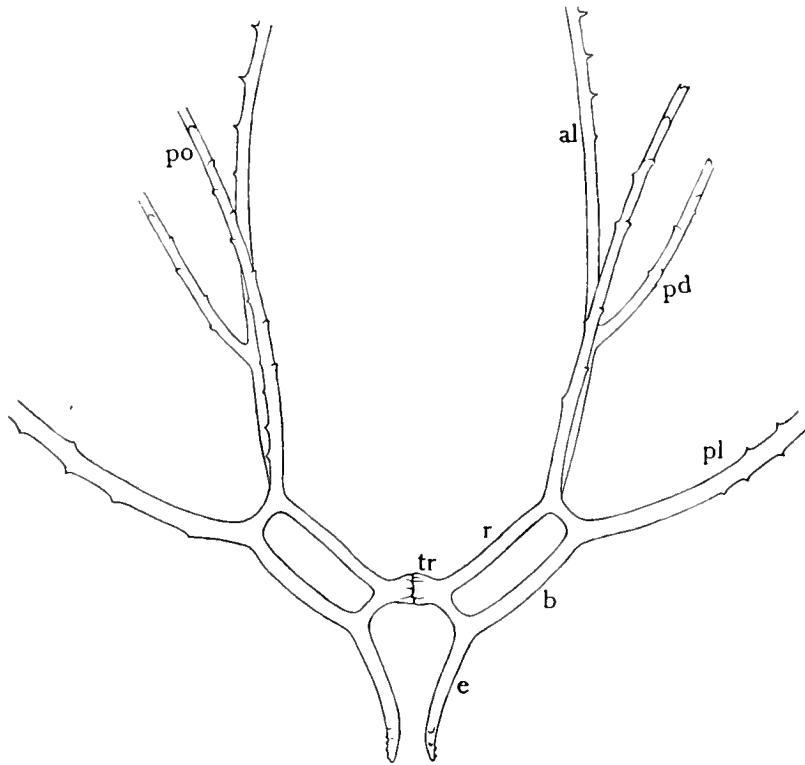


Fig. 91. Skeleton of *Ophiopluteus pusillus*, species a. Letters as in fig. 85.

but remains straight in the middle part. The posterolateral arms are about  $1\frac{1}{2}$  body length. There is no distinct widening at the point of the arms.

The body skeleton (Fig. 91) is slender, the meshes being rather large, rectangular; the end rods are fairly long and slender, with one or a few small side branches somewhat above the tip, which is very gently curved; the outer edge near the point may be finely serrate. There is no process from the recurrent rod. The posterolateral rods are provided with short thorns of about equal size on both the outer and the inner side, the postoral and posterodorsal rods with small thorns, placed mainly along the ventral side of the former and along the dorsal side of the latter, so as to appear mainly as transverse lines on these rods in ventral or dorsal view of the larva.

A dozen specimens of this larva were found in a plankton sample from Misaki, Japan, 17/VI. 1914. A specimen from off Koh Kam, Gulf of Siam (4/II. 1900) differs from the Japanese specimens in lacking the small side-branches of the end rods, but otherwise so closely resembles the latter that I have no doubt in referring it to the same species.

Species **b**. (Pl. XXIX, Figs. 2—3). This species agrees with species **a** in the character of the spinulation of the posterolateral and the other rods,

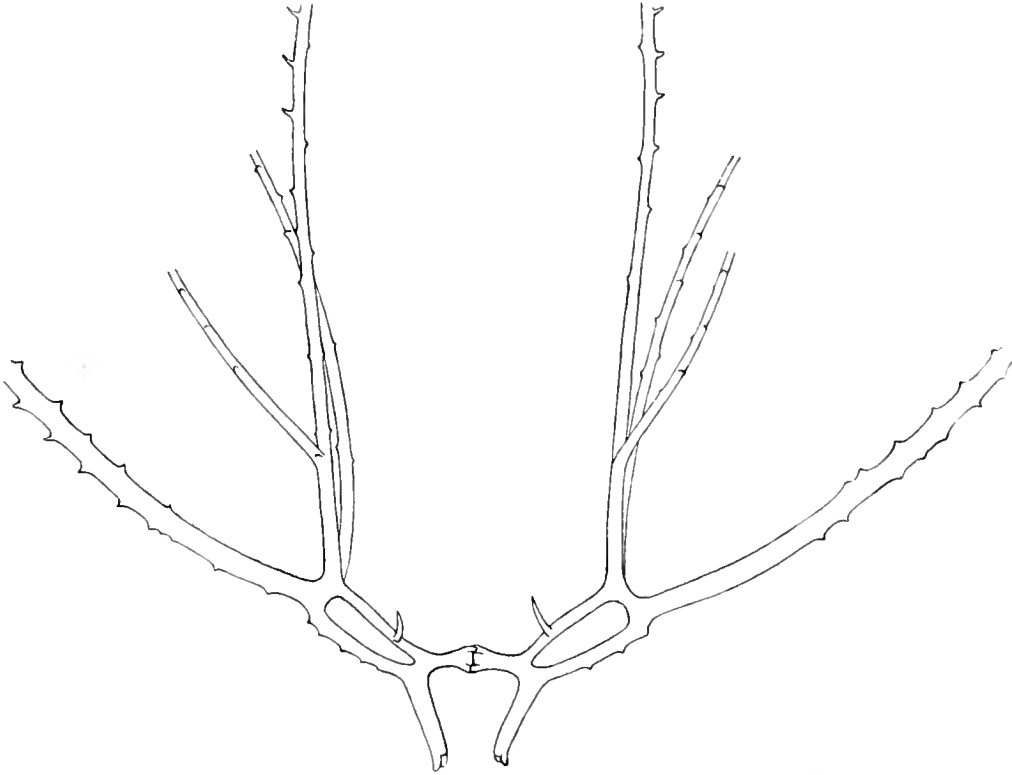


Fig. 92. Skeleton of *Ophiopluteus pusillus*, species **b**.  $\frac{290}{1}$ .

but differs markedly from the latter species in the shape of its body skeleton (Fig. 92). The meshes are not quite rectangular, but generally distinctly narrowing downwards, and there is a conspicuous process from the recurrent rod. The transverse rods are somewhat longer than in species **a**, in accordance with the insertion of the recurrent rod nearer the body rod. The end rods are somewhat shorter and quite straight, and the side branches are placed close to the tip. Otherwise it agrees very closely with species **a** in its general shape, only the postoral and posterodorsal arms being still somewhat shorter: they reach only to about the level of the preoral band.

A very interesting stage of metamorphosis is represented in Pl. XXIX, Fig. 3. As in *Ophiopl. formosus*, sp. **a** (Pl. XXX, Fig. 2) and *O. undulatus*,

sp. a (Pl. XXIV, Fig. 3) the vibratile band is seen to pass directly across the body, below the developing Ophiurid, so as to continue directly from one posterolateral arm to the other. A distinct anterior band is represented by the former preoral band of the larva, and moreover in this specimen distinct traces of other vibratile bands are seen, the accordance with the pupa-stage of the Holothurians being thus still more emphasized. There can then be no doubt, that we have really in these Ophiurid larvæ a true pupa-stage. — Also in the metamorphosis-stage of *O. formosus* there are

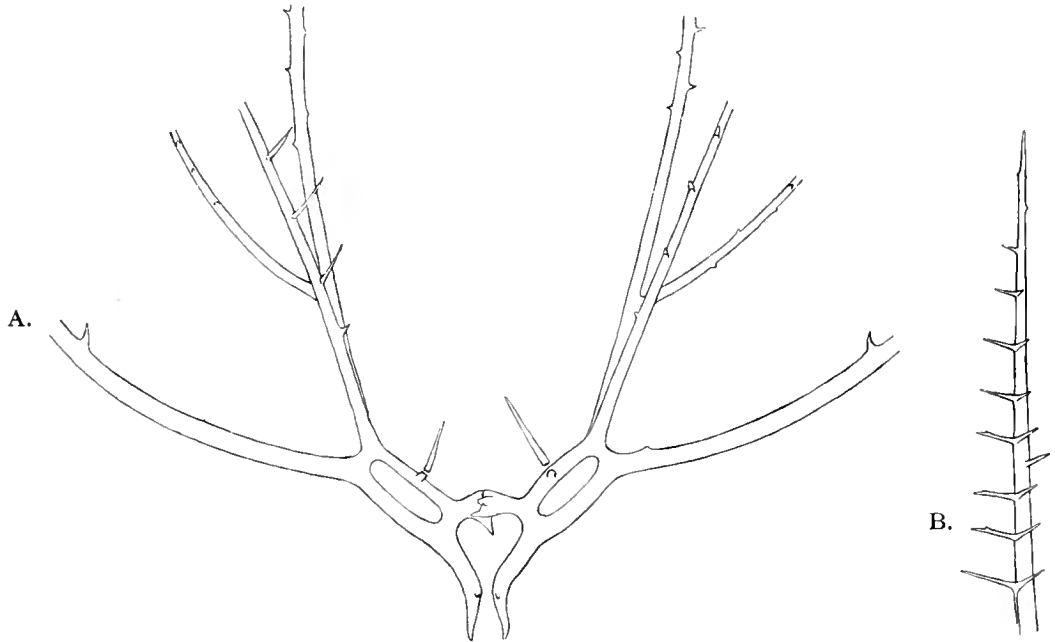


Fig. 93. *Ophiopluteus pusillus*, species c. A. body skeleton; B. outer part of postoral rod. <sup>290</sup>/<sub>1</sub>.

very slight indications of small parts of vibratile bands in the median part of the body. Most probably they will prove to exist in all forms having a distinct pupa-stage.

This species was found in the Gulf of Panama, at the island of Taboga, in December 1915; 12 specimens.

Species c. (Pl. XXIX, Fig. 4). The present species differs markedly from the two preceding species in the character of the posterolateral rods, which are provided with long thorns along the inner side, but entirely smooth on the outer side. The body skeleton (Fig. 93, A) forms a pair of rather small, oval meshes, and there is a long often somewhat thorny process from the recurrent rod; this process is directed ventrally or dorsally, and it is therefore generally broken in the preparations, as also seen in the figure. This thorn may, however, sometimes be lacking. The end rods are rather long, gracefully curved, with a small side branch at some



distance from the point. The backward projecting process from the transverse rods seen in the figure is no constant feature. The thorns on the postoral rods and apparently also on the posterodorsal rods are very long, and lend this rod a very peculiar pectinate appearance; but as they are directed ventrally they can be seen distinctly only when they (or the rod itself) are (is) broken. As seen in Fig. 93, B they may be bifid or even trifid at their base, and there may further be a small side branch near the point. Whether this complicate structure is a constant feature is hard to ascertain, as it can only be seen when the rod is broken and lies in a favourable position. Neither can the possibility be denied that these minor differences really are specific characters, so that more than one species may be included under the larval form designated here as *O. pusillus*, species **c**. This cannot be decided from the study of preserved material alone. None of the other species of the *O. pusillus* type appear to have such long thorns on the postoral rods. — The body of the present species is somewhat shorter and comparatively broader than that of the two preceding species. Also the frontal area is comparatively lower and the preoral vibratile band less arched.

A considerable number of specimens were found in a plankton sample taken by my brother, Mr. H. Mortensen, off Colombo, Ceylon, 13/II. 1898. Further I have specimens from the Gulf of Aden, 3/V. 1900 (1 specimen), and the Malacca Strait, 30/XI—1/XII. 1899 (8 specimens).

This species has several points of resemblance with *Ophiopl. retrospinus*, species **b**, and probably they are nearly related. The possibility that they are really only one, very variable species cannot even be denied. Only the study of living material can decide the question.

Species **d**. (Pl. XXIX, Fig. 5). The shape of the body is like that of species **c**, short and rather broad, with a very small frontal area; it differs from the other species in the posterior extremity of its body being more rounded. As seen in the figure the nervous system may be distinctly observable, showing the typical arrangement<sup>1)</sup>.

This species differs from the preceding ones in the shortness and rather robust character of the body skeleton (Fig. 91); there is no process from the recurrent rod. The end rods are short, straight, and with the small side branch close to the point. The posterolateral rods are provided with long thorns along the inner side, the outer side being smooth. The thorns of the postoral and posterodorsal rods appear to be more bilaterally arranged than in the other species and are especially much less developed than in species **c**.

<sup>1)</sup> Th. Mortensen. Notes on the development and the larval forms of some Scandinavian Echinoderms. p. 158—160.

This species was found in the Gulf of Panama, at the Island of Taboga, in December 1915, a dozen specimens.

Evidently it stands more apart from the other species and possibly does not really belong to the same type; still I have thought it preferable to

include it under the type of *O. pusillus*, to which it bears in several regards a close resemblance.

It is impossible to have any opinion of the relationship of this larval type. That it occurs both at Panama, Japan and in the Indian Ocean is by no means a sufficient foundation for any suggestion as to this point. Too many Ophiurid genera are common to the Pacific coast of

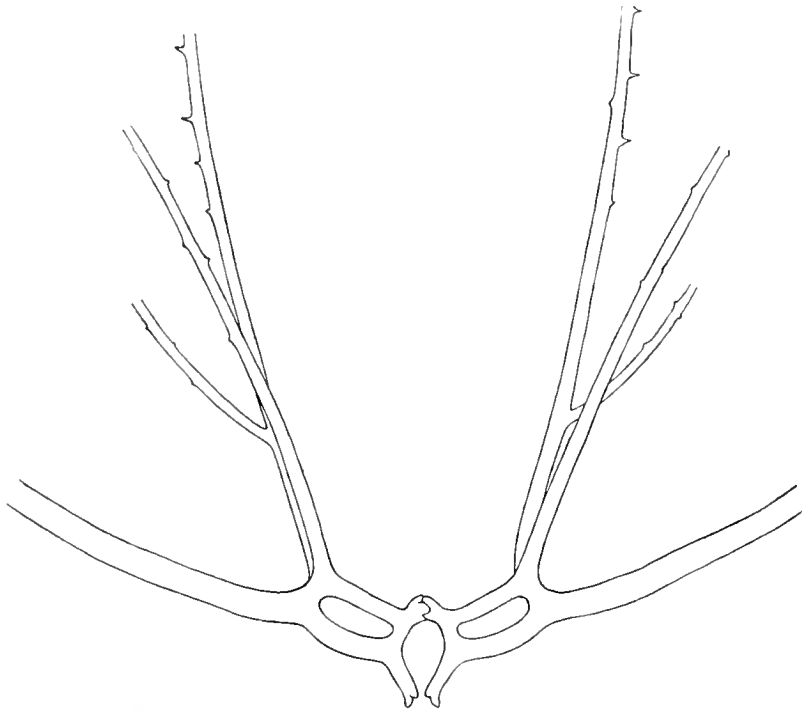


Fig. 94. Skeleton of *Ophiopluteus pusillus*, species d. <sup>290</sup>/<sub>1</sub>.

America and the Indo-Pacific region to allow any such conclusions at our present stage of knowledge.

### ***Ophiopluteus diegensis* nova forma.**

Pl. XXIX, Fig. 6.

In its general appearance this small larva (0.27 mm body length) very much resembles *Ophiopluteus pusillus*. The posterolateral arms are scarcely longer than the body, and the point of the anterolateral arms is at about the level of that of the former ones, while the postoral and posterodorsal arms remain very short. The frontal area is quite low. The posterolateral rods are set with short thorns along both the outer and the inner side, and the anterolateral rods have rather long thorns along their outer side, as in *pusillus*. The postoral rods are strongly curved, with few, small thorns. The body skeleton is simple; there is generally a small thorn on the outer side near the base of the body rod. The end rods are straight, with a small branch close to the point. The transverse rods have the same structure

as in *O. pusillus*, with small obtuse, interlacing branches at the slightly swollen end; there is no median process (Fig. 95). — In the posterior part of the body some comparatively large grains, evidently pigment cells, are seen.

In the specimen figured the hydrocoel has not yet begun to form the primary lobes; this is, however, the case in other specimens, and as the arms are not longer in these than in the one figured, it seems beyond doubt that the arms will not be much longer in the fully formed larva.

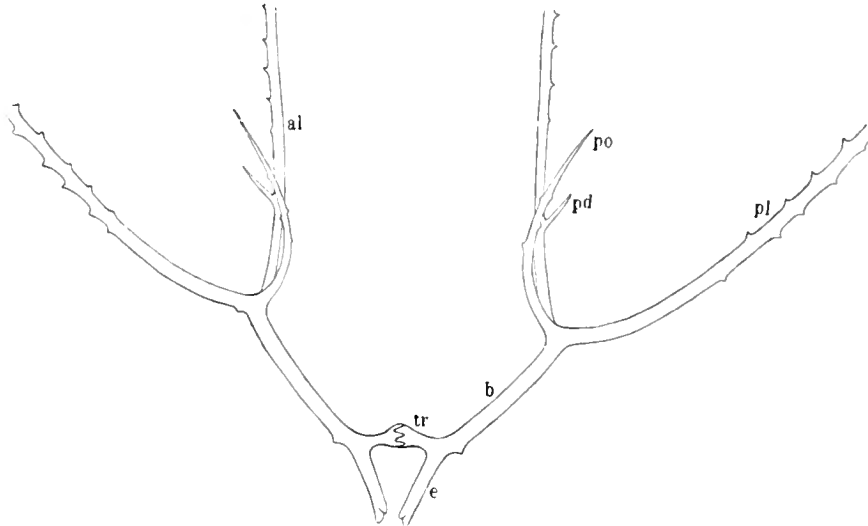


Fig. 95. Skeleton of *Ophiopluteus diegensis*.  $\frac{200}{1}$ . Letters as in fig. 85.

A number of specimens were found in a plankton sample from San Diego, California, 7/IX. 1915.

This species bears so close a resemblance to *Ophiopluteus pusillus*, especially species **b**, that the suggestion lies at hand that it is really related to it, in spite of the apparently essential difference in the structure of the body skeleton. On the other hand, it also bears some resemblance to *Ophiopluteus fusus*. At our present state of knowledge it is impossible to ascertain which is the correct reference, especially so long as we do not definitely know the value of that conspicuous character of the body skeleton, the simple or the compound structure.

### **Ophionereis squamulosa** Kœhler.

Pl. XXXI. Figs. 1—6.

During my stay at Tobago, B. W. I., with the Carnegie Expedition I had the good fortune of seeing (on the 13th of April 1916) a specimen of this species discharge its eggs, which were at once fertilized, a male speci-

men among those kept in the same dish discharging its sperm at the same time. The eggs were few in number, amounting only to ca. 90; the specimen, however, still contained some more, so that, evidently, not all the eggs are discharged at the same time, as is the case in *Ophiothrix angulatus*, in which they are all discharged at one time, almost as by an explosion. — The specimen was not observed to assume a special attitude while discharging its eggs, such as is the case in *Ophioderma brevispina*, according to the observations of Grave.

Owing to the small number of eggs the material was insufficient for a complete study of the details of the interior changes during the metamorphosis, a study which would have been of the greatest interest for a comparison with the results obtained by Caswell Grave<sup>1)</sup> in *Ophioderma brevispina*. Although I tried many times to get another culture, I did not succeed, so I had to make a very careful use of the little material available and to preserve no more specimens of the different stages than strictly necessary.

The size of the eggs is 0.2 mm; they are red coloured. They were lying free at the bottom, not floating at the surface, as did those of *O. brevispina*. The cleavage is regular and total. In the course of 15 hours the embryos were found to be in the gastrula stage, pearshaped, of a beautiful pink colour, especially towards the pointed anterior extremity; they were swimming close to the bottom. In the course of ca. 24 hours it became evident that the larva would turn out to be of the vermiform type, like that of *O. brevispina*, as described by Grave. At that age the embryo has an elongate, triangular shape, with a narrowing below the anterior end, which thus becomes like a rounded knob (Pl. XXXI, Fig. 6). It is ciliated all over, without any ciliated bands as yet; what looks like a transverse band in the figure quoted is not really one; it is due to the fact that a transverse fold is formed in the posterior end of the body, on the ventral side, the apparent band being only the edge of the lobe. In this fold the gastrula mouth lies which is thus no longer in the posterior edge of the embryo; it appears to be closed already at this stage. The embryo keeps swimming close to the bottom as in its youngest stages.

Pl. XXXI, Fig. 5 represents a frontal section of a larva 26 hours old. It shows a double sac at the upper end of the archenteron, apparently still in connection with the latter — but the histological preservation is not sufficiently good to allow the definite ascertaining of this question. The larger of these sacs doubtlessly represents the hydrocoel, while the smaller apparently is the anterior right enterocoel. In the posterior end two

<sup>1)</sup> Caswell Grave. *Ophiura brevispina*. Mem. Nat. Acad. of Sc. VIII. Baltimore 1900. (Mem. Biol. Lab. Johns Hopkins Univ. 4).

accumulations of nuclei are seen which, no doubt, represent the posterior coelomic vesicles. There is an indication that one of them is in connection with the ectoderm, but it cannot be stated definitely to be the case. — It is very unfortunate that the material available does not allow a detailed study of the process of formation of the hydrocoel and the coelomic vesicles, so that a comparison with Grave's researches on *O. brevispina* might be made. Especially his statement<sup>1)</sup> that the epigastric coelom originates as a separate invagination from the ectoderm is so remarkable that it would have been of the greatest interest to see, whether it originates in the same peculiar way in this species also. There is, as stated above, an indication that it really does so, but it can by no means be ascertained as a fact.

The specimen represented in Pl. XXXI, Fig. 6, although of the same age, is somewhat more advanced in its development, the hydrocoel having formed the five primary lobes. The small sac lying at the upper end of the stomach apparently is the right anterior coelomic vesicle: the posterior coelomic vesicles could not be discerned. —

At the age of 40—45 hours the larva has reached its full development and has a very characteristic shape (Pl. XXXI, Figs. 1—2). The anterior end forms an elongate, rounded lobe with a ciliated band around it, situated a little below its middle; below and above the band the lobe is narrowing, at the point there is a large ciliated tuft, which is of a bright pink colour. In the middle of the posterior part of the body there is another spot of pink colour, larger than the apical spot, but less intense. It coincides with the central part of the young Ophiurid, which has already developed its first pair of tubefeet.

Two ciliated bands are found in the posterior, main part of the body, one at the level of the mouth of the developing Ophiurid, the other at the posterior end. Both are incomplete; the band in the middle of the body consists of a median part on the dorsal side and two lateral parts, while the posterior band consists of two parts, a larger one on the right side and a smaller one to the left. Possibly the posterior band has been complete, surrounding a posterior lobe in a former stage, before the developing Ophiurid has reached so far in its development. That the band in the middle of the body is not the broken up rests of a formerly complete band would seem evident from the fact that in the next stage figured (Pl. XXXI, Fig. 3), of a larva 2½ days old, the band is much more developed and nearly complete across the dorsal side.

At the age of 10—15 hours the skeletal plates begin to appear. In the

<sup>1)</sup> Caswell Grave. *Ophiura brevispina*. II. An Embryological Contribution and a Study of the effect of the Yolk substance upon development and developmental processes. Journ. of Morphology. Vol. 27. 1916.

specimen figured in Pl. XXXI, Fig. 2 the six primary plates of the dorsal side have appeared and three of the terminal plates have just begun to develop, beginning with the posterior radius, as is evident from the relative size of these three rudiments. On the ventral side no skeletal plates have been formed as yet. There is not the slightest trace of a larval skeleton.

In specimens  $2\frac{1}{2}$  days old (Pl. XXXI, Fig. 3) the terminal plates have been fully formed, the unpaired, terminal tentacle lying within it as in a tube. (Although the skeleton has been dissolved in all the specimens of this age preserved, this fact can be distinctly ascertained). Inside the first formed pair of tentacles indications of another pair of much smaller outgrowths from the radial canals are seen. This is in accordance with the interesting fact observed by Grave in *Ophioderma brevispina*, that the buccal tentacles are formed after the second pair. The same observation was also made by Krohn<sup>1)</sup> in a similar Ophiurid larva which was found at Madeira. It seems highly probable that this is really the usual order of appearance of the oral tentacles in Ophiurids.

As stated above, the median band is nearly complete across the dorsal side, while on the ventral side it is, of course, interrupted by the mouth opening of the Ophiurid. The left part of the posterior band has developed towards the mouth so that there are now three distinct bands reaching the mouth edge, one to the right, two to the left side. The rest of the posterior band remains at the right side of the posterior end.

At this stage the larva evidently has reached its fullest development, and it is worth mentioning that it was observed now to swim fairly actively, while on the other hand, it could also now attach itself to the bottom by means of its tubefeet, so firmly that it was hardly possible to wash it off by means of a pipette. — Also in the stage of 40—45 hours the larvæ were observed now and then to swim free in the water.

At the age of 6 days the anterior lobe of the larva is still distinct, with its ciliated bands, but it is very much shortened and evidently in the course of being absorbed (Pl. XXXI, Fig. 4). The median ciliated bands have nearly disappeared, but a small trace of each of the three bands reaching the mouth in the foregoing stage is still observable at the edge of the body; the posterior band is still quite distinct. — The primary skeletal parts have all been formed, and the teeth and the first spines have appeared. Very prominent is the torus angularis, a fact the more remarkable since this plate is hardly observable in the adult specimens. In the two anterior radii two ventral plates are seen, one inside the other; the inner one of them doubtlessly represents the first, rudimentary, inner

<sup>1)</sup> A. Krohn. Über einen neuen Entwicklungsmodus der Ophiuren. (Müllers Archiv. 1857. p. 370. Taf. XIV. B. Fig. 1).

ventral plate; it is not formed in all the radii; I find it present sometimes in three radii, sometimes only in two or one, but not in more than three radii in any of the specimens available. —

In fig. 96 part of a young specimen, 12 days old is represented. The second pair of lateral plates has begun to form; the inner (in reality the second) ventral plate has assumed an elegant hourglass-shape. The buccal plates have not yet been formed. Inside the ventral plate a pair of small, irregularly halfmoon-shaped plates has appeared, representing the adoral plates. (This interpretation is not in conformity with that usually adopted; I cannot, however, enter here on a discussion of the morphology of the oral skeleton of Ophiurids).

When the young Ophiurids had reached this age, the sojourn at Tobago ended and put a stop to the experiments, and the few specimens left were preserved. But I cannot have the slightest doubt that it would be very

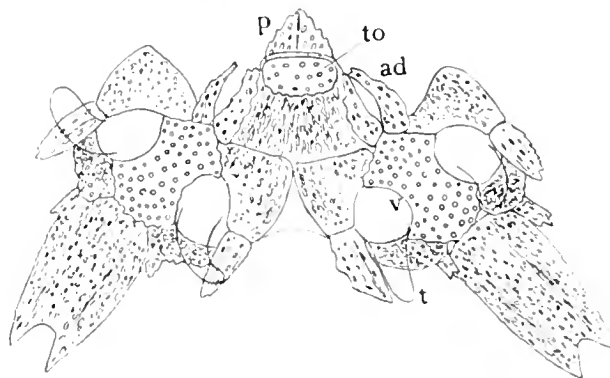


Fig. 96. Part of a young *Ophiureis squamulosa*, 12 days old. ad, adoral plate; p, mouth papilla; t, tubefoot; to, lorus angularis; v, ventral plate.  $220/\mu$ .

easy to rear the young Ophiurids of this species to a much later stage, since it is very easy to give them suitable conditions. The species is found in quite shallow water on the coral reef, in the sand under old coral blocks, together with a number of other species of Ophiurids. The experiments carried out thus far indicate that here is a lot of interesting work to be done.

Quite recently a notice on the development of another species of *Ophiureis*, *O. Schayeri* (M. Tr.), was published by H. B. Kirk<sup>1)</sup> indicating the highly remarkable fact that in this species the development is absolutely direct, no larval form apparently occurring at all, the young star forming already within the tough envelope by means of which the eggs are attached to the under surface of stones. Unfortunately, the identification of the species is not beyond doubt, the deposition of the eggs not having been observed and the young Ophiurids not having been reared until they could be identified with certainty.

It would be exceedingly interesting to study the development also of other species of this genus; although thus (probably) two species of the genus have been shown to develop without the Pluteus larval stage, it is

<sup>1)</sup> H. B. Kirk. On the much-abbreviated development of a sand-star (*Ophiureis Schayeri*). Preliminary Note. Transact. & Proc. New Zealand Inst. Vol. XLVIII. 1916, p. 383—384.

quite possible that other species may have a Pluteus-larva, corresponding to the fact shown in this work that within the genus *Asterina* some species have a typical Bipinnaria-larva, while others have a shortened, direct development as in the classical case of *Asterina gibbosa*. —

The larva of *Ophionereis squamulosa* belongs to the same type as that of *Ophioderma brevispina*, described by Caswell Grave. There are some minor differences in the shape of these two larvæ, that of *Ophionereis squamulosa* having the anterior lobe distinctly longer than that of *Ophioderma brevispina*. Also the arrangement of the vibratile bands is somewhat different, especially the posterior band, as a comparison of Pl. XXXI, Fig. 3 with Pl. III, Fig. 22 of Grave's Memoir will make evident.

The statement of Grave (Op. cit. p. 83) that the usual Pluteus skeleton is formed in the larva of *Ophioderma brevispina*, while there is no trace of a larval skeleton in *Ophionereis squamulosa*, would appear to indicate a very important difference between these two larvæ. Later on, however, Grave has announced<sup>1)</sup> that he mistook the beginning skeletal plates of the Ophiurid for the larval skeleton. There is thus no larval skeleton in the larva of *Ophioderma brevispina* either.

A larva closely resembling that of *O. brevispina* was taken pelagically at Taboga, Gulf of Panama, 18/XI. 1915. Probably it belongs to one of the Panamic species of *Ophioderma*. It would seem superfluous to give a closer description or figures of it. — To the same larval type belongs that described by Joh. Müller<sup>2)</sup> from Triest under the designation "wurmformige Asterienlarve", and also those described from Madeira by Krohn<sup>3)</sup>. It may perhaps be suggested that the Mediterranean form belongs to *Ophioderma longicauda*.

In the "Echinodermenlarven d. Plankton-Exped." I designated also these worm-shaped larvæ as Ophiopluteus. Hamann<sup>4)</sup> objects to this designation, because there is neither a ciliated band nor a larval skeleton in these larvæ, not to mention that the usual larval arms are totally lacking. I would, however, still think it justifiable to use this designation. In the larva of *Ophiura affinis*<sup>5)</sup>, *Ophiopluteus Metschnikoffi* and *O. Claparèdei* we have different stages of the reduction of the typical Pluteus-shape. From

<sup>1)</sup> Caswell Grave. On the occurrence among Echinoderms of larvæ with cilia arranged in transverse rings; with a suggestion as to their significance. Biol. Bull. V. 1903. p. 173.

<sup>2)</sup> Joh. Müller. Über die Larven u. die Metamorphose d. Holothurien u. Asterien. III. Abhandlung. Abh. d. Akad. Berlin. 1850. p. 26. Taf. VI. 8—12. VII. 1—4.

<sup>3)</sup> A. Krohn. Über einen neuen Entwicklungsmodus d. Ophiuren. Müller's Archiv. 1857. p. 369, 373. Taf. XIV. B. Fig. 1—4.

Th. Mortensen. Echinodermenlarven d. Plankton-Exp. p. 65—66.

<sup>4)</sup> O. Hamann. Die Schlangensterne. Bronn. Klassen u. Ordn. III. 1901. p. 860.

<sup>5)</sup> Th. Mortensen. Notes on the development and the larval forms of some Scandinavian Echinoderms. p. 135.



the latter species, in which the skeleton is reduced to a pair of simple, small rods, there is only a very small step to the one of Krohn's larvæ, (*O. elongatus*) which was observed by that author also to have a rudimentary skeleton (— unfortunately, he does not give any figures of it —). We have thus an unbroken series from the typical *Ophiopluteus* through the worm-shaped *Ophiopluteus elongatus* with a larval skeleton to the larvæ of *Ophioderma brevispina* and *Ophionereis squamulosa* with no larval skeleton, and further on to *Ophionereis Shayeri* with the larval stage completely eliminated.

### ***Amphiura vivipara* H. L. Clark.**

Pl. XXXI, Figs. 7—9.

The discovery of this new viviparous *Amphiura* was one of the results of the Carnegie Expedition to Tobago, B.W. I., in April 1916<sup>1)</sup>. As emphasized by Ludwig in his paper on "Brutpflege bei Echinodermen"<sup>2)</sup> the viviparous Ophiurids hitherto known all belong to the colder regions (arctic-subarctic or antarctic-subantarctic), with the sole exception, besides the nearly cosmopolitan *Amphiura* (or, more correctly, *Amphipholis*) *squamata*, of *Hemipholis cordifera* Lyman (*elongata* Say); moreover, the viviparity of the latter is, no doubt, only apparent, as I have shown recently.<sup>3)</sup> It was then of considerable interest to find a truly viviparous Ophiurid living here, even under the most tropical conditions, viz. on a coral reef. (It was mainly found in thick cushions of *Corallina*, which covered large patches on the reef lying dry at ebb tide).

It was at once evident from the considerable size of the eggs, 0.5 mm, that the interest attached to this case was more than that of having found a tropical viviparous Ophiurid. In the only viviparous Ophiurid hitherto studied, *Amphipholis squamata*, the eggs are very small, only ca. 0.15 mm, and the cleavage total and regular; the embryo has a rudimentary larval skeleton and is, evidently enough, only a reduced Pluteus. In the present species all this is different. First of all the cleavage is meroblastic. The nuclei, in the first cleavage stages, lie irregularly spread in the yolk substance and there is no trace of cell division; then they gradually arrange themselves in a more regular order along the surface of the egg, forming thus the ectoderm (Pl. XXXI, Figs. 7—8), while in the interior they remain without distinct order till a much later stage. The details of the embryonal and postembryonal development cannot be given here, as I cannot spare

<sup>1)</sup> H. L. Clark. Brittle-Stars, new and old. Bull. Mus. Comp. Zool. LXII. 6. 1918. p. 268.

<sup>2)</sup> Zoologische Jahrbücher. Suppl. VII. 1904.

<sup>3)</sup> Th. Mortensen. On Hermaphroditism in viviparous Ophiurids. Acta Zoologica. I. 1920. p. 4—5.

the time, at present, for this apparently very difficult study. It must suffice at the present occasion to state only that there is formed at the place destined to form the oral side of the Ophiurid an accumulation of nuclei, like a germinal disk, from which the formation of all the main structures of the Ophiurid proceeds, while the large yolk mass remains undifferentiated, simply as a reservoir of food, covered only by a thin ectodermal coat. The arms of the young Ophiurid gradually as they grow are folded up over the yolk mass (Pl. XXXI, Fig. 9).

The embryos proved unfavourable objects for a detailed study of the development of the oral skeleton. The usual primary plates are formed in the skin of the dorsal side. There is no trace of a larval skeleton. — The embryos are not liberated until they have reached a comparatively large size, with ca. 10 armjoints; the paired infradental mouth papillæ have then already appeared; they do not appear till the teeth have been fully formed, the latter being among the first parts of the oral skeleton to appear.

That this type of development will prove to be of more general occurrence in viviparous Ophiurids can hardly be doubted, viz. in such forms as have large eggs, rich in yolk; but not in all of them. In *Stegophiura nodosa* (Ltk.), the eggs of which are 0.5—0.6 mm in diameter and rich in yolk the cleavage is total and regular. A detailed study of the development of these two Ophiurids, both having large, yolk-laden eggs, but one of them having superficial, the other total and regular cleavage, would, evidently, be of exceptional interest. This is, however, entirely out of the scope of the present work. But it is worth emphasizing that *Amphipholis squamata* is so far from representing the usual type of development among viviparous Ophiurids that it appears in reality to be exceptional in this regard.

The interesting observation that *Amphiura vivipara* is hermaphroditic like *Amphipholis squamata* may be recalled here. It led to an examination of other viviparous Ophiurids which resulted in the establishment of the surprising fact that out of the twenty viviparous forms of Ophiurids known sixteen are hermaphroditic, three alone having separate sexes (one remaining unknown as regards its sexual characters). This fact, the more conspicuous since not a single case of hermaphroditism is known otherwise in Ophiurids, shows that there is some relation between viviparity and hermaphroditism in Ophiurids, though it remains enigmatical, wherein this relation consists. (Comp. the author's paper "On hermaphroditism in viviparous Ophiurids").

**Ophionotus hexactis** (E. A. Smith).

PL. XXXII.

In the paper quoted above "On hermaphroditism in viviparous Ophiurids" (p. 17) the observation was mentioned that this species, in spite of being viviparous, has a true, well formed larva, the development being intraovarial. While in that paper the hermaphroditic character of the species was established, I may here take the opportunity of giving a description of the remarkable intraovarial development of the no less remarkable larva.

The previous observers, Studer<sup>1)</sup> and Lyman<sup>2)</sup> assumed that the young were enclosed in the much widened and very thin-walled bursæ, or "rather, perhaps, in pockets leading out of the bursæ"; this latter expression shows that Lyman has seen something of the real fact; the understanding of the whole astonishing fact could, however, not be gained through simply examining how the large young are lying within the parent specimen. Only an examination of the ovaries could disclose the fact, almost unique among the Echinoderms<sup>3)</sup>, that the young are really lying within the distended ovaries.

The structure of the young ovaries differs somewhat from that generally observed in the female gonads of Ophiurans. While generally they are completely filled with eggs so as to be solid organs, they are in *O. hexactis* hollow vesicles, the eggs attached to the walls not nearly filling out their lumen (Pl. XXXII, Fig. 9). The eggs are of various sizes, one or a few of them being larger than the rest; the size of the ripe egg is about 0.2 mm. When ripe the egg falls into the cavity of the ovary, but it does not pass out into the bursa, as should be expected; it remains within the ovary and, after being fertilized there, goes on developing, the embryo passing its whole development within the ovary.

Gradually as the embryo grows, the walls of the ovary are distended. The other eggs remain attached to the wall as flat buttons, gradually wider and wider apart from one another. In the same time they gradually diminish in size and ultimately they disappear completely. It seems beyond doubt that they must serve as nourishment for the young contained within the ovary. Traces of eggs on the ovarian walls may still be seen when the young has about 4—5 armjoints (Pl. XXXII, Fig. 8). As the young grow

<sup>1)</sup> Th. Studer. Über Geschlechtsdimorphismus bei Echinodermen. Zool. Anzeiger. 1880.

<sup>2)</sup> Th. Lyman. Ophiuroidea of the "Challenger". 1882. p. 41. Pl. XLV, Fig. 1; Pl. XLVII, Fig. 2.

<sup>3)</sup> Intraovarial development is known to occur only in one other Echinoderm, *Chirodota contorta* Ludw. Ludwig. Holothurien d. Hamburger Magelh. Sammelreise. 1898. p. 77—81.

to a relatively very large size, — about 8 mm diameter of disk and ca. 20 mm length of the arms, which may have up to about 40 joints — before they are liberated, the ovaries must be distended to quite an enormous extent, and on account of the growing long arms of the young, which need considerable room even if bent up, must occupy any space left between the stomach and the body wall. These are the sacs observed by Studer and Lyman and taken by these authors to be the bursæ themselves (Studer) or pockets from the bursæ (Lyman); as a matter of fact they have nothing at all to do with the bursæ; they are nothing but the distended ovaries. The bursæ themselves are of the typical shape, not at all especially widened, and they never contain young.

The question, how the young are liberated cannot be directly answered. Considering the great number of young found in adult specimens, it should be expected that specimens having emptied out their young would show distinct traces of the way the young have been passing. Only three ways are possible; either they must pass directly through the body wall, rupturing the sac within which they have developed, or they must pass through the bursal wall, likewise after rupturing the ovarian sac, or finally there may be a natural opening from this sac through the bursal wall, through which they may pass. As there is never seen any traces of scars on the disk, and not on the bursal wall either, in specimens which have emptied the young, and the empty ovarian sacs are likewise unruptured, there can hardly be any doubt that there must be an opening from the ovarian sac through the bursal wall. As no such opening can be seen, it must be capable of widening to a very large extent and then completely closing again. — Through this opening also the spermatozoa must enter for fertilizing the egg. — It is a remarkable fact, however, that nobody appears to have observed specimens with the young in the act of being liberated, such as is seen so very often in other viviparous Ophiurids.

After the liberation of the young the ovarian sacs shrink very considerably, the wall contracting and becoming much thicker; it remains attached to the body wall and the stomach and bursal walls through numerous trabecules of connective tissue, as observed by Lyman. But they do not disappear or reassume the original shape of an ovary.

The propagation begins at a very early stage; already in a specimen of 13 mm diameter of disk a large young was found, so that the sexual activity must have started here at a size of only ca. 12 mm diameter of disk. In another specimen of 16 mm only larvæ, not yet metamorphosed, were found. But this specimen was unusually late in beginning its sexual activity, which may be stated to begin, as a rule, at a size of ca. 13—14 mm diameter of disk, that is to say very soon after they are born. In such

young specimens generally only the ovary at the outer corner of the bursal slit is found to contain a young, and mostly of the same size in all the radii. A very large specimen, 39 mm diameter of disk, was found to have all the young, except two of them, liberated. The ovarian sacs were contracted as described above. In the same time new ovaries, containing young developmental stages, had been formed; so far as could be ascertained these new gonads were formed within the old ovarian sacs. In this specimen in two of the radii testes had been formed in the former female gonad on the corner, even two testes in each. Otherwise the testes were in the normal position and in the usual number of three. Another specimen of 37 mm diameter of disk was quite empty; but here no embryos were found in the ovaries; the gonads were evidently abortive and the specimen quite senile. It was probably such specimens that were taken by Studer to be male specimens.

Generally only one young is found in each ovarian sac. In the said large specimen, however, there were in several cases two embryos in the same ovary, mostly in exactly the same stage of development. One ovary was found to contain three embryos in different stages and another even six embryos, in two different stages of development.

The embryonal development proves to be of exceptional interest. Cleavage stages were not observed, but it cannot be doubted that it is total as in *Amph. squamata*; this may be safely concluded from the fact that a regular blastula is formed. The embryo develops into a comparatively well formed larva, with a distinct vibratile band and a rudimentary larval skeleton (Pl. XXXII, Figs. 1—6). The vibratile band remains in a primitive condition, corresponding, in fact, exactly to the diagrammatic figure of the ideal type of an Ophiurid larva represented in Joh. Müller's classical memoir "Über den allgemeinen Plan in der Entwicklung der Echinodermen" (Taf. II, Fig. II. 2<sup>1</sup>). No larval arms are developed, and the larva thus retains a shape like a young *Auricularia*; the rudimentary larval skeleton, however, shows it to be a rudimentary Ophiopluteus. Nothing can be said about the typical character of this larval skeleton, it being altogether too rudimentary to be relied upon in this regard, and no conclusions can be drawn as to its relation to other, free Ophiurid larvæ. It is almost always seen to consist of two main parts, as in typical Ophiurid larvæ, but I never saw an embryo with both parts equally developed.

The posterior end of the larval body is produced into a tip, bearing a rather large tuft of cilia, as it is found, e. g. in the larva of *Ophiura albida* and in several other Ophiurid larvæ. Mostly the larvæ are quite regularly

<sup>1</sup>) Abh. d. Berliner Akad. 1853.

shaped, sometimes, however, they are more or less irregular, the vibratile band forming lobes, as in the specimen figured in Pl. XXXII, Fig. 7.

The interior organisation of the larva is quite typical, though, as might be expected, the digestive organs are to some degree rudimentary, in accordance with the fact that the larva has no opportunity of feeding on other organisms, as do the free pelagic larvæ. The esophagus is somewhat less developed than in the typical larvæ, and especially the mouth opening is smaller, sometimes irregular in outline. The stomach is large and of the typical shape; the rectum is sometimes quite unusually large, but apparently there is no anal opening (Pl. XXXII, Fig. 6). A more or less distinct line of nuclei in the oral area (Pl. XXXII, Fig. 3) would appear to represent the larval nervous system.

The enterocoel and hydrocoel vesicles are large and very distinct, the hydrocoel having at first only 5 lobes; the sixth appears to form between the 2nd and 3rd primary lobes. On metamorphosis the hydrocoel grows upwards over the esophagus. In some cases there is a distinct right anterior vesicle (Pl. XXXII, Fig. 1); in two cases a normally lobed right hydrocoel was found, no trace of a left hydrocoel being observable (Pl. XXXII, Fig. 4). There is not the slightest reason to doubt that these "right"-specimens would have developed normally. This case is quite unique in Echinoderm embryology. Larvæ with both a right and a left hydrocoel have been observed repeatedly, rarely in the free, but not so rarely in cultures, and, as shown by MacBride<sup>1)</sup> can be produced artificially; but, so far as I know, larvæ with a right hydrocoel alone have never before been observed, in nature or in artificial cultures. The theoretical interest connected with this case is very considerable. This is, however, not the place to enter on a discussion of this matter.

Regarding the structure of the young Ophiurid I would only call attention to the fact that there is not one prominent central plate as is usually the fact in young Ophiurids, but two or three of somewhat irregular shape (Pl. XXXII, Fig. 8). Mostly the young Ophiurids have the oral tentacles very much extended (— the specimen figured is exceptional in this regard, having the oral tentacles for the greater part retracted —); they are further conspicuous by the granulated appearance of their point. The suggestion lies near that these tentacles may perhaps have some kind of absorbing function. In any case it is clear that the food contained in the substance of the small egg can by no means account for the large size attained by the young within the brood sac. Nourishment from the parent

<sup>1)</sup> E. W. MacBride. The artificial production of Echinoderm Larvæ with two water-vascular systems, and also of Larvæ devoid of a water-vascular system. Proc. R. Soc. B. Vol. 90. 1918. p. 323—48. Pls. 4—10.

specimen must be absorbed in some way or other. At first it is evidently the other, not developing, eggs within the same ovary that serve as food for the growing young, not directly, but by being dissolved gradually and thus absorbed, perhaps by the digestive organs of the larva and the young Ophiurid. But since these eggs have completely disappeared a long time before the young Ophiurid has reached the size at which it is to be liberated, it must be fed on some sort of nutritive fluid secreted by the parent specimen. It would not seem improbable that the oral tentacles of the young have something with the absorption of this nourishing fluid to do.

The remarkable fact that this species, although representing one of the most highly specialized cases of viviparity, passes through a distinct Pluteus-stage, more developed than many a truly pelagic larva, evidently has an important bearing on the question of the phylogenetic meaning of this larval form. But that is for another opportunity.

### III. Asteroidea.

The Asteroids, upon the whole, lend themselves rather easily to artificial fertilization and are among the favourite objects of experimental embryological studies, although much less so than the Echinoids. A curious fact which renders them somewhat less favourable objects for such a study is this that the spermatozoa are very often found to be quite immovable when taken from the testes and diluted with water, though the specimens be evidently perfectly ripe and ready to empty the content of the gonads. It is, of course, impossible to obtain fertilization by means of such immovable sperm. On adding, however, some drops of sodium hydroxyd (NaOH) to the water and thus raising the alkalinity it is easy enough to stir the spermatozoa to activity and then fertilization is easily obtained<sup>1</sup>). But it is surprising how much NaOH must sometimes be added, before they begin to move. The spermatozoa of Asteroids are evidently exceptionally sensible to changes in the alkalinity of the water, that is to say, they cannot stand any lowering of the normal alkalinity of the water, while they do not object to an amount of alkalinity considerably beyond that of the water of their normal surroundings.

The eggs are very rarely found to be fully mature when taken out of the ovaries, even though the specimens look ever so ripe; they have nearly always a large germinal vesicle. But if they are left for some hours in the water, the germinal vesicle disappears, and they are then ready for fertilization.

<sup>1</sup>) Comp. the author's paper "On the development of some British Echinoderms", p. 7. (*Luidia ciliaris*).

Many starfishes have large eggs, rich in yolk. It appears to be next to impossible to obtain fertilization of such eggs, unless they are shed in the natural way by the females. In this regard the Asteroids — together with the Holothurians — are in remarkable contrast to the Echinoids, in which large and yolky eggs are as easily fertilized as are the small, transparent eggs, with little yolk substance.

The development of the Asteroid-larvæ generally takes a rather long time, which fact partly accounts for the comparatively poor results achieved in the rearing of these larvæ. A stay of two—three months in some place is, in general, not long enough for obtaining satisfactory results in the rearing of Asteroid-larvæ. The fact that the main characters of the larvæ do not appear until they have reached their full size and are near metamorphosis, makes this only more evident. The rearing of the young larval stages alone does not serve to give much more than the proof that the species in question has pelagic larvæ, while in the Echinoids even the first larval stage may give very important information of the larval characters.

To rear the young starfish from larvæ in beginning metamorphosis, taken pelagically, is generally easy enough, and much may certainly be achieved in that way, under suitable laboratory conditions. But a fairly long time will be necessary for rearing them far enough to identify them with certainty; this cannot be achieved during a stay of two—three months. — The experiments of Mead<sup>1)</sup> showing how exceptionally rapid growth may be in these animals, if a rich food supply is given them, while on the other hand a poor food supply delays growth very considerably, is of special interest in this connection. (That the food supply acts in the same way on the larvæ, accelerating their development when available in good quality and sufficient quantity and delaying it when poor and insufficient, is a well known fact, which I have also had a rich opportunity of observing).

The lacking of a skeleton interferes in some way with the preservation of Asteroid larvæ. Not that they are difficult to preserve well, if carefully treated; on the contrary! When taken up a little cautiously in a pipette and then dropped directly into alcohol or formalin they will generally not contract at all; even such forms as have long, contractile arms may be preserved perfectly in this way<sup>2)</sup>. Thus far the Asteroid larvæ are much more easily preserved in a satisfactory way than Echinoid- and Ophiurid larvæ, which will nearly always contract as much as the skeleton allows.

<sup>1)</sup> A. D. Mead. On the correlation between growth and food supply in starfish. *American Naturalist*. XXXIV. 1900. (No. 397).

<sup>2)</sup> Still better results may be achieved with such larvæ if they are narcotized, by means of magnesium sulfate, drops of alcohol or the like, before they are killed.



But on a less careful preservation the result will mostly be very poor; which accounts for the fact that Asteroid larvæ from plankton samples are generally of little use, being often unidentifiable, in contradistinction to the Echinoid- and especially the Ophiurid-larvæ, where the skeleton affords sufficient characters for identification, so that such larvæ may be very well utilized, even if the soft parts of their bodies are in a poor state of preservation. — In the present work I have made little use of such material of Asteroid larvæ from plankton samples, although I have quite a good deal of them, some of them representing types of Bipinnariæ hitherto unknown. They are, however, not of so considerable importance that I deem it desirable to publish descriptions of them, which cannot be in any way satisfactory.

***Astropecten scoparius*** Müller & Troschel.

Pl. XXXIII, Figs. 3—5.

This species, which occurs abundantly in shallow water near the Biological Station at Misaki, was found to have ripe sexual products in June; fertilization was undertaken on June 21st 1914, the sperma being treated with NaOH. The embryo is in the blastula-stage very much folded, looking almost like a walnut, the folds disappearing when the embryo leaves the egg-membrane. I have no notices on the progressive development of the embryos, so that the details of the transformation of the embryo into the Bipinnaria-larva cannot be given. At the age of 7 days they had developed into beautiful Bipinnariæ, the enterocoel pouches having, however, not yet united in the anterior end of the larval body. At the age of 19—21 days the larvæ were in beginning metamorphosis. Beyond this stage it was not possible to rear them, my stay at Misaki ending by that time.

The larva (Pl. XXXIII, Figs. 3—5) is of a very typical Bipinnaria-shape, with short, rounded processes. The preoral band forms a high arch, while the postoral band curves only slightly downwards in the middle. The postoral processes are very distinct, as are also the posterolateral, posterodorsal and anterodorsal processes. The median processes are of about equal size, short, rounded, the ventral one being somewhat ventrally directed (this accounts for its apparently being much shorter than the dorsal process in Fig. 5). Preoral processes are not distinct, the frontal area only being narrowed at the base of the median process, especially so in the metamorphosis stage; also at the base of the dorsal median process there is a distinct narrowing, the vibratile band from the two sides sometimes nearly joining in the midline. The frontal area is distinctly convex, the sides lying much deeper than the middle part, as is especially distinct in the metamorphosis stage. — There is a distinct suboral cavity, narrow

but fairly deep, reaching down to the upper edge of the stomach or even some distance beyond. Fine, redbrown pigment grains are scattered all over the body. The length of the fully formed larva is ca. 0,5—6 mm.

Although metamorphosis was not completed, the development proceeded far enough to show definitely the important fact that this larva has no *Brachiolaria*-stage; this is what was to be expected from the evidence of the only other *Astropecten*-species, the metamorphosis of which has been studied, viz. *Astropecten aranciaca* (the "Bipinnaria von Triest" of Joh. Müller, IV. Abhandl. Taf. V.).

### ***Astropecten polyacanthus* Müller & Troschel.**

A few specimens of this species, containing fairly ripe sexual products, were obtained at Misaki on the 18th of June 1914, and fertilization was

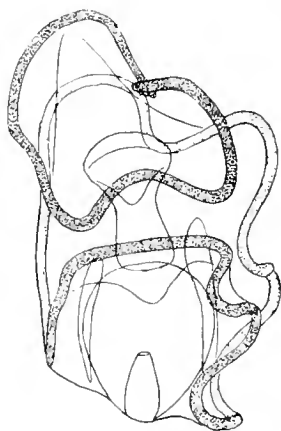


Fig. 97. Abnormal larva of *Astropecten polyacanthus*, 10 days old. <sup>105/1</sup>.

undertaken, resulting, however, in only a small culture, the eggs not being as ripe as desirable, and therefore only comparatively few being fertilized. The sperma, as usual, had to be treated with NaOH in order to obtain active movement of the spermatozoa. Only a few of the embryos survived the gastrula stage, and only a single specimen reached far enough (at the age of 10 days) to show the characters of the larvæ. Moreover, this specimen was abnormal, its right side remaining in a rudimentary condition. But the left side of this larva was typically developed, and, in spite of all, this specimen (Fig. 97) makes it sufficiently evident that the larva of *A. polyacanthus* is so closely alike that of *A. scoparius* that it will be hard to distinguish them. The fact

that the postoral band is straight in the *A. polyacanthus*-larva, while it is concave in the larva of *A. scoparius*, is not likely to be a reliable distinguishing character. The *polyacanthus*-larva differs, however, from the *A. scoparius*-larva in being devoid of pigment. It was also found to be considerably more active in its movements than the latter species.

### ***Asterina (Patiria) pectinifera* (Müller & Troschel).**

Pl. XXXIII, Figs. 1—2.

Th. Mortensen. On the development of some Japanese Echinoderms. p. 550.

This strikingly beautiful starfish occurs fairly abundantly on the rocky shores near the Biological Station at Misaki. Fertilization was undertaken in the end of May and the beginning of June, but the cultures obtained

were not very good, the embryos developing only to the beginning formation of the Bipinnaria; the somewhat unexpected fact that this species has a typical pelagic larva was, however, already proved by this first attempt. On the 18th of June I had the pleasure of seeing a female specimen, kept in a dish together with a number of other specimens, discharge its eggs, from which an excellent culture was obtained. I regret not having noticed the exact size of the eggs, only stating that they are small; I think I remember that they were of yellowish colour. The cleavage began very soon after the fertilization; the fact that I have made no notices about the cleavage process most likely indicates that it is of the usual, regular type. After 16 hours the gastrula stage was reached, and at the age of two days the embryos had the typical Bipinnaria-shape. The larvæ were generally found swimming close to the bottom of the dish. At the age of 10 days the enterocoel pouches had united in the anterior end of the body. At the age of 18 days some few of the larvæ were in the metamorphosis-stage and, accordingly, had reached the full larval shape.

The young larva (Pl. XXXIII, Fig. 1) looks very much like the *Astropecten*-larva, with small, non-contractile processes; there are no postoral or preoral processes. The suboral cavity is small, not very deep. It is especially noticeable that the vibratile band of the ventral median process is as distinctly developed as the rest of the bands, contrary to what is generally the case in larvæ having a Brachiolaria-stage. It was, therefore, a great surprise to me to see that this larva in its final stage really is a Brachiolaria (Pl. XXXIII, Fig. 2), though of another type than the Brachiolaria of *Asterias*. At each side of the fairly large sucking disk there is a small brachiolarian process with a few papillæ at the end. I was unable to ascertain the exact number of these papillæ, as also to ascertain whether the vibratile band continues along the paired brachiolarian processes. The median process is only slightly transformed, retaining its flat shape, and its vibratile band bordering it as in the younger stage; only a row of small papillæ, 3—5 in number, along each side, inside the band, indicates its brachiolarian character. The other processes remain unaltered, short and small. The length of the fully formed larva is ca. 0,6—7 mm. It is unpigmented.

#### ***Asterina (Patiriella) regularis* Verrill.**

Among a large number of specimens of this species which I collected on the rocky shore at the Island Bay, outside Wellington, New Zealand, on the 17th of February 1915 I found a few specimens to contain partly ripe sexual products. The artificial fertilization which I undertook was not

very successful, still I succeeded in obtaining a small culture of larvæ, which I carried along with me to Sydney. They developed fairly normally unto the Bipinnaria stage, but I did not succeed in rearing them unto metamorphosis. — Later in the year, in June, Professor H. B. Kirk again undertook a fertilization of this starfish and sent me the larvæ he had reared. None of them, however, had reached a more advanced stage of development than those of my own culture. There is, accordingly, no definite proof that also this larva has a Brachiolaria-stage, but there is, on the other hand, no reason to doubt that it will prove to have a Brachiolaria-stage of the same type as that of *A. pectinifera*.

The young larva (Fig. 98) is of the same type as that of *A. pectinifera*. The preserved material, including the larvæ sent from Prof. Kirk, is not in a very good state of preservation, the best specimen being also somewhat abnormal in the anterior end; I shall therefore not try to point out the specific differences between the two larvæ, these differences being, evidently, very trifling and unimportant, at least as far as the young Bipinnaria-stage is concerned.

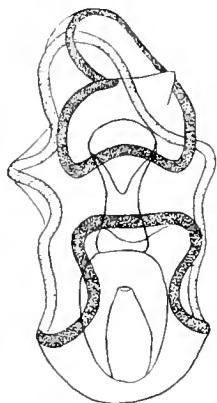


Fig. 98. Larva of *Asterina regularis*; 9 days old. <sup>105/1</sup>. The larva is slightly abnormal in the anterior end; the fold across the frontal area is probably due to contraction on preservation.

I may here call attention to the fact, which has apparently been overlooked, that besides *Asterina gibbosa* one more species of *Asterina*, viz. *A. (Patiriella) exigua* (Lank.) has been recorded to have a shortened development. This observation was made by Th. Whitelegge, who in his "List of the Marine and Fresh-water Invertebrate Fauna of Port Jackson and Neighbourhood" (1889, p. 40) states that "the ova of this species are deposited on stones in shallow rocky pools and are to be found from June to December. They are particularly well adapted for study, inasmuch as after the young leave the egg-case they do not swim away, but remain round about the empty egg-cases and never leave until they assume the true starfish-form. The larvæ are remarkably hardy and may be kept in confinement without change of water until they have passed through the larval stages."<sup>1</sup>) During my stay in Sydney I had the opportunity of confirming Whitelegge's observations, in the beginning of March 1915, which shows that the breeding season of this species is considerably longer than stated by Whitelegge; more probably it will be found to breed all the year round. (In *Asterina gibbosa* the breeding

<sup>1</sup>) I have thought it proper to quote Whitelegge's short statement in full, as his paper may not be so easily accessible outside Australia.

season is confined to the months March—July, in the Mediterranean mainly to April—May).

I shall not enter on a description of the developmental processes in *A. exigua*; no doubt, it would be of considerable interest to see how far this species agrees in this regard with *A. gibbosa*, but such a study would be out of the scope of the present work, the more so as the discovery that this species has a direct, shortened development, like *A. gibbosa*, is not mine. I would only call attention to the fact that the brachiolarian processes are in general more distinctly developed in the embryos of *A. exigua* than in those of *A. gibbosa* (Fig. 99). The sucking disk is not very much developed, still it is distinct enough.



Fig. 99. Embryos of *Asterina exigua*, in different views. <sup>66</sup>/<sub>h.</sub>

— The interpretation, first set forth by Ludwig<sup>1)</sup>

that these processes of the *Asterina*-embryo are homologous with the Brachiolarian processes of the *Asterias*-larva, is definitely proved to be correct through the fact that the larva of *Asterina pectinifera* passes through a Brachiolaria-stage.

In his paper “Über die Genitalorgane der *Asterina gibbosa*”<sup>2)</sup> Ludwig mentions the fact (previously observed by Gasco) that the genital openings of *Asterina gibbosa* are found on the ventral side, while in all other Asteroids thus far observed they are found on the dorsal side. The fact of the two species *A. pectinifera* and *regularis* having pelagic larvæ raises the question whether the genital openings in these species are found in the same position as in *A. gibbosa* or on the dorsal side, as is the rule in Asteroids. It is very easily seen that there are no genital pores on the ventral side in the two said species; on the dorsal side it is not easy to ascertain, which of the pores seen there are genital pores, as they do not differ in size from the papular pores; on following the genital ducts they are however easily found, and it is thus ascertained that the genital pores are really situated on the dorsal side. In *A. exigua* they are found on the ventral side as in *gibbosa*. This contradicts the statement of Ludwig, in the paper quoted, who maintains that in *A. pentagona* v. Martens, which is generally regarded as a synonym of *A. exigua*, the pores are found on the dorsal side. The discrepancy is probably due to *Asterina*

<sup>1)</sup> H. Ludwig. Entwicklungsgeschichte der *Asterina gibbosa* Forbes. Zeitschr. f. wiss. Zool. Vol. 37. 1882. (Morphologische Studien an Echinodermen. II. p. 151).

<sup>2)</sup> Zeitschr. f. wiss. Zool. Vol. XXXI. (Morphol. Studien an Echinodermen. I. p. 290).

*pentagona* not being the same species as *A. exigua* as it is generally thought to be. It is also on zoogeographical grounds very probable that the specimens from Cape are not the same species as the Australian form. Unfortunately, Ludwig does not state from which locality his specimens came. But, in any case, the fact thus ascertained that the genital pores are on the ventral side in the Australian specimens, on the dorsal side in specimens from some other locality (Cape?) shows that what has hitherto been included under the name of *Asterina exigua* is not all one and the same species.

It can hardly be doubted that the ventral situation of the genital pores<sup>1)</sup> in *A. gibbosa* and *exigua* is not a character of greater systematic value (— the two said species are referred to different genera in Verrill's revision of the Asterininæ<sup>2)</sup> —), but only an adaptation to their breeding habits, and it seems then legitimate to draw the conclusion that the same habits will be found in other species showing the same position of the genital pores. An examination of the material of *Asterina* in the collections of the Copenhagen Museum, which contains most of the known species of the genus (s. lat.), shows that, with one single exception, these species have dorsal genital pores, and it may therefore be concluded that pelagic larvæ are the rule in the *Asterina*-group, direct development exceptional. Only in one case, besides *A. gibbosa* and *exigua*, I find ventral genital pores, viz. in a small *Asterina* from the littoral region of Misaki, Japan, which appears to represent a new species; at least it is not identical with any of the species mentioned from Japan by Goto<sup>3)</sup>. It may accordingly be expected that also this species will prove to have a shortened development. — This species, moreover, is interesting in being selfdividing in its younger age, the only other case of selfdivision hitherto known among the Asterinidæ being *Asterina Wega* Perr. While the species is normally 5-rayed, the specimens arising through divisions are often 6- or 7-rayed. Only very small 6—7-rayed specimens were found. (Possibly this selfdividing form is not really the same species as that with the ventral genital pores).

<sup>1)</sup> It is interesting to notice that also the male specimens of *A. exigua* have ventral genital openings; Ludwig does not state, whether this is likewise the case in *A. gibbosa*, but it may seem probable from analogy with *A. exigua* that it is so.

<sup>2)</sup> A. E. Verrill. Revision of the genera of starfishes of the subfamily Asterininæ. Amer. Journ. Science. 4. Ser. XXXV. 1913. p. 477.

<sup>3)</sup> Seitaro Goto. A descriptive Monograph of Japanese Asteroidea. I. Journ. Coll. Science Tokyo. Vol. XXIX. 1914.

**Gymnasteria carinifera** (Lamk.).

Pl. XXXIII, Fig. 6.

This species was found, though not very commonly, in the rock-ponds near Hilo on Hawaii, and proved to have ripe genital products during the time of my stay there. Fertilization was undertaken on the 7th of April and proved successful. The next day the embryos were in the blastula-stage; the ectoderm is folded as in *Astropecten*, *Luidia* etc. At the age of two days they were in the gastrula-stage, being somewhat elongate in shape; on the third day the formation of the mouth and the enterocoel-pouches was beginning, and on the fifth day the embryos had the shape of young Bipinnariæ, showing, when disturbed, the usual contraction of the dorsal side, so characteristic of young Bipinnariæ. At the age of three weeks the larvæ were well developed Bipinnariæ of the rather characteristic shape shown in Pl. XXXIII, Fig. 6. The most conspicuous feature is the great width of the dorsal side in the anterior part, which very considerably surpasses that of the frontal area. The preoral band is much raised in the middle, forming almost an acute angle; the frontal area is much narrowed at the base of the median process, but there are no preoral processes. Both the ventral and dorsal median processes are broadly rounded and rather unusually short, though not quite as short as they appear in the figure; the specimen figured is somewhat contracted on the dorsal side, these processes thus being somewhat dorsally directed so as to appear shorter than they are in reality. The posterolateral processes are very short, merely indicated, the posterior end of the body being rather narrow. There are no postoral processes; the postoral transverse band is straight. — The larva is unpigmented; I have noticed in the living larvæ the existence of fine, isolated muscle fibres. The body length of the larva is ca. 0,4 mm.

Beyond the stage described the larvæ did not develop. The culture was kept for a little while yet (the specimen figured is 26 days old), but no further development was observed. The important question must then be left undecided, whether this larva has a Brachiolaria-stage. This is to be expected, since another form of the same family, *Porania pulvillus*, has a Brachiolaria-stage; but the proof is wanting.

**Ophidiaster Guildingii** Gray.

During my sojourn at Tobago, B. W. I., with the Carnegie Expedition in April 1916 I found some few ripe specimens of this species on April 19th, which were used for fertilization. The eggs are very small, only 0.11—0.12 mm. The cleavage is quite regular; the gastrula is formed, before the

embryo leaves the egg membrane. At the age of four days the embryos had assumed the shape of young Bipinnariæ.

By that time I had to leave Tobago; the culture was carried along with the other larval-cultures to Trinidad, but after a few days it was found to be all dead. Accordingly I can give no further information about the shape of the larva; but the fact here established that this species has a typical pelagic larva is in itself of no small interest. — I have not thought it worth while giving a figure of the young larva, partly because the few specimens preserved are in a rather poor condition, partly because the larvæ are not yet far enough developed for giving any information about the special characters of this larva.

### *Asterias calamaria* Gray.

Th. Mortensen. Development of some Japanese Echinoderms: p. 551.

The breeding season of this widely distributed pacific species was found to begin (in Japan) towards the end of June, and fertilization was under-

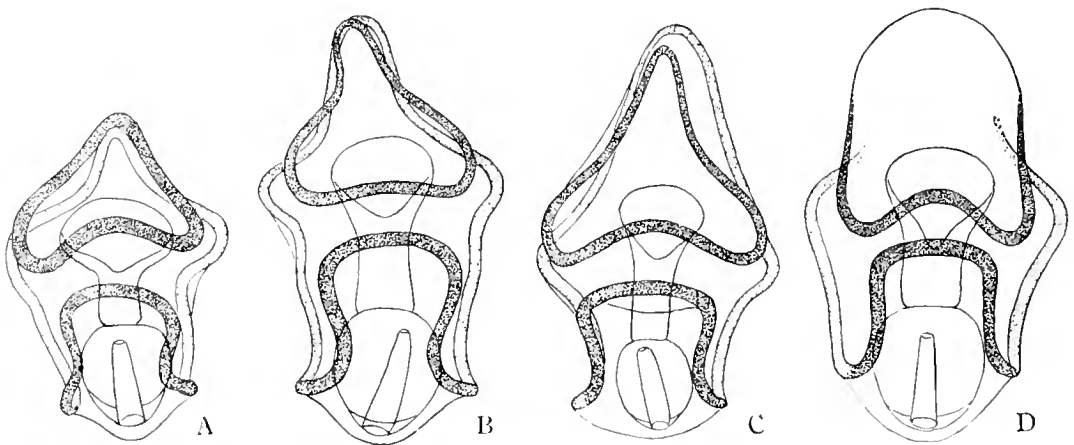


Fig. 100. Young Bipinnariæ of *Asterias calamaria* (Fig. A), *Pisaster ochraceus* (Fig. B), *Euasterias Troscheli* (Fig. C.) and *Orthasterias leptolena* (Fig. D.). A—C.  $\frac{150}{1}$ ; D.  $\frac{130}{1}$ .

taken on June 25th. The development of this species being rather slow, as usually in the Asterids, there was no hope of rearing the larvæ to full shape, as I had to leave Misaki already on the 12th of July. By that time the larvæ had reached the stage represented in Fig. 100, A. It is, of course, not sufficiently advanced for showing the specific characters, and it is, especially, not to be seen, whether it will develop into a Brachiolaria. The result achieved with this species is then in the main confined to the proof of its having pelagic larvæ. I have no notices about the first developmental processes.



The observation mentioned in the preliminary notice may be recalled here, that this species is very often infested with a parasitic organism (Cirripedian?), which castrates its host, the parasite occupying the place of the genital organs of the starfish.

#### ***Pisaster ochraceus* (Brandt).**

Among the numerous Asteroids occurring near the Biological Station at Nanaimo, Vancouver Isl., this species is especially conspicuous on account of its remarkable gregarious habits, generally assembling in shoals on rocks, where it may be above the water for several hours during ebb tide; the specimens are very closely aggregated, with interwoven arms. It was found to have ripe sexual products by the end of May, and fertilization was undertaken on May 21th. It was unusual in the spermatozoa being very active in natural sea-water, without addition of NaOH. The eggs are small, not very transparent. The blastula-stage was reached after about 24 hours (the ectoderm is not folded) and the gastrula-stage in the course of the second day; at the age of four days the embryos were beginning to assume the Bipinnaria-shape, and at the age of six days they were beautiful small Bipinnariæ of typical shape. Although the culture was kept alive and apparently in good health for about four weeks the larvæ did not develop beyond this stage; in some of the specimens of this age the enterocoel pouches had begun to grow forwards into the anterior end of the body, but they had not yet fused.

The shape of the larva is shown in Fig. 100, B (the specimen figured is 30 days old); it does not offer any marked special features. The fact that the ciliated band of the ventral median process is rather weak indicates that the larva is going to develop into a Brachiolaria. It is pigmented all over with fine, yellow spots.

#### ***Euasterias Troscheli* (Stimpson).**

This species, which is also very common at Nanaimo, although not so much so as the preceding one, (— it may also be found above the water for several hours during ebb tide, but it is not gregarious —), was likewise found to have ripe sexual products by the end of May. Artificial fertilization was undertaken on May 25th. The eggs are exceedingly numerous, very small, not very transparent; the spermatozoa were very active in natural sea-water, without addition of NaOH. The cleavage stages were very beautiful, perfectly regular. The embryos were not liberated from the egg membrane till after 24 hours, the gastrula stage being reached on the

second or third day; on the fourth day the embryos were beginning to assume the Bipinnaria-shape. The culture was kept for nearly four weeks apparently in good health (— the larvæ kept swimming near the bottom of the dish, not rising to the surface as usual —); but none of the larvæ reached beyond the young Bipinnaria-stage, the enterocoel-pouches not yet at that age having begun prolongating forwards.

The shape of the Bipinnaria (Fig. 100, C; the specimen figured is 23 days old) does not offer any very marked features distinguishing it from the young larva of *Pisaster ochraceus*. It is provided with small, yellow pigment spots, especially along the vibratile band.

#### **Orthasterias leptolena** Verrill.

Fertilization of this species was undertaken repeatedly in June 1915 at the Biological Station, Nanaimo, but the cultures were not very successful, only in one case the young Bipinnaria-stage being reached. The eggs are of a faint reddish tint; the cleavage stages, blastula and gastrula are very beautiful, perfectly typical. The young Bipinnaria (Fig. 100, D; the specimen figured is 7 days old) differs rather considerably from that of the other forms in being broadly rounded in the anterior end; the vibratile band is not developed along the anterior edge of the body, which indicates almost certainly that the larva will develop into a Brachiolaria.

#### **Pycnopodia helianthoides** (Brandt).

This large and strikingly beautiful Asterid, which occurs quite commonly at Nanaimo, was found to have its breeding season in May—June. Fertilization was undertaken repeatedly, but a good culture never resulted. The embryos never reached more than just beyond the gastrula stage. All the information acquired of the development of this species thus amounts only to this that it has pelagic larvæ; but what they look like or whether they have a Brachiolaria-stage remains an open question.

As stated above (p. 185) the material of pelagic Echinoderm larvæ found in the plankton samples includes a number of Bipinnariæ, among which some interesting new forms which would very well deserve to be figured and described. Unfortunately, they are nearly all of them in a poor state of preservation, so that it is hardly possible to give a reconstruction of their true shape. I have therefore thought it better to desist from describing them here. Only one form I shall briefly mention, viz. the larva in the Brachiolaria-stage represented in Pl. XXXIII, Fig. 7. It affords the inter-

esting feature that the ventral median process is transformed, carrying papillæ, only in its lower part, while its outer part retains its normal shape unaltered. This larva was taken in the Red Sea, 6/V. 1900.

Quite a considerable number of Asteroids apparently have direct development. This may fairly safely be concluded from the fact that they have large, yolky eggs. It is to be expected that these forms will have only a rudimentary larva as it is known in e. g. *Solaster* and *Echinaster sepositus*. I have observed the eggs to be of this character e. g. in *Ctenodiscus crispatus*, *Hippasteria phrygiana*, *Ceramaster japonica*, *Mediaster lævis*, *Psilaster andromeda*, *Pontaster tenuispinus*. In spite of many attempts I have never succeeded in obtaining artificial fertilization of any of these forms.

#### IV. Holothurioidea.

The Holothurians are, next to the Crinoids, the poorest of all Echinoderms for artificial fertilization. The numerous Dendrochirotes have, probably, all of them large, yolk-laden eggs, which completely resist artificial fertilization; but also in the Aspidochirotes, where the eggs are generally small and transparent, artificial fertilization is rarely successful. I have myself succeeded in fertilizing and rearing the larva of *Holothuria nigra* (in Plymouth, 1913<sup>1)</sup>), and in the present work I have three more fertilizations and rearings to record, viz. *Stichopus californicus*, *St. Kefersteini* and *Holothuria* sp. But in all these cases it was only a very small percentage of the eggs which were fertilized, and with many other species I tried in vain to obtain fertilization. It is also rather troublesome to get the necessary material for the study of the different stages of development, when only a small culture is available. A much more easy way to obtain fertilization and normal development of the larvæ is that employed by Selenka<sup>2)</sup> and Edwards<sup>3)</sup>, who put a number of specimens together in a large live-box, the cracks and upper side of which were covered by gauze, the box then being sunk to the bottom in an easily accessible place in the sea, in a depth of ca. 1½ meters. Fertilized eggs were then soon after found in considerable numbers lying on the bottom of the box, and the embryos thus secured were found to develop normally. For obtaining the normal larvæ this method will doubtless prove to be excellent in many cases, not only in Holothurians but in many other kinds of marine animals which do not

<sup>1)</sup> Th. Mortensen. On the development of some British Echinoderms. Journ. Mar. Biol. Ass. N. 1913. p. 17.

<sup>2)</sup> E. Selenka. Zur Entwicklung der Holothurien (*Holothuria tubulosa* und *Cucumaria doliolum*). Zeitschr. f. wiss. Zool. XXVII. 1876. p. 157.

<sup>3)</sup> Ch. L. Edwards. The development of *Holothuria floridana* Pourtales with especial reference to the ambulacral appendages. Journ. of Morphology, XX. 1909. p. 212.

lend themselves very easily to artificial fertilization nor to breeding in aquaria. I was not prepared to use that method during my voyage, partly because my former experiments with *Holothuria nigra* did not make clear to me the difficulties generally met with in the study of the development of Holothurians by means of artificial fertilization, partly because it would have been rather troublesome to carry along such a live-box on the long voyage.

As is the case with the Asteroid-larvæ, the larvæ of the Holothurians are as a rule not found very well preserved in plankton samples, and the material which I have gathered in that way is not very important, presenting no new larval types. The contribution to the knowledge of the Holothurioid-larvæ which I can give here, is accordingly rather small, especially as compared with that of the Echinoid- and Ophiuroid-larvæ.

### ***Stichopus californicus* (Stimpson).**

Pl. XXXIII, Figs. 8—9.

This species, which occurs fairly commonly along the rocky shores near the Biological Station at Nanaimo, was found to have ripe sexual products in June. Fertilization was undertaken repeatedly and with good success, though the percentage of the fertilized eggs was always rather small. I have no notices about the first developmental processes, except that the embryos were found in the blastula stage one day, in the gastrula stage two days after fertilization; the formation of the Auricularia may begin on the second day. At the age of about 6 days the larvæ were typical Auriculariæ, provided with a starshaped calcareous body in the left posterolateral process. In this stage the larvæ remained till the age of ca. 3 weeks, no further development taking place.



Fig. 101. Spicules from larva of *Stichopus californicus*.  $\frac{800}{1}$ . The small spicule to the right from the right posterolateral process.

The shape of the larva (Pl. XXXIII, Figs. 8—9) is somewhat elongated. The preoral band is highly arched; there are no preoral processes, but the frontal area is distinctly constricted at the level of the upper end of the oral cavity, the anterior part forming a rounded lobe; the corresponding part on the dorsal side is much narrower. The dorsal and posterolateral lobes are fairly distinct. The postoral band is strongly convex in the middle so as almost to suit the shape of the preoral band. The anal area is markedly constricted at the lower end of the body, the posterior edge of which is distinctly concave. The calcareous body (Fig. 101) has the shape of an irregular star; very rarely there is a small, irregular calcareous body also

in the right posterior corner. The larva is colourless, excepting for a slight yellowish tint along the vibratile band. The larval nervous system was not distinctly observed.

### **Stichopus Kefersteinii** Selenka.

Of the rather numerous Holothurians occurring along the rocky shores of Taboga, in the Bay of Panama, several species were found to contain ripe sexual products in October—November 1915; many attempts were made to obtain their larvæ through artificial fertilization, but the results were very poor. With the present species a fertilization was undertaken on October 23rd, which resulted in a small number of embryos. At the age of two days these latter were beginning to assume the Auricularia-shape; on the 3rd day all the embryos had died. A number of specimens were examined in order to have started a new culture, but all were empty by this time. The information acquired about the development of this species accordingly does not go beyond the fact that it has a typical pelagic larva.

### **Holothuria** n. sp. (?)<sup>1)</sup>

Pl. VI, Figs. 5—6.

Like the preceding species this one was found to contain ripe sexual products in October; fertilization was undertaken on the 21st of this month 1915. The eggs were found to ripen after lying about 3 hours in the water; they then readily accepted the spermatozoa and quite a large percentage was fertilized. The cleavage is perfectly regular; the gastrula-stage was reached at the age of one day, and at the age of two days the embryos showed the beginning formation of the Auricularia. Three days old they were typical young Auricularias of the characteristic shape shown in Pl. VI, Fig. 5, with the anterior part very broad, almost bell-shaped. At the age of 8 days the larvæ had reached the stage shown in Pl. VI, Fig. 6. On the dorsal side the vibratile band now almost joins in the midline in the anterior end; otherwise the larval shape is still quite simple, without any indication of processes. The frontal area may perhaps be somewhat

<sup>1)</sup> This appears to be an undescribed species, allied to *H. kapiotania* Bell. It may be shortly thus characterized: Length 5—6 cm. Dorsal side brown, with two rows of small, black spots; ventral side pale; tentacles yellow. Deposits in the skin: slightly curved, very spinous rods; well developed end-plates in the pedicels. Calcareous ring high, without a deep notch posteriorly. Genital tuft long; only one Polian vesicle. The madreporite is single, fastened on the mesentery, with lancet-shaped head; the stone canal is s-shaped. Cuvierian organs present. — Locality: Taboga, Gulf of Panama, Littoral.

I am indebted to Miss E. Deichmann for the above remarks on this species.

In the list of the Echinoderms the development of which has been studied in the present work, given in the Introduction (p. 17—18), this species was forgotten.

too narrow in the figure, as the specimen has apparently contracted somewhat on preservation (it is slightly distorted, which has been corrected in the figure). The posterior end is rather elongated, with a somewhat indistinct, round body at one side, and some accumulated cells which probably indicate the presence in the fully formed larva of some kind of calcareous bodies. It has a faint greenish colour. — Beyond this stage I did not succeed in rearing the larvæ, and no more specimens containing ripe sexual products were obtained, the breeding season of the species being evidently passed by the beginning of November.

### **Auricularia nudibranchiata** Chun.

Since Chun observed this magnificent larva at Orotava in March 1887 it has never been recorded again from the Atlantic. I was therefore very pleased in finding a specimen during my stay at Tobago, B. W. I., in April 1916, proving thus its occurrence also in the West Indian seas. It has further been found in plankton samples from the following localities in the Sargasso Sea and in the vicinity of the Azores: 45° 32' N. 25° 50' W., 24/VI, 1911 (1 specimen); 40° 47' N. 21° 10' W. 21/III. 1911 (1 specimen); 39° 22' N. 22° 49' W. 20/III. 1911 (2 specimens); 36° 13' N. 33° 50' W. 15/III. 1911 (1 specimen); 34° 39' N. 40° 54' W. 13/III. 1911 (several specimens); 33° 55' N. 43° 40' W. 12/III. 1911 (several specimens); 30° 30' N. 49° 57' W. 22/II. 1911 (2 specimens). This shows that it is fairly widely distributed over the ocean, the time of its occurrence extending at least from February to June. None of the specimens exceed the largest specimens found by Chun in length (6 mm), and none of them are in a further stage of development than the more advanced of Chun's specimens.

While the species had not been rediscovered in the Atlantic till now, it was recorded in 1911 by H. Ohshima<sup>1)</sup> as occurring in the seas of Japan (the Sagami Sea), and quite recently MacBride<sup>2)</sup> has recorded it from off the North end of New Zealand. It is, of course, beyond doubt that these larvæ from the Japanese and New Zealand seas really belong to the type of *A. nudibranchiata*; but it is equally certain that they are not the same species as the Atlantic form. In accordance with the nomenclature here adopted I shall designate the three forms respectively as species **a**, **b** and **c**, the Atlantic form being, of course, designated as species **a**.

<sup>1)</sup> Hiroshi Ohshima. Note on a gigantic form of *Auricularia* allied to *A. nudibranchiata* Chun. Annot. Zool. Japon. VII. 1911. p. 347.

<sup>2)</sup> E. W. MacBride. Echinoderma (Part II) and Enteropneusta. Larvæ of Echinoderma and Enteropneusta. British Antarctic ("Terra Nova") Expedition. 1910. Zoology. Vol. IV. p. 88.

Species **b**, the Japanese form, differs from the Atlantic first in its much larger size, reaching 15 mm, the latter not being known to surpass a length of 6 mm, the stage of development being the same in both. Further I find on a comparison of some specimens, kindly sent me by Dr. Ohshima, with those of species **a**, that the body is distinctly narrower in species **b** than in species **a**, and also the projecting lobes of the vibratile band are larger and more prominent in the Japanese species. Through this strong development of the vibratile band, in fact, the sides of the larva are wider than its dorsal and ventral sides, and the preserved specimens therefore generally lie on the side, while specimens of species **a** generally lie on the dorsal or ventral side. Whether the small difference in the structure of the calcareous deposits pointed out by Ohshima — viz. that the edge is finely serrated in the Japanese specimens, while Chun states it to be smooth in the Atlantic species — is a reliable difference needs to be verified by a reexamination of the latter; I am sorry to be unable to settle this question, all my specimens having been preserved in formaline, and the deposits thus having been dissolved.

Species **c**, the New Zealand form, is likewise considerably larger than species **a**, the single specimen known measuring "at least a centimetre in length". Otherwise it is impossible to state by which other characters it is distinguished from species **a** and **b**, no description or figures having been given of it. Only in one feature it is stated to differ from the two other species, viz. in the median ventral pouch from the intestine being paired, while in the two other species it is unpaired. It would appear from the expression used by MacBride (Op. cit. p. 89), running thus: "This single diverticulum is supposed to be a rudimentary representative of the gill-(lung-)trees of other Holothurioidea; but the discovery that the pouch is paired deprives this argument of its ground", that he thinks Chun's statement of the pouch being unpaired in the Atlantic form to be wrong. I would then take the opportunity of confirming Chun's statement. There is not the slightest doubt that the pouch is really unpaired, as figured by Chun, and the same is the case in the Japanese species.

On account of this intestinal pouch Chun was inclined to refer this larva to some Elaspod, and I have joined him in this opinion. MacBride, however, thinks this a mistake. Having found in a species of *Cucumaria* the gill-trees to appear only in a rather advanced stage of development, he finds it "exceedingly unlikely that a rudiment of these gills should appear in the *Auricularia* larvæ; they probably only begin to develop when the cloacal function of sucking in and ejecting water has been established. I conclude, therefore, that the intestinal pouches of *A. antarctica* and *A.*

*nudibranchiata* have nothing to do with gills; and if this be admitted, there is no reason why *A. nudibranchiata*, like *A. antarctica*, should not be the larva of a Synaptid, to which group its wheels naturally ally it." Without entering on a discussion of the time of appearance of the gill-rudiments in *Cucumaria* I would merely point out the fact that there is no structure in the Synaptids into which this pouch could possibly develop. This would then mean that this large organ of the Auricularia should completely disappear again on metamorphosis. This is certainly not very likely. The question about the parental origin of this larva can hardly be definitely settled except through the rearing of the larva; it seems only safe to say this much that the intestinal pouch proves that it must belong to some form with gill-trees, and accordingly cannot be a Synaptid, in spite of the Auricularian wheels.

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## GENERAL PART

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### I. Classification.

**A**FTER the description given above of the new larvæ reared or otherwise gathered it now remains to see, whether this material, together with that known from previous researches, gives any answer to the original question, which was the guiding principle in the author's studies, namely this: is there any correspondance between the different larval forms and the natural groups of the adult forms — or to put it more definitely: is there a larval classification corresponding to that of the adult forms, each group of the adults (genus, family or order) having a distinct type of larvæ differing from that of the other groups?

It is known already from Joh. Müller's magnificent researches that at least each class of Echinoderms has its own distinct larval type — the Holothurians the Auricularia, the Asteroids the Bipinnaria, the Ophiuroids the Ophiopluteus and the Echinoids the Echinopluteus<sup>1</sup>), the Crinoids alone having no separately named larval type, which is also unnecessary as long as we do not know a single case of a typical pelagic Crinoid-larva. But are "orders" and "families" to be distinguished within these four larval types? The question may at once be answered, at least partly, in the affirmative. A more detailed discussion is, however, necessary.

Starting with the **Echinoid-larvæ** it was clear already from the previous researches that the Spatangoid-larvæ form a very distinct type, characterized by the unpaired posterior process, which does not normally occur in any of the other Echinoid-larvæ, so far as hitherto known<sup>2</sup>). They also differ from all other Echinoid-larvæ in having well developed anterodorsal arms. We now know the larvæ of quite a number of Spatangoids, viz. of

<sup>1</sup>) Joh. Müller designated both the Ophiurid- and the Echinoid-larvæ simply as Pluteus; the separation of these two larval types under the names of Echinopluteus and Ophiopluteus was introduced in the present author's work "Die Echinodermenlaven d. Plankton-Expedition."

<sup>2</sup>) Prouho in his "Recherches sur le *Dorocidaris papillata*" (Arch. de Zool. expér. génér. V. 1888) describes and figures (p. 141, Pl. XXV, fig. 9) an abnormal larva of this species with an unpaired posterior process.

the genera *Spatangus*, *Echinocardium*, *Moira*, *Brissus*, *Brissopsis*, *Meoma*, and besides a number of other Spatangoid-larvæ (*Echinopluteus fusus*, *solidus* and others) are known to exist. They all of them agree in having the unpaired posterior process, and there is not the slightest reason to expect that there will be any exception to this rule. We have then here a larval type corresponding to the order of the Spatangoidea, forming a distinct larval "order."

Is it possible to distinguish larval "families" within this order, corresponding to the families of the adult Spatangoids? We are not yet in possession of sufficient facts for answering this question definitely; but the facts which are known would seem to point in the direction that also "families" may be distinguished within this larval order.

The Spatangoid-larvæ may be divided into two main groups, viz. those with posterolateral arms and those without. Of the latter group only one species has been referred to its parental form, viz. that of *Brissopsis lyrifera*; but there is some reason to suggest that also the larvæ of the genus *Brissus* belong to this type (comp. above, sub *Brissus Agassizi*, p. 119). A larva of the same type, which was found in the Gulf of Panama I would be inclined to refer to *Meoma grandis*. That would tend to indicate that this larval type is characteristic of the family of the Brissidæ. But it can be nothing more than a suggestion at the present state of our knowledge; moreover the fact that Metschnikoff<sup>1)</sup> has found a larva of this type occurring in great numbers at Triest, where *Brissus unicolor*, otherwise common in the Mediterranean, apparently does not occur, would seem to prove that this larval type may also be found in other Spatangoids. Metschnikoff refers this larva to *Schizaster canaliferus* "da sie dort unter den Echinoidenlarven ebenso vorherrschend ist, wie Schizaster unter den erwachsenen Spatangoiden."

The larvæ of the genera *Echinocardium*, *Spatangus* and, probably, *Moira*<sup>2)</sup> agree in having posterolateral arms, supported by a simple rod, not widened at the base. This would point in the direction of this larval type being characteristic of one group of Spatangoids. The existence of several species of the type of *Echinopluteus fusus* might indicate that this

<sup>1)</sup> E. Metschnikoff. "Studien über die Entwicklung d. Echinodermen u. Nemertinen." Mém. Acad. St. Pétersbourg. VII. Sér. XIV. 1869. p. 46. Taf. VIII—IX.

<sup>2)</sup> Caswell Grave has reared the larva of *Moira atropos* through metamorphosis, but unfortunately does not give any information of the shape of the larva. On my applying to him for the information wanted, he kindly sent me some slides containing some of the larvæ. It turned out, however, that there were two different species of larvæ in the slides, one with posterolateral arms, the other without. Having called his attention to this fact I was informed by him that he thought it almost certain that the form with the posterolateral arms was the *Moira*-larva, but full certainty could not be obtained any more from the material still preserved.

larva is characteristic of another group. But all this can, of course, be nothing more than mere suggestions—working hypotheses in the light of which future investigations should be carried out. It must be remembered that the classification of the Spatangoids is very far from being settled. In fact, H. Lyman Clark in his work on the Spatangidæ (“Hawaiian and other Pacific Echini”)<sup>1)</sup> states that “a satisfactory classification of the Echini here included in the Spatangina is in the present state of our knowledge simply impossible.” I agree with Clark herein as far as the *Amphisternata* are concerned, while I think the classification of the *Meridosternata* in fairly good order. The amphisternous “families” Hemiasteridæ and Spatangidæ, as comprised in Clark’s work, are certainly unnatural, which is, however, not to be wondered at, his classification being “purely one of convenience, worked out in the endeavour to make an artificial key to all the genera and species of living Spatangoids.” But no better classification exists, and it seems at least that the family Palæopneustidæ, as comprised by Clark, is fairly natural, and thus far his classification represents a progress. — I would expect that the study of the larvæ will prove of great importance for establishing the natural relationship between the numerous forms of Spatangoids.

That the *Asternata*, or at least the Cassidulids, do not really belong to the Spatangoids, but are more nearly related to the Clypeastroids seems rather probable alone from the study of the *Echinobrissus*-larva. The study of the development of forms like *Echinotampas* and *Echinoneus* will be of the greatest importance for settling the question of the natural relationship of these interesting forms.

Another very distinct larval type is that of the Clypeastroids. The order of the Clypeastroidea being a very well limited one, and there being no doubt that the forms referred to that group are really naturally related, the study of the Clypeastroid-larvæ will afford a critical test to the theory of the value of the larvæ as lending proof of the natural relations of the adult forms. It must be claimed, of course, that if the larvæ really are of such classificatory value, the larvæ of the Clypeastroids should form a uniform group, as do the adult forms. As we now know, through the previous researches and those recorded in the present work, larvæ belonging to 10 different genera, viz. *Echinocyamus*, *Clypeaster*, *Echinarachnius*, *Dendraster*, *Encope*, *Mellita*, *Astriclypeus*, *Arachnoides*, *Laganum* and *Peronella*, we can form a fair judgment of the character of the Clypeastroid-larvæ in general. The result fully bears out the expectations. These larvæ form a very uniform group, so uniform that it is even in some cases hard to distinguish the larvæ of different genera. The Clypeastroid-larvæ

<sup>1)</sup> Mem. Mus. Comp. Zool. XLVI. 1917, p. 98.

form a distinct larval "order", corresponding to the natural order of the adult Clypeastroids, and accordingly testify the correctness of the suggestion of the classificatory value of the larvæ.

The Clypeastroid-larvæ are characterized by the body skeleton forming a basket structure, which very often develops into a large complicate, fenestrated plate in the posterior end of the body. Although the body skeleton is partly absorbed in the fully formed larva, there is no change in the body shape, so that we cannot speak of a first and a second larval stage. No posterior transverse rod is formed, and there are no vibratile epaulets, whereas there are small ventral and dorsal vibratile lobes. The postoral and posterodorsal rods are generally fenestrated.

The question whether different groups of these larvæ, corresponding to the families of the Clypeastroids, are to be distinguished, cannot be answered at present. It is noticeable that the single *Clypeaster*-larva known as yet differs rather conspicuously from the other larvæ, excepting the *Echinocyamus*- and the *Laganum*-larva (— the modified larva of *Peronella Lesueurii* does not count in this connection —), in its skeleton being much simpler, apparently not forming a fenestrated plate in the posterior end of the body; this may possibly indicate a family character. But very much more information is needed before we can form a real judgment of the value of this difference. Another very noticeable fact is this that the larva of *Arachnoides placenta*, so unique among the Clypeastroids through the aboral position of its periproct, does not differ in any way markedly from the larvæ of the other Scutellids.

It is worth pointing out that the peculiar property of turning green on preservation in alcohol or on being damaged or dying, so characteristic of Clypeastroid tissue, is found also in the larvæ and the young, metamorphosing sea-urchin.

Within the Regular Echinoids we may first dismiss the order of the Cidaroida, altogether too little being known of their larvæ for judging about their essential characters. If the unexpected should turn out that *Echinopluteus transversus* belongs to Cidarids, it will be very hard to reconcile its highly specialized characters with the primitive character of Cidaroid structure, as also it would be most surprising to find so different larvæ as *Echinopluteus transversus* and the larva of *Cidaris cidaris* (*Doricidaris papillata*) within the same family (the Cidarids apparently forming only a single family). — But there is no reason to trouble with this problem so long as it has not been definitely settled that *Echinopluteus transversus* really is a Cidaroid-larva.

The few facts known about the development of Diadematids tend to show that their larvæ are characterized by their skeleton forming in their

first stage a typical basket structure, while in their full shape they have the characteristic shape of the larva represented in Joh. Müller's VII. Abhandl. Taf. V, Figs. 1—3, and in the present work, Pl. V, Fig. 7, with very long postoral and posterodorsal arms, a posterior transverse rod, very large vibratile lobes but no epaulets. There is then reason to expect that the Diadematid-larvæ will prove to represent a distinct, well characterized larval "family."

The Echinothurids, unfortunately, remain entirely unknown as regards their development. While at least some of the deep-sea forms may be expected, on account of the large size of their eggs, to have a direct development, the small eggs of *Asthenosoma varium* indicate that this species will have pelagic larvæ. It will be exceedingly interesting to see whether its larva will prove to resemble the type of the Diadematid-larvæ, as it might perhaps be expected on account of the relation which undoubtedly exists between the Echinothurids and the Diadematids, in spite of the remarkable difference in their test structure.

Entirely unknown as regards their development are also the Salenidæ. Judging from their small genital pores they may be expected to have small eggs and, therefore, probably pelagic larvæ, in spite of their being mainly deep-sea forms. It will be most interesting to learn whether their larvæ resemble those of their nearest relatives among recent Echinoids, the Arbaciidæ.

Within the family Arbaciidæ we now know the larvæ of three species of the genus *Arbacia*, viz. *A. lixula*, *punctulata* and *stellata*, these three being so closely alike that they are to be distinguished only by very unimportant characters. One more larva of the same type is known (Pl. VI, Fig. 1), which may perhaps belong to another genus; in any case there can be no doubt that it is also an Arbaciid-larva. The facts thus far made known decidedly indicate that there is a very distinct type of larva belonging to the family of the Arbaciidæ, characterized in its first stage by the skeleton forming a basket-structure, in its second stage by the existence of a posterior transverse rod which ends in a pair of long posterolateral arms of the same shape as the other arms. The postoral and posterodorsal rods are of the fenestrated type, but the holes are generally small or entirely lacking in a greater or lesser part of the rod. There are large ventral and dorsal vibratile lobes, but no epaulets.

It will be of very great interest to learn whether the larvæ of the comparatively few other forms belonging to this very well limited and unquestionably quite natural family are in conformity with the *Arbacia*-larvæ, as they should be, according to the views of the present author. The polyporous *Tetrapygyus niger* is easily enough accessible for study, and

also *Coelopleurus* may be got at without too much trouble, while the rare, small deep-sea forms *Podocidaris*, *Habrocidaris* etc. will, at any rate, not be within easy reach. But the study of the two first named forms will suffice for meeting reasonable claims to the knowledge of this larval "family."

It is, however, especially the larvæ of the Camarodonta which we must consider in discussing the classificatory value of the larvæ. This great group comprises the bulk of the recent regular Echini, and here the views of the various authors regarding what would be a natural arrangement are most diverging. May not perhaps the larvæ give us the clue to their real interrelations? We now know, more or less completely, the larvæ of so many of these forms that we are at least able to form a fair judgment, whether the larvæ will give us any support for the solution of the problem.

Two main views regarding the classification of the Camarodonta are prevailing among recent authors. One is that of H. Lyman Clark and R. T. Jackson, the other that of Döderlein and myself. While according to the two former authors the test structure alone affords valid characters by which to distinguish genera and families, the minor microscopical structures, the pedicellariæ and spicules affording characters of no higher value than for distinguishing species, I have expressed the view that also the microscopical structures, especially the globiferous pedicellariæ, afford a valid basis for the higher systematic divisions, the genera and even the families, and that these characters should be taken into consideration as well as the structural characters of the test. The latter characters are, of course, regarded as the more important, but it is maintained that where the structural characters of the test do not give the clue to the natural interrelationship of the forms, as is mostly the case in the great and uniform group of the Camarodonta, there the microscopical characters set in. The classification worked out on the base of these principles, which was set forth in the author's work on the Echinoidea of the Danish "Ingolf"-Expedition, Part I—II. (1903—7) was fully accepted by Döderlein, who is even inclined to ascribe still more importance to the microscopical characters than I can agree to. — In the said work I have especially pointed out that the character of the ambulacra, the oligoporous or poly-porous condition, is of no value as a character of larger groups, as it has, evidently, developed separately in different groups. Also the elongation of the test in *Echinometra* and some allied genera is regarded as invalid as a family character. H. L. Clark on the contrary regards these two characters as of primary value for the classification, although he cannot deny that the poly-porous condition has developed in at least two separate groups (his families Strongylocentrotidæ and Echinometridæ).

The two classifications are evidently irreconcilable. It is clear that we know perfectly well all the characters which are at all available as a base for the classification. The internal anatomy is so uniform within the whole group that there is no hope of finding therein any characters of value for the classification. Only the structural characters of the test and the organs attached to it, viz. the spines, tubefeet, pedicellariæ, and the spicules found in the skin of these organs are available. (The sphæridiæ do not afford characters of classificatory value). The divergences in the two main views on the true relationship of these forms then depend on subjective apprehension, and further discussion will hardly alter the views on any side<sup>1</sup>). Only new arguments may be expected to settle the problem and give us a clue as to which of the views regarding the interrelation between the forms within this uniform group comes nearest the truth. Such an argument I have expected to find in the study of their larval forms. The present researches have added so considerably to our knowledge of these larval forms that it is possible to form a reasonable judgment, whether that expectation is justified or not.

One of the families within the Camarodonta is unquestionably a quite natural group; viz. the Temnopleuridæ, or rather the subfamily Temnopleurinaë, the other subfamily, the Temnechininaë or Trigonocidarinaë being less distinctly circumscribed. If the larvæ are of real value to classification it must be a just claim that the larvæ of the Temnopleurinaë should form a corresponding natural group. While hitherto not a single Temnopleurid-larva was known, we now know, more or less completely, the larvæ of *Temnopleurus loreumaticus*, *Tennotrema sculpta* and *Mespilia globulus*, and it is indisputable that they do really agree in several important characters, so that it has the appearance that there is really a distinct larval type peculiar to the Temnopleurids (or at least the Temnopleurinaë). Some larval forms taken pelagically and most probably, belong-

<sup>1</sup>) A classification differing again from both the above mentioned has been set forth by J. Lambert & P. Thiéry in their "Essai de Nomenclature raisonnée des Échinides" (I—IV. 1909—14). These authors have made a point of working out the natural classification of the Echinoids, taking both the recent and the fossil forms equally into consideration. This is, of course, in itself an excellent principle; in fact, nobody could deny this to be the only natural way → if only the fossil forms were sufficiently well preserved for this use. But this, unfortunately, they are not. When the other authors have confined themselves mainly to the recent forms, it is because they recognize the fact that the fossil forms are imperfectly preserved, so that their characters can only be incompletely ascertained, and accordingly the relation between the recent and fossil forms must remain more or less doubtful. Lambert & Thiéry, however, have adopted the view that the classification of the whole group, recent and fossil forms, has got to be based alone on the characters which can be found in the fossil forms, viz. on the test structure alone. Regardless of all facts known they construct their classification strictly on this principle. As, moreover, the nomenclature is worked out on the principle of the priority rule in its strictest, most literal sense, it is no wonder that the result is so absurd that it can hardly be taken seriously.

ing to the same group serve to emphasize the distinctness of this larval type.

This larval "family" appears to be characterized in the first stage through the skeleton forming no basket-structure; the fairly elongate body rod divides at the end into two rather long horizontal branches. In the second stage a posterior transverse rod is formed, from which a pair of short, branched posterolateral rods may issue; the latter may, however, be lacking. There are four vibratile epaulets, but no vibratile lobes.

The rest of the Camarodonta was arranged by the present author in the families Echinidæ, Toxopneustidæ and Echinometridæ, while Clark will not acknowledge the family Toxopneustidæ, the forms referred to that family being redistributed in the Echinidæ and in a new family Strongylocentrotidæ. The family of the Echinometridæ is regarded by Clark as containing only the polyporous, oblong forms, the other, more primitive forms referred to this family by the present author being also redistributed by Clark in the Echinidæ and Strongylocentrotidæ. According to my view Clark's families Echinidæ and Strongylocentrotidæ are quite heterogeneous, while his family Echinometridæ is quite natural, only, in my opinion, not wide enough. We shall see now what the larvæ will teach us about this matter.

It may first be stated that, as regards the various genera and the species referred to them, Clark and I in general agree, only with regard to the genus *Strongylocentrotus* we disagree in some important points, as is stated below.

To the family Echinidæ Clark refers the genera *Psammechinus*, *Lytechinus*, *Echinus*, *Parechinus*, *Nudechinus*, *Evechinus*, *Toxopneustes*, *Triopneustes* and *Gymnechinus*; according to my view only *Psammechinus*, *Echinus* and *Parechinus* belong to this family, *Evechinus* being an Echinometrid, while the rest of them belong to the Toxopneustidæ. No larvæ belonging to the genera *Parechinus* (in the sense of Clark, which I adopt), *Nudechinus* or *Gymnechinus* are known, while of the other genera we know quite a fair number of larvæ, so that we can see whether they favour Clark's views or those of the present author.

The two species known of the genus *Psammechinus*, *miliaris* and *microtuberculatus*, have both been studied as regards their development, *miliaris* being very completely known, while there is no description of the fully formed larva of *microtuberculatus*. The larva is characterized by having, in the first stage, long body rods, widening in the end; no basket structure. In the second stage the larva has four epaulets, situated at the base of the four main arms. There is no posterior transverse rod or posterolateral processes.



Of the species referred to the genus *Echinus* s. str. two have been studied as regards their development, viz. *esculentus* and *acutus*. The larvæ of these two species are so closely alike that they are hardly distinguishable. In the first stage they have elongated, clubshaped body rods, but no basket structure; in the second stage they have four epaulets, at the base of the four main arms, and besides a pair of laterally placed epaulets which may form an almost closed ring round the posterior end of the body. There is no posterior transverse rod or posterolateral processes.

The larva of the nearly related *Sterechinus Neumayeri* (which Clark regards only as a synonym of *Echinus margaritaceus* — or *Sterechinus Agassizi*, as I think its correct name should be) is known in its second stage. It agrees with the two *Echinus*-larvæ in all essential features.

The larvæ of these forms accordingly agree very well in their main characters as should be expected, since they are indisputably closely related. But now those of the other genera! Here the matter lies quite differently. Within the genus *Lytechinus* we now know the larvæ of the species *variegatus*, *anamesus* and *pictus* in both the first and second stages, and of the species *panamensis* and *verruculatus* in the first stage. The young larvæ have a short, rounded body, the body rod being short, branching at the end; the recurrent rod is well developed but does not unite with the branch from the body rod so as to form the basket structure, except in the *verruculatus*-larva. In the second stage there is a transverse rod, and posterolateral lobes, while the presence of epaulets is not definitely settled. — The larva of *Tripneustes esculentus* agrees with the *Lytechinus*-larvæ, differing only in the body skeleton of the first stage forming a typical basket structure. The *Tripneustes gratilla*-larva in its first stage has the same structure, while the second stage is unknown. Of *Toxopneustes* we know with certainty only the young stage of the larvæ of *T. pileolus* and *roseus*; they agree completely with the *Tripneustes*-larva in the skeletal structure. Finally the larva of *Evechinus chloroticus* has in its first stage a more complicated body skeleton than that of the *Tripneustes*-larva, though essentially of the basket-type, recalling that of the *Echinometra*-larva, and in the second stage (almost certainly) a posterior transverse rod and posterolateral processes.

It must be conceded, at least, that the facts from the larvæ do not lend support to Clark's view regarding the relationship of these genera.

Clark's family Strongylocentrotidæ encloses the genera *Echinostrephus*, *Pseudoboletia*, *Paracentrotus*, *Loxechinus*, *Cænocentrotus*, *Pachycentrotus*, *Heliocidaris* and *Strongylocentrotus*. Of these the genera *Echinostrephus*, *Cænocentrotus*, *Pachycentrotus* and *Heliocidaris* according to me belong to the family Echinometridæ, *Pseudoboletia* to the Toxopneustidæ, *Paracen-*



*trotus* and *Lovechinus* to the Echinidæ; the relation of *Strongylocentrotus* appeared uncertain, though I have thought it probably nearest related to the Toxopneustidæ. Unfortunately, the larvæ of most of these genera are still unknown; but we know those of *Paracentrotus lividus*, *Heliocidaris tuberculata* (— the reduced larva of *H. erythrogramma* does not count in this connection —) and some “*Strongylocentrotus*”-species.

The larva of *Paracentrotus lividus* agrees with the *Echinus*-type; the body rod is elongated, clubshaped, and no basket structure is found in the first stage; there is no posterior transverse rod or posterolateral processes in the second stage. Anterior but no posterior epaulets (as in *Psammechinus miliaris*). In the larva of *Heliocidaris tuberculata* the body skeleton in the first stage forms a very complicate basket structure, as in the *Echinometra*-larva; in the second stage there is a posterior transverse rod and posterolateral lobes; vibratile lobes are present, but no epaulets.

Within the genus *Strongylocentrotus* we know the larvæ of the species *drobachiensis* and *franciscanus* fairly completely, that of *pulcherrimus* nearly so and that of *purpuratus* in its first stage. They all agree in the body skeleton forming no basket-structure, the body rod being clubshaped, elongate (less so in *franciscanus*); in the second stage there is no posterior transverse rod or posterolateral processes, but both anterior and posterior epaulets as in the *Echinus*-larva (presence of epaulets in the *pulcherrimus*-larva uncertain).

To the genus *Strongylocentrotus* Clark also refers the mediterranean species *granularis*, otherwise unanimously regarded as the type of a separate genus, *Sphaerechinus*. According to my view this genus belongs to the family Toxopneustidæ, representing a polyporous development within that family. The larva of this species differs most conspicuously from those of the above named *Strongylocentrotus*-species. The body skeleton forms a basket-structure in the first stage; in the second stage a posterior transverse rod is formed, and there are posterolateral processes, vibratile lobes and anterior but no posterior epaulets. That the postoral rods are fenestrated is another conspicuous difference from the *Strongylocentrotus*-larvæ, though of minor morphological importance. Thus it is evident that the characters of the larva of *Sph. granularis* bear decided testimony against classifying that form with the “*Strongylocentrotidæ*”, or even referring it to the genus *Strongylocentrotus* itself, while on the other hand there is perfect agreement between the larval characters of *S. granularis* and those of the other Toxopneustid-larvæ thus far known.

To the genus *Strongylocentrotus* Clark also refers the Japanese species *depressus*, which, according to my view, represents the type of a separate genus, *Pseudocentrotus*, of the family Toxopneustidæ. The little bit of in-

formation that has been given here of its larva is sufficient to show that it differs very markedly from the true *Strongylocentrotus*-larvæ in its body skeleton in the first stage forming a basket-structure; there is then very good reason to expect that also in its second larval stage it will prove to agree with the Toxopneustid larval type. At least the facts known are decidedly not in favour of Clark's views.

Regarding the genera referred by Clark to the family Echinometridæ there can be no doubt that they really form a natural group, *Parasalenia* alone being doubtful. It must then be claimed that the larvæ of these forms should be in conformity with one another in their essential features. It is a pity that we do not know much about these larvæ, only one species, *Echinometra lucunter*, having been reared to its full larval shape and through metamorphosis. But it is known that the larvæ of *Echinometra oblonga* and *Colobocentrotus atratus* agree with the *Ech. lucunter*-larva in the very characteristic feature of the recurrent rod being double, and it is highly probable that the same character applies to the larvæ of *Echinometra Mathæi* and *Heterocentrotus mamillatus*. Thus the facts hitherto known regarding the larvæ of the Echinometridæ agree very well with the results derived from the study of the adult forms as to their natural affinities.

Summarizing now the preceding discussion it must be stated that the study of the larvæ most decidedly lends support to the author's views as to the classification of the Camarodonta, and thus also gives proof of the correctness of ascribing comparatively great importance to the minor microscopical characters of pedicellariæ and spicules in the classification of this group. The classificatory results reached on using these characters, combined with the characters of the test, have been splendidly confirmed through the study of the larvæ. Disregarding these characters, Clark was led e. g. to such an absurdity as to include *Sphærechinus granularis* in the genus *Strongylocentrotus*, otherwise so naturally circumscribed through the peculiar character of its globiferous pedicellariæ. There is no reason to enter here on a discussion of the objections raised especially by Clark against using these microscopical characters in classification, as it may now be regarded as an established fact that they are really of eminent classificatory value. Thereby I do not mean to maintain that my classification was correct in all details. Thus e. g. the position assigned by me to the genus *Strongylocentrotus*, mainly on account of the structure of its globiferous pedicellariæ, as being probably related to the Toxopneustidæ, was evidently incorrect. The study of the larvæ shows that it is most likely to be an offshoot from the Echinidæ s. str. Upon the whole I would emphasize that the true position especially of the forms belonging to the Camarodonta, (excepting

the Temnopleurinæ), cannot be taken as definitely established, until **all** the characters available, including the structure of the larvæ, have been studied and duly taken into consideration. The structure of the pedicellariæ, of course, does not in itself give definite proof of their affinities; also these characters may, doubtless, have developed separately along different lines, as is seen from the case of *Strongylocentrotus*, not to mention *Glyptocidaris crenularis*<sup>1)</sup>. Therefore I would not consider e. g. the position of the genus *Loxechinus* in the family Echinidæ as definitely established, until it has been proved that its larva also belongs to the Echinoid type. Still less can the position of forms like *Notechinus magellanicus* and *Pseudechinus albocinctus*, where the characters of the pedicellariæ are very indistinct, be regarded as settled, as long as we do not know anything about their larvæ. Upon the whole, the natural classification cannot be found through arranging the forms diagrammatically after this or that character; the interrelations and affinities being the result of organic evolution and descent it is not likely that we will find the true expression thereof by means of a diagram.

As a definite result it may be stated that there is a definite larval type characteristic of each of the three families, the Echinidæ, the Toxopneustidæ and the Echinometridæ. They may be shortly characterized thus:

The larvæ of the Echinidæ have in their first stage an elongated body, supported by a long, more or less club-shaped body rod, the skeleton forming no basket-structure. In the second stage there is no posterior transverse rod, no posterolateral or vibratile lobes; epaulets are developed at the base of the four main arms, often also one pair at the posterior end of the body. Fenestrated rods are not known to occur within this type.

The larvæ of the Toxopneustidæ have in their first stage a short body, the body rod being short and, together with the recurrent rod, forming a basket-structure (excepting the genus *Lytechinus*). In the second stage there is a posterior transverse rod; posterolateral and vibratile lobes are found, and there are often (always?) epaulets at the base of the four main arms. The rods of the main arms simple or fenestrated.

The larvæ of the Echinometridæ have in the first stage a short, obliquely truncated body, supported by a complicate basket-structure, the recurrent rod being double. In the second stage there is a posterior transverse rod; posterolateral and vibratile lobes are found, but no epaulets. The rods of the main arms are fenestrated.

<sup>1)</sup> Comp. the author's "Echinological Notes." II. A new principle of Classification. Vid. Medd. Naturh. Foren. København. 1910. p. 31 note.

Turning to the **Ophiurid-larvæ** we find matters much less clear than is the case with the Echinoid-larvæ. In fact, our previous knowledge would hardly seem to warrant any other conclusion than this, that these larvæ form a rather chaotic assemblage; thus e. g. the larvæ of forms so closely related as *Ophiura affinis*, *albida* and *texturata* are so different, that they would rather seem to belong to different families than to closely related species. The present researches, however, tend to prove that matters do not stand quite as badly.

It may be regarded as an established fact that within the genus *Ophiothrix* the larvæ are of a very uniform character, so uniform, indeed, that it is in many cases impossible to distinguish the various larval species. Whether this type is peculiar to the whole family of the Ophiothrichidæ, and not to the genus *Ophiothrix* alone, remains to be proved. But in any case we have here a distinct larval type common to the very numerous species within this genus, and there is not the slightest reason to believe that the larvæ of any of these species should prove to differ markedly from the common type. This is then in perfect accordance with the legitimate claim, that nearly related forms should agree in regard to their larval characters.

Another conspicuous case is afforded by the *Ophiocoma*-larvæ. The four (or five) larvæ hitherto known are so closely alike that it may be safely stated that there is a distinct larval type of this genus, characterized through the transformation of the central part of the body skeleton into a sort of link, and through the existence of vibratile lobes. Whether this larval type is peculiar also to the family Ophiocomidæ remains uncertain.

The study of the great variety of Ophiuroid larvæ of unknown origin has disclosed the important fact that also among these larvæ several distinctly characterized types may be distinguished, each comprising several species. After the analogy of the genera *Ophiothrix* and *Ophiocoma* it may very reasonably be concluded that these types represent various genera, the larvæ of the different species within these genera being upon the whole closely alike, as should be claimed upon the theory of the classificatory value of the larvæ. Such larval types are especially *Ophiopluteus undulatus*, *O. arcifer*, *O. pusillus*, *O. serratus-bimaculatus*.

It is then hardly to be denied that definite proof has been given that, also within the Ophiuroids, the larvæ of closely related species are in general similar, agreeing in their main characters. The conclusion to be derived from this fact must needs be this that the conspicuous difference between the larvæ of *Ophiura albida*, *affinis* and *texturata* proves these forms not to be so very closely related, in spite of the fact

that, even after the recent subdivision of the great genus *Ophiura* (Matsumoto, H. L. Clark), these two species are left in the same subdivision, the genus *Ophiura* s. str., which would mean that a further subdivision of this genus is necessary. In this connection it is important to notice that most probably *Ophiura affinis* and the mediterranean *O. Grubei*, which has unjustly been made a synonym of the former, have larvæ of almost identical structure<sup>1)</sup>. Further the *Ophiopluteus fusus*, described in the present work, recalls the *Ophiura albida*-larva to a considerable degree, so that it might well seem that here again we have the larvæ of two really related forms. (— *O. fusus* being found at the Azores, one might perhaps think of *Ophiura Thouletii* Koehler as its parental form —). Regarding *Ophiura texturata*, the larva of which is quite unique among the Ophiurid-larvæ hitherto known through its fenestrated posterolateral rods, it is worth pointing out that this species is very peculiar by its series of pores along the ventral midline of the arms, therein differing markedly from the other species of the genus. Upon the whole, I would think it very probable that the genus *Ophiura* (or *Ophioglypha*) in its wider sense is a parallel to the Camarodonta within the Echinoids, that is to say, representing the most specialized type, in which the "coarser" characters, if I may use such an expression, have reached such a point of specialization and uniformity that they do not afford a sufficient base for further classification. The generic characters would then have to be looked for among the minor, morphologically less important structures, just as in the Camarodonta the characters of the pedicellariæ and spicules set in, where the morphologically much more important characters of the test structure are failing as a sufficient base for classification. This is, of course, only meant as an idea to be tested by further studies. But in any case, it would seem perfectly absurd, in view of the facts here made known regarding the Ophiurid larvæ, to draw the opposite conclusion that, since the larvæ of forms so closely alike as *Ophiura albida*, *affinis* and *texturata* differ so markedly from one another, the Ophiurid larvæ have no classificatory value at all.

While it thus seems an established fact that within the Ophiuroid-larvæ several very distinct generic types may be discerned, it is, at the present state of our knowledge, impossible to say whether "family"-types also may be distinguished. There is some probability that the family Ophiothrichida has a distinct larval type of its own, perhaps also the Ophiocomidæ have a distinct larval type — but very much more knowledge is required, before we can form a safe judgment of this problem.

<sup>1)</sup> Comp. the author's paper "Notes on the development and the larval forms of some Scandinavian Echinoderms", p. 135.

Within the **Asteroid-larvæ** the facts previously made known, together with those given in the present work, decidedly tend to show that there are distinct "family" types of the larvæ, corresponding to the families of the adult. Unfortunately, our knowledge is still very limited, so that there is only a poor foundation for the conclusions; but the little we know speaks rather clearly.

Within the Astropectinidæ we know the larvæ of four different species, all agreeing in their main features: the processes are very short, rigid, and the larvæ do not develop into a Brachiolaria. By the metamorphosis the whole larval body is absorbed. — Within the Luidiidæ we know the larvæ of the two species *Luidia Sarsi* and *ciliaris*, which both agree so closely in their characters that it is difficult to distinguish them. They are characterized by the great elongation of the anterior part of the body which apparently forms an active swimming organ: all the paired arms, which are long and movable, are situated close together in the posterior part of the body. There is no Brachiolaria-stage, and the larval body is not absorbed by the metamorphosis but apparently simply cast off, when metamorphosis is completed. — The fact that "*Bipinnaria asterigera*" is recorded from the Celebes-Sea (in the "Summary of Results" of the "Challenger", p. 836) indicates that at least one more species of Luidiæ has a similar larva, which lends support to the conclusion that we have here a distinct larval type, characteristic of the genus *Luidia*. Whether we may conclude this much that these two larval types represent the larvæ of the families of the Astropectinidæ and Luidiidæ, is, of course, doubtful. But, at least, there is nothing to disprove it.

Within the other families the few facts known of the development of the Asterinidæ and the Gymnasteridæ hardly form a sufficient base for any conclusion as to the characters of their larvæ. I would only say that the character of the rudimentary larvæ of *Asterina gibbosa* and *exigua*, combined with the fact that the larva of *Asterina pectinifera* develops into a Brachiolaria, tend to show that within this genus (s. lat.) the larvæ typically have a Brachiolaria-stage.

Within the genus *Asterias* the development of the species *A. rubens* and *vulgaris* has been studied very completely, and of a third, *A. glacialis*, enough is known to state that its larva agrees very closely with those of the other two species. It appears that we have here a very distinct larval type, characterized through its long, movable processes, and developing into a Brachiolaria with round arms, crowned by a circle of papillæ. On metamorphosis the larval body is completely absorbed. The characters of the young larvæ of some other forms, *Orthasterias leptolena*, *Euasterias Troscheli*, seem to indicate that these forms also have a Brachiolaria-stage;

further the species with shortened development, *Asterias Mülleri*, *groenlandica*, *hexactis*, through the fact that their rudimentary larvæ have distinct Brachiolarian processes, lend support to the suggestion that this larval type is characteristic of the whole family Asteriidae.

So little is known as yet of the development of **Holothurians** that hardly anything can be concluded as to how far the larvæ may be arranged in groups, corresponding to the orders or families of the adults. A single larva is all that is known of the Synaptids; three larvæ of the genus *Holothuria* are known, but none of them in their full shape, and it is uncertain whether they adopt a more complicate structure in their more advanced stages. That they are very much alike in the younger stages, all being of a very simple shape, is in good accordance with what should be expected, but much stress cannot be laid on this fact.

Of more weight is the fact that three different species are known of the type *Auricularia nudibranchiata*, resembling one another so closely that it is difficult enough to distinguish them. This proves that we have here a case of the larvæ of closely related species agreeing very closely in their characters. (Although we do not know to which genus the *A. nudibranchiata* belongs, there can hardly be any doubt that all these larval species belong within the same genus, or, at least, — in case MacBride's statement that the intestinal pouch of species *c* is a paired organ be correct — very closely related genera). It would not seem unreasonable to suggest that *Auricularia antarctica*, *plicata* and *minor* belong to the same group as *A. nudibranchiata*, and then we would here really have a "family" of Holothurian-larvæ, fairly well characterized through several features (e.g. the peculiar shape of the oral region, the peculiar folding of the vibratile band). But as long as we do not know anything with certainty about the parentage of these larvæ, we may only hint at this as a possibility.

It appears to be a rule that the Dendrochirotes have a shortened development, without a typical pelagic larval stage. Without entering here on a discussion of the question, whether the simple larva of the Dendrochirotes is a secondary adaptation or whether it represents the most primitive condition of Echinoderm-larvæ, it is clear that it has no bearing on the problem of the classificatory value of the typical pelagic larvæ.

The **Crinoids** are the poorest of all Echinoderms in regard to the present subject, as we do not know one single truly pelagical Crinoid-larva, corresponding to the other four main types of Echinoderm larvæ. Till now only Comatulids have been studied as regards their development, and it seems very likely that within this whole group the development is of the



type without a typical pelagic larva, the Comatulids thus offering a case analogous to that of the Dendrochirote Holothurians. It may perhaps be expected that typical pelagic larvæ will be found to exist in some of the stalked Crinoids; but till now nothing is known about that, and accordingly the Crinoids do not contribute to the solution of the problem here discussed and must be left out of consideration for the present.

After this summary review we may state as the result of these researches that the facts hitherto brought to light are decidedly in favour of the view that the larvæ of the Echinoderms have an important bearing on the classification of the adult forms. It seems a sufficiently established fact that the larvæ of closely related species are upon the whole very much like one another, often hardly distinguishable, and, further, that the larvæ of allied genera agree in important characters, so that we get groups of larvæ, larval "families", "orders", corresponding to the groups (families, orders) of the adult forms. Accordingly the very important conclusion seems justified, that when forms, which were supposed to be nearly related, prove to have essentially different larvæ, these forms are not in reality nearly related<sup>1)</sup>. The study of the larvæ will thus form a most important criterion for our classification, giving, so to say, the final judgment of its true value, and we are justified in stating that no classification which is in contradiction to the evidence given by the larvæ can give an adequate expression of the natural relationship of the adults. — These results probably apply also to other animal groups than the Echinoderms; but this side of the problem will not be discussed on the present occasion.

Although the facts already known seem to warrant the above conclusions, I would maintain most emphatically that the present researches are only to be regarded as a reconnaissance in this field. Proof is given that the way entered upon is the right way, and we may be sure that further researches will yield important results. But there is a long way to go. What has been obtained as yet is nothing more than random samples, taken here and there. It must be claimed that all the various forms should be studied, and not only the genera; it will be equally important to have all the species within the various genera made the object of study, even though they are, apparently or really, ever so closely related, and it is equally desirable that the larvæ should be studied and figured alive. Thus we will gradually acquire a sum of knowledge of the greatest importance for reaching the end of all systematic work, the comprehension of the multitude of living forms in their natural relationship.

<sup>1)</sup> Provided, of course, their embryological conditions be the same. That closely related species may differ in one having typical larvæ, the other having abbreviated development or being viviparous, is quite a different thing, and does not interfere with the above conclusion.

## II. Morphology; Phylogeny; Biology.

The general homology of the four main types of the Echinoderm larvæ was so clearly pointed out by Joh. Müller in his classical memoir "Über den allgemeinen Plan in der Entwicklung der Echinodermen"<sup>1)</sup> that very little has had to be corrected<sup>2)</sup> or added, the main thing being that the separate frontal band of the Asteroid-larvæ does not represent an essential difference from the other larvæ, as Joh. Müller thought it to do. In the light of the more extensive knowledge of the larval forms now acquired it may be worth while to pay some attention to the special development within each of the four types, to see how they develop from the primitive generalized shape into more or less highly specialized forms or, on the other hand, are reduced into forms so simple that they are hardly recognizable as forms derived from the true pelagic larval type.

The Auricularia is the type in which the least amount of specialization appears to have taken place, due allowance being made for the fact that we know comparatively less about the Holothurioid larvæ than of the three other main groups. The simplest form is that found within the genus *Holothuria* (— unless it should turn out to be much more specialized in the more advanced stages of development, which does, however, not seem very likely —). The vibratile band hardly shows an indication of the typical larval processes, the larva in fact looking almost like a diagram of the primitive Echinoderm-larva, as regards its outer shape (— as to its inner structure it is less simple —). Only simple calcareous bodies are known to occur, irregular stars or spherical bodies<sup>3)</sup>, no wheels. — The larvæ of *Synapta* and *Stichopus* are only a little more specialized, the vibratile band forming small processes corresponding to those of the other Echinoderm-larvæ. In the *Synapta*-larva calcareous bodies are formed in the shape of elegant wheels.

The *Auricularia paradoxa* being in all probability only a decalcified *Echinopluteus transversus*, only one group of Holothurian larvæ is known, which represents a more specialized form of the Auricularian type, viz. the larvæ *Auricularia minor*, *plicata* and *nudibranchiata*. While *A. minor* is still comparatively easily referred to the primitive type, *A. plicata* is considerably more specialized, but the climax is reached by *A. nudibranchiata* in which the vibratile band develops to such an extraordinary degree of complication that it is difficult enough to recognize the original type. *Auricularia antarctica*, though somewhat specialized in other directions,

<sup>1)</sup> Abhandl. d. Akad. Berlin. 1853. Taf. II.

<sup>2)</sup> Comp. the author's Memoir "Die Echinodermenlarven d. Plankton-Expedition" p. 8.

<sup>3)</sup> The *Auricularia sphaerigera* (Joh. Müllers's "Auricularia mit Kugeln") may well be suggested to belong to the genus *Holothuria*.

seems fairly evidently to belong to this same larval group. As might be expected in such a specialized type, the calcareous bodies are wheels of a very elaborate structure.

While in *A. nudibranchiata* the Auricularian type has reached its highest perfection (— it is very interesting that also in regard to size this larva represents the climax —), the Dendrochirote larva represents the opposite extreme, being simply worm-shaped, with none of the characters of the Auricularia, its vibratile rings recalling those of the Auricularian pupa, not the band of the Auricularia itself. For deciding the question, whether this simple larva is a true primitive form (as maintained by Caswell Grave<sup>1</sup>) or merely a reduced form, it would be of importance to know whether transitional forms exist, as is the case in the Ophiurans. Of this, however, we are ignorant as yet; but considering the very imperfect stage of our knowledge of the development of Holothurians, it would not seem unreasonable to expect that such an interesting case might ultimately turn up.

The Bipinnaria in its simplest type differs so slightly from the simpler forms of the Auricularia that it may sometimes be difficult enough to decide to which of them such a form belongs. This primitive type is, as far as hitherto known, peculiar to a genus of starfishes which is unanimously regarded as one of the more primitive of recent Asteroids, viz. *Astropecten*. It is especially an important fact that no Brachiolaria-stage occurs in this type of Bipinnaria. The same fact applies to that more specialized type, the *Luidia*-larva, in which the anterior part of the body has undergone a development into an apparently active swimming organ. Also the remarkable *Bipinnaria antarctica* recently described by MacBride<sup>2</sup>) evidently agrees with the *Astropecten*- and *Luidia*-larvæ in having no Brachiolaria-stage, as MacBride justly infers from the fact that even in a fairly advanced stage of metamorphosis the ventral median process retains its typical shape, no trace of Brachiolarian arms having yet appeared. If the reference of this larva to *Cheiraster gerlachei* is correct, we have here another case in support of the assumption that in the more primitive Asterids upon the whole the larvæ do not develop into Brachiolaria. This said larva represents the most specialized form of all known Asteroid-larva in regard to the vibratile band, which forms dense folds or crenulations along the strongly developed arms, a case analogous to *Auricularia nudibranchiata*.

<sup>1</sup>) Caswell Grave. On the occurrence among Echinodermis of Larvæ with cilia arranged in transverse rings, with a suggestion as to their significance. Biol. Bull. V. 1903. p. 169.

<sup>2</sup>) E. W. MacBride. Echinoderma (Part II) and Enteropneusta. British Antarctic ("Terra Nova") Expedition, 1910. Zoology. IV. 1920. p. 90.

While it would thus appear to be a rule that the larvæ of the Phanerozonia have no Brachiolaria-stage, the facts known of the development of the Spinulosa and the Forcipulata (Cryptozonia) seem to indicate that their larvæ are characteristic through having a Brachiolaria-stage<sup>1)</sup>. The differences between the various types of Brachiolarias are very unessential, consisting mainly in the median Brachiolarian process being now round, with a crown of papillæ, now flat with a series of papillæ along the edges; this need not be considered here. The point to be emphasized is that the Brachiolaria-stage is known to occur only in the more specialized Starfishes, and the Brachiolaria-arms and the sucking disk connected therewith are therefore later acquired, specialized structures. Accordingly the homology generally supposed to exist between the sucking disk of the Brachiolaria and the Pelmatozoan stalk is only apparent, and the great part it has played in phylogenetic speculations is unjustified, not being supported by facts acquired from an extended study of the development of Asteroids. Of course, I agree that very much more knowledge is needed for finally establishing this statement as a fact beyond dispute. The metamorphosis of the *Astropecten*- and *Luidia*-larvæ need being studied in a much more detailed way than has hitherto been done. It would also be of the greatest interest to study the development of such Astropectinids and other Phanerozonia as have large, yolky eggs and to see whether the larvæ of such forms possibly develop Brachiolarian processes and a sucking disk, as do e. g. the *Solaster*-larvæ. If my views on the development of Asteroids are correct, they should not develop such processes, or, at least, no sucking disk. (Processes might not necessarily be homologous with the Brachiolarian arms). Anyhow, the facts hitherto known of Asteroid development seem to me to enforce the above conclusions.

It is of importance to notice the fact that during the metamorphosis of

<sup>1)</sup> If the larva figured on p. 119 of my paper "Notes on the development and the larval forms of some Scandinavian Echinoderms" really belongs to *Stichaster roseus* as supposed by me there, that will be an exception to the rule indicated by the direct observations on the development of the said groups of starfishes. I would not be inclined to think this probable and therefore now doubt the correctness of that suggestion. The larva figured would then belong to *Astropecten irregularis*.

Gemmill in his paper on "The larva of the Starfish of *Porania pulvillus* (O. F. M.) (Qu. J. Micr. Sc. Vol. 61. 1915) concludes from the fact that he has found this larva to have a Brachiolaria-stage that "it is evident that the division of Asterids into Phanerozonia and Cryptozonia is not necessarily associated with fundamental differences of development." As, however, the position of the family Gymnasteridae (or Asteropidae), to which *Porania* belongs, within the Phanerozonia is doubtful, this conclusion may not be justified. The fact of the *Porania*-larva being a Brachiolaria at most may serve to prove that this larval stage makes its appearance in the most specialized group of the Phanerozonia.

Asteroids no breaking up and subsequent rearrangement of the ciliated band into transverse rings has been observed, such as it occurs especially in Holothurians, but also, more or less distinctly, in Ophiuroids and Echinoids; accordingly we cannot speak of a pupa-stage in Asteroids corresponding to that of Holothurians and (more or less modified) of Ophiuroids and Echinoids. Neither do the forms with direct development (*Henricia*, *Solaster* etc.) develop ciliated rings, as do the Crinoids and Holothurians with abbreviated or direct development; there is only a general ciliation in these reduced starfish-larvæ. It is, of course, possible that larvæ with ciliated rings may occur among those of the Phanerozoia which have direct development; but as yet we do not know a single case of such larvæ within the Asteroids — and this fact is not in favour of the suggestion that the simple, wormshaped larva provided with ciliated rings, like the Comatulid- and the Dendrochirote-larvæ, represents the primitive Echinoderm-larva.

Two more forms of starfish-larvæ have been described, which would appear to represent special types differing essentially from the main types treated above. They must be briefly mentioned here.

In my Memoir on "Die Echinodermenlarven d. deutschen Südpolar-Expedition"<sup>1)</sup> p. 89 notice is given of a larva with more than 20 Brachiolarian processes, the general shape of the larva being otherwise like that of a typical *Asterias*-larva; the larva itself I had not examined, the description being founded on observations of the living specimen made by Vanhöffen during the stay of that Expedition in the Antarctic Sea. As later on the specimen of this larva was examined by me, those numerous Brachiolarian arms were found to be a mistake; they were nothing but the spines of the young metamorphosing starfish. — A correction of the description was given in the "Vorwort" to the said volume of the "Deutsche Südpolar-Expedition", p. VI; but as this correction is very likely to be overlooked I have found it my duty to mention it here.

In 1906 Koehler & Vaney<sup>2)</sup> published the description of a remarkable new Asteroid-larva, taken in the vicinity of the Azores, which was named *Stellosphera mirabilis*. Only two stages were observed, the younger being provided with clusters of large spines, which were absent in the later stage, so that a remarkable, regressive development of the calcareous bodies in the larval skin takes place during the progressing development

<sup>1)</sup> Deutsche Südpolar-Expedition 1901—1903. Bd. XIV. Zoologie VI. 1913.

<sup>2)</sup> R. Koehler et Cl. Vaney. Description d'une nouvelle larve d'Astérie appartenant très vraisemblablement à une forme abyssale. Bull. Mus. Océanogr. Monaco. No. 61. 1906.

The description was reprinted in Koehler's great work "Échinodermes provenant des campagnes du yacht Princesse Alice (Astéries, Ophiures, Échinides et Crinoïdes). Rés. d. Camp. Scient. Monaco. Fasc. XXXIV. 1909. p. 131—136. Pl. XXIV.

of the larva. The crossed pedicellariæ, present in both larval stages, definitely prove that it belongs to the suborder of the Forcipulata, and reasons are given for the suggestion that it is the larva of a deep-sea form. It is a noticeable fact that no traces of a vibratile band are found.

Through the kindness of Professor Jules Richard I have received from the Musée Océanographique of Monaco some specimens of this very interesting larva. The examination of these specimens has led me to an interpretation differing rather considerably from that given by Koehler & Vaney. Both the stages described are far advanced metamorphosis stages, so that the true shape of the larva is not to be made out, the larval body most probably (— as may be inferred from a comparison with the later metamorphosis-stages of *Asterias* —) already being for the greater part absorbed. But this much is still clear, that the larva belongs to the Brachiolaria-type. In fact, there can be no doubt that what Koehler & Vaney take to be the mouth of the larva is really the sucking disk of the Brachiolaria, round which are found the three typical Brachiolarian arms. They are of quite typical shape, ca. 2—5 mm long, cylindrical, the point being covered with small papillæ; furthermore there is a close series of similar small papillæ from the base of the median, anterior Brachiolarian arm backwards to each side of the sucking disk. On the larval body there are besides found the last vestiges of the other larval arms, mostly reduced to mere papilliform processes, which can no longer be identified with certainty, excepting only the unpaired, median dorsal process, situated behind the median Brachiolarian arm. The larva is in a stage corresponding very closely with that represented in Pl. 21, Fig. 13 of Gemmill's Memoir on the development of *Asterias rubens*<sup>1)</sup>. If only the body and arms were a little more contracted — as they would certainly be on a not very careful preservation — we would here have a figure very well representing the *Stellosphæra*. If we now look upon the figures on Pl. XXIV of Koehler's work, it is evident that the figure 10 represents a larva seen from the apical pole, showing the sucking disk in the middle, with the three Brachiolarian arms (very poorly represented — they have evidently been unusually contracted in that specimen; the papillæ on the point of these "pédicelles péribuccaux" were also observed by Koehler & Vaney). The smaller papillæ scattered over the body are the remnants of the larval arms, not at all the beginning tubefeet of the young starfish, as would seem to be the opinion of the authors. The six large calcareous plates with the clusters of spines are the terminal plates of the starfish. Another curious result of this examination is that the I. stage of Koehler & Vaney is really the older, more advanced stage, their II. stage being

<sup>1)</sup> Phil. Trans. Ser. B. Vol. 205. 1914.

the younger. Accordingly the remarkable absorption of the plates and spines, supposed by the authors to take place during the progress of development, does not take place at all, the facts being quite the inverse. The peculiar stage represented in fig. 1 of Koehler's work, showing what appears like two filaments at the "mouth" is only a later stage of development, where the Brachiolarian arms have been almost absorbed, the other arms completely so.

In 1915 Gemmill<sup>1)</sup> described a new Asteroid-larva, *Brachiolaria hibernica*, characterized by the point of the Brachiolarian arms being wholly covered with small papillæ, and through the presence of a row of small papillæ on each side of the sucking disk, which latter is transversely elongated. The single specimen observed (taken in the Atlantic, 50 miles to the W. of Ireland, in a vertical haul from 2165 meters) was in an advanced stage of metamorphosis, the larval arms being reduced to short cylindrical prominences, but Gemmill thinks it very probable that in its younger stages it has the shape of a typical *Brachiolaria* larva. The characters of this larva exactly agree with those of *Stellosphæra mirabilis* pointed out here, and the figures of the larva given by Gemmill also recall the *Stellosphæra* to such a degree that I cannot doubt that it is really the same larva. It is true that Gemmill does not say anything about its being six-rayed, as is *Stellosphæra*. But his Fig. 1 shows, besides the five young arms, a sixth prominence, which is indicated in the explanation of the figure only as a "prominence of soft tissues in the aboral notch." I can hardly doubt that this is really the beginning 6th arm. (The skeleton, which would have settled the question, was, unfortunately, dissolved).

Thus, I would think, the "*Stellosphæra mirabilis*" has been definitely deprived of its remarkableness and been reduced to a, probably, quite ordinary *Brachiolaria* in an advanced stage of metamorphosis. — The suggestion of Koehler & Vaney that it belongs to a deep-sea Asteroid was apparently for a great part due to its supposed fundamental difference from the typical pelagic larvæ of littoral Asteroids. The larvæ were taken in vertical hauls with open nets, from 3000 m. to the surface: there is thus — as Koehler & Vaney of course admit — no certainty about the depth in which these larvæ were taken. As also other larvæ, belonging undoubtedly to littoral Echinoderms, have been observed far away from the coasts (see below, the chapter on the geographical distribution of the larvæ), there seems thus far to be no special reason for regarding the "*Stellosphæra*" as the larva of a deep-sea Asteroid. Still it is possible that it was really taken in greater depths, and if we look up the forms of Starfishes to which it

<sup>1)</sup> James F. Gemmill. On a new brachiote Asteroid larva and on the advanced Bipinnaria of *Luidia ciliaris* (Philippi) Gray. Proc. R. Phys. Soc. Edinburgh. XIX. p. 191.

might possibly belong, it seems indeed probable that it does belong to one of the forms occurring in greater depths. The facts that the young starfish is 6-radiate and that it belongs to the Forcipulata (as proved by its pedicellariæ) considerably restrict the number of forms which may come into consideration. Among the starfishes known to occur in the littoral regions of the Azores there is not one having normally 6 arms; *Asterias tenuispina* Lank. however sometimes has this number of arms, though there are generally seven or eight. In case the "*Stellosphæra*" should belong to this species, it must evidently start with six arms, since the metamorphosing starfish apparently always has this number of arms. The larger number of arms in *A. tenuispina* then must be due to additional arms formed by regeneration after selfdivision. This is by no means improbable, and it is therefore thus far very well possible that we have in the "*Stellosphæra*" the larva of *Asterias tenuispina*. If this is not the case, the only other forms known to which it could belong are *Asterias Richardi* Perr. (not recorded from the Azores, but not unlikely to occur there), *Pedicellaster sexradiatus* Perrier and *Freyella sexradiata* Perrier, all of them deep-water forms. As the larva was found in considerable numbers it is very unlikely that it belongs to the rare *Freyella sexradiata* or to *Asterias Richardi*, not known with certainty to occur in the Azorean waters. Thus *Pedicellaster sexradiatus* alone remains. The fact that this species has small eggs (— as I have had the opportunity to ascertain —) makes it highly probable that it has a typical pelagic larva (in contradistinction to *Pedicellaster typicus*, which has large, yolky eggs).

One might expect that the structure of the pedicellariæ would decide the question to which of these species the larva belongs. This is, however, not so, the crossed pedicellariæ of the two forms being hardly different at all. On the other hand the pedicellariæ of the young starfish, as figured by Koehler & Vaney, differ from those of the two species mentioned in having only one series of teeth along the edge, while there are two series in both *Ast. tenuispina* and *Pedicellaster sexradiatus*. This structural difference might rather bear testimony against the referring of the larva to any of the two said species. It is, however, very well possible that the single series of teeth in the young is an embryonal character. I therefore would not deem this structural difference of sufficient importance to counterbalance the fact that no other starfish, which might come into consideration as its parental form, is known from the locality where the larva occurs. (The specimens of the larva examined by me all had their calcareous structures dissolved, so that I have been unable to ascertain myself the correctness of the figures of the pedicellariæ given by Koehler & Vaney). — The occurrence of the larva off Ireland, which may be regarded almost



as an established fact through the "*Brachiolaria hibernica*" of Gemmill, affords another important aid for settling the question of the parentage of the larva. *Asterias tenuispina* does not occur in the Atlantic to the North of 40° Lat. N. Accordingly its larva could hardly be found off Ireland. On the other hand *Pedicellaster sexradiatus* is not known to occur farther North than the Biscayan Gulf; but it is by no means improbable that it does, however; occur in the deep-sea off Ireland. The result is then that it seems highly probable that the "*Stellosphæra mirabilis*" is the larva of *Pedicellaster sexradiatus*.

The Ophiopluteus, in spite of the great number of "species" known, appears to show only unimportant deviations from the original simple type, which may perhaps be most nearly represented by the *Ophiothrix*-larva. In the shape of the body there are only few features which may be regarded as a higher specialization; such feature is the presence of vibratile lobes at the base of the posterolateral arms in the *Ophiocoma*-larva. The presence of a ciliated tuft at the posterior end of the body, occurring in various forms, may also be a specialized feature, probably acquired separately in various groups. But too little is known for forming a definite judgment of the value of this character. The ciliated ring in the posterior end of the body of *Ophiopluteus coronatus* ("Echinodermen-Larven d. Plankton-Exped." Taf. VI, Fig. 6), as yet quite a unique feature in Ophiurid-larvæ, may perhaps represent a further specialization of the apical tuft. But so long as we do not know anything about the affinities of that larva (— its skeletal structure is still unknown —) this question must remain unsettled.

The length of the arms varies very considerably. The posterolateral arms are generally much the longer and form the main floating apparatus of the larva; this is especially evident in the *Ophiothrix*-larva and *Ophiopl. opulentus*, where these arms are entirely unaltered during metamorphosis, the young Ophiurid remaining attached to them and simply leaving them by the time it is giving up pelagic life. The arms of Ophiurid-larvæ never become actively movable swimming organs, no muscles connecting the two parts of the body skeleton being present, contrary to what is often the case in Echinoid larvæ. Generally the arms are very thin and narrow, more rarely broad and flat (as in *Ophiopl. paradoxus* and the *Ophiocoma*-larva). The widening of the arm points often found in preserved specimens is probably only due to preservation. It is a curious fact that the right anterolateral arm is often longer than the left one.

A very conspicuous feature is the absence of posterodorsal arms in the larva of *Amphiura filiformis* (*Ophiopluteus mancus*). Also in *Ophiopluteus dubius* (Echinodermen-Larven d. Plankton-Exped. Taf. IV, Fig. 9—10) the

posterodorsal arms would appear to be absent. It is very tempting to suggest that this larva may belong to *Amphiura Chiajei*. In that case the absence of this pair of arms would seem to be characteristic of the *Amphiura*-larvæ in general. However, the fact that among the numerous Ophiurid-larvæ examined by me from so many parts of the world, there is no one lacking the posterodorsal arms, makes this suggestion very doubtful, as it is, indeed, hard to assume that in all that multitude of forms there should not be at least some larva of one or another of the numerous *Amphiura*-species occurring in nearly every locality. But, anyhow, the lacking of the posterodorsal arms, being quite a normal feature at least in the larva of *Amphiura filiformis*, is a very noteworthy, probably regressive, specialization. — In contradistinction to this stands the formation of small extra arms in *Ophiopluteus opulentus*. It seems beyond doubt that these arms are due to the branches from the postoral and anterolateral rods pushing out the vibratile band so as to form a beginning arm; but as this is apparently the case also with the other arms, the growing skeletal rod being the primary factor in the formation of the arms, it seems perfectly justified to regard these small extra arms as having the value of true arms, and one might very well fancy that other larval forms may exist in which these arms reach a size similar to that of the other arms. These additional arms of *Ophiopluteus opulentus* form an interesting analogy with the formation of anterodorsal arms in the Spatangoid-larvæ.

It is, however, the skeletal structure that shows the more interesting diversities within this larval type. Two main types are to be distinguished, one having simple body rods, the other a compound body skeleton, a ventral and a dorsal recurrent rod forming together with the body rod two meshes in each side of the body. It would seem fairly certain that the simple type is the more primitive. The only larva with a compound body skeleton, the origin of which has been definitely ascertained, is that of *Ophiactis balli*<sup>1)</sup>; but it is clear that all the many different forms having a compound body skeleton cannot possibly belong to the family Ophiactidæ. It is evident, therefore, that this type of skeletal structure must have developed independently along various lines, and accordingly the character of the body skeleton, whether simple or compound, cannot be of primary importance from a classificatory point of view. If I was right in referring the *Ophiopluteus gracilis*, described in my Memoir on the Echinoderm larvæ of the German South Polar-Expedition (p. 89), to *Ophiura gelida*, it becomes evident that the compound type of body-skeleton is at most a genus-character, not a family-character. The fact that the larva of *Ophiactis balli* has a compound body skeleton, while the larva of *Ophio-*

<sup>1)</sup> Th. Mortensen. On the development of some British Echinoderms; p. 11.

*pholis aculeata*, apparently a near relative of it, has a simple body skeleton tends to prove the same thing.

The end rods and the transverse rods reach an extraordinary degree of specialization in the *Ophiocoma*-larvæ, in which they are so much reduced in size as to form together merely a sort of link between the two halves of the skeleton. Otherwise the end rods show only a small amount of diversity, less so than the transverse rods which often afford important specific characters. More interest, however, is attached to the median processes from the transverse rods, present in a number of forms; these rods may show a high degree of development, especially in the larvæ of the *serratus-arcifer*-group; also *Ophiopluteus monacanthus* must evidently represent a remarkable specialization of this skeletal part. These median processes are generally directed horizontally outwards from the transverse rods and thus considerably enlarge the body volume, which may serve to increase the floating power of the larva. In no case the vibratile band is produced along the body prominences formed by these rods.

The remarkable preoral rod of *Ophiopluteus costatus*, as yet quite a unique feature in Ophiurid-larvæ, may possibly have originated as a further development from the median process; but nothing definitely can be stated about this at our present state of knowledge. There is a certain analogy between this preoral rod and the dorsal arch of Echinoid larvæ — but, of course, it is only a quite superficial analogy, by no means a homology, as, upon the whole, there is no direct homology between the skeleton of Ophiurid- and Echinoid-larvæ, the skeleton having certainly been acquired separately in each of these two larval types.

The rods of the inner pairs of arms (postoral, anterolateral and posterodorsal) show but little diversity. The various degree of development of their thorns is a feature of interest here; it is not improbable that the strong development of thorns along the aboral side in the outer part of the anterolateral arms in forms like *Ophiopluteus pusillus* may prove of some importance. A more conspicuous feature is, however, the development of special rods supporting the anal area in *Ophiopluteus fulcitus*; but this is also a feature as yet unique among Ophiurid-larvæ, about the morphological meaning of which it is not safe as yet to state anything definite. It recalls the ventral transverse rods of Echinoid-larvæ, with which there is, however, no homology, of course.

The posterolateral rods show the greatest diversity of all skeletal parts of the Ophiurid-larvæ, and afford especially important diagnostic characters. The more usual type is a simple rod provided with strong, curved thorus along the inner (adoral) side; more rarely thorns are found also along the outer (aboral) side. A most remarkable specialization is the un-

dulating rod of *Ophiopl. undulatus*. In some forms the posterolateral rod is canaliculate to a greater or lesser extent (*O. costatus*, *opulentus*), in others it is composed of two closely apposed, parallel rods (*O. affinis*), and finally it reaches its highest specialization in the larva of *Ophiura texturata*, in which it is fenestrated — another feature unique among Ophiurid-larvæ. This character also recalls the Echinoid-larvæ in which fenestrated rods are of general occurrence; but, as was pointed out already by Metschnikoff<sup>1)</sup> (comp. also "Echinodermen-Larven d. Plankton-Exp." p. 53) the structure of the fenestrated rods of the *O. texturata*-larva is markedly different from that found in the Echinoid-larvæ, in accordance with the fact that this character has been acquired separately in the two types and is a highly specialized feature in the Ophiurid-larvæ, while in the Echinoid-larvæ it is, evidently, a primitive character.

Some Ophiurid-larvæ are more or less rudimentary, showing various degrees of reduction from the typical Pluteus-shape to a mere worm-shape which has no longer any likeness whatever to the Pluteus-form. The first stage of reduction may perhaps be represented by the larva of *Amphiura filiformis*, in which the posterodorsal arms have disappeared, the larva otherwise being typical in shape. A somewhat more advanced stage of reduction is probably represented by the larva of *Ophiura affinis* or that figured by Joh. Müller on Taf. VII, Fig. 5 of his VI. Memoir on the development of Echinoderms. Unfortunately, only the metamorphosis-stage is known, however, so that we do not know how far the reduction has gone: in any case the posterolateral arms are completely developed. A much more reduced stage is represented by the larva figured by Metschnikoff (Op. cit. Taf. XII. B. Fig. 1—5) (*Ophiopluteus Metschnikoffi*) and a still further reduced stage by the larva figured by Claparède<sup>2)</sup> (*Ophiopl. Claparèdei*). In these two larvæ, which I have reproduced in figure 102, the Pluteus-shape is, especially in the latter, hardly recognizable any more; the rudimentary skeleton of *O. Metschnikoffi* still distinctly recalls the typical Ophiopluteus-skeleton, while in *O. Claparèdei* it is reduced to a pair of simple rods. In the larva represented in fig. 102, C, which was discovered by Krohn (*Ophiopluteus elongatus*) the Pluteus-shape is no longer recognizable, but traces of the larval skeleton are stated by Krohn<sup>3)</sup> to be found. Through these forms we reach to the larvæ of *Ophioderma brevispina*,

<sup>1)</sup> E. Metschnikoff. Studien über die Entwicklung d. Echinodermen u. Nemertinen p. 29.

<sup>2)</sup> E. Claparède. Beobachtungen über Anatomie u. Entwicklungsgeschichte wirbelloser Tiere. 1863. Taf. I Figs. 11—12.

<sup>3)</sup> "Im Embryo liess sich soweit ausser kleineren Kalkablagerungen . . . deutlich ein gerader, starker, bis in die beiden Enden reichender Kalkstab unterscheiden." A. Krohn. Über einen neuen Entwicklungsmodus d. Ophiuren. Müll. Archiv 1857. p. 373.

*Ophionereis squamulosa* (and doubtless many other Ophiurids), in which also the larval skeleton has disappeared completely, no trace of the Pluteus-form remaining. In these latter larvæ ciliated rings are formed, as in the barrel-shaped larvæ of Comatulids and Dendrochirotes, and in the pupa-stage of other Holothurians.

The existence of a true pupa-stage in Ophiurids was first shown by Caswell Grave<sup>1</sup>). (Very likely the larva, in which the rearrangement of the vibratile band into an indication of rings was observed by Grave, was a species of the type described here as *Ophiopluteus opulentus*). My own observations in the main agree with those of Grave, however, differing

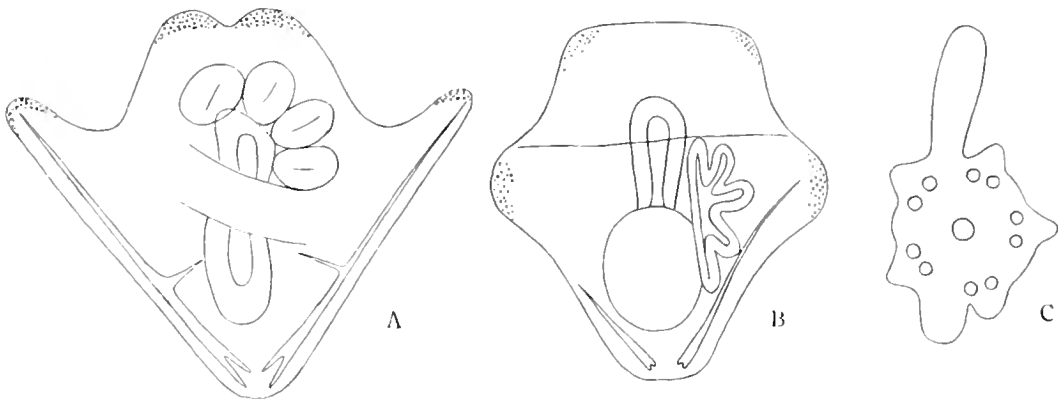


Fig. 102. A. *Ophiopluteus Metschnikoffi* (after Metschnikoff); B. *Ophiopl. Claparèdei* (after Claparède; modified so as to represent the larva in ventral view); C. *Ophiopl. elongatus* (after Krohn).

from them in some minor points. I find the rings less distinctly indicated than shown by Grave, which may, however, be due to my not having observed the metamorphosing larvæ in the same lateral position as that in which they are represented in Grave's fig. 8, but from the ventral or dorsal side. The anterior "ring" I have not found to be complete, but it may very well be so in a later stage of metamorphosis such as that figured by Grave, the stages in which I have noticed this rearrangement of the vibratile band being less advanced (Pl. XXIX, Fig. 3; Pl. XXX, Fig. 2). I have been able to ascertain that the anterior band of the "pupa"-stage is derived directly from the preoral band of the larva. Another interesting fact is that in some cases, at least, the vibratile band of the posterolateral arms in an advanced stage of metamorphosis coalesces in the midline of the larval body, below the developing Ophiurid; how far this is a general rule remains to be ascertained.

<sup>1</sup>) Caswell Grave. On the occurrence among Echinoderms of larvæ with cilia arranged in transverse rings, with a suggestion as to their significance. Biol. Bulletin. V. 1903, p. 175.

The *Echinopluteus* affords the greatest diversity of forms of all Echinoderm larvæ, and several well marked types are to be distinguished. It does not immediately appear which of these represents the more primitive type. Considering, however, the fact that the larvæ in which the body skeleton in the first stage forms a basket-structure, and which have in their second stage a posterior transverse rod and more or less developed posterolateral processes, are characteristic — so far as we know — of the Cidarids, Diadematids and Arbaciids, that is to say of the more primitive forms of Echinoids, it can hardly be disputed that we have got to regard this larval type as the more primitive form. Consequently the larval type characteristic of the family Echinidæ s. str., with the elongated, club-shaped body rods, with the recurrent rod rudimentary or absent, and without a posterior transverse rod or posterolateral processes, is a highly specialized and exceptional larval type. It is therefore not at all justifiable to make this larval type represent the Echinoid larvæ in general, as is done in most text-books.

Characteristic of the larval body of the primary type are the vibratile lobes; in the more specialized types, the larvæ of the Echinidæ s. str., and of the Spatangoids these lobes have disappeared, while the Clypeastroid-larvæ have retained them to some degree. A further specialization from the lobes are the epaulets occurring in the higher types of the Regularia.

Both the vibratile lobes and the epaulets evidently serve to increase the floating power of the larva. This object is attained to a still higher degree in several larval forms of Regular Echini and Clypeastroids in which muscles connect the lower ends of the rods of the four main arms, so that these arms become actively movable. These larvæ, when floating, keep the four main arms in a more or less horizontal position, raising them when disturbed. This is not yet an active swimming movement, the muscular apparatus being too simple for performing regularly repeated movements. Only one Echinoid larva appears to be able to swim actively, viz. the remarkable *Echinopluteus transversus*, in which a complicate muscular system is developed, as described above (comp. fig. 31, p. 88), the body-skeleton being most extraordinarily adapted for serving as a support to the muscles.

The four main arms, the postoral and posterodorsal, are the most diversified of the larval arms. They are always rather long, but sometimes (Diadematidæ) attain a very great length. This is carried to an extreme in *Echinopluteus transversus*, as regards the postoral arms, while the posterodorsal arms have disappeared. In some forms these arms are broad and flat, especially so in the *Mespilia*-larva. The anterolateral and preoral arms are very uniform in character throughout the whole class. The postero-

lateral arms, always the most prominent of the Ophiopluteus-arms, are developed as true arms only in Arbaciids and Spatangoids, in the rest of the larvæ they have the shape of broad, earshaped lobes or are entirely lacking.

As regards the skeleton it is a noteworthy fact that the fenestrated rods represent a primary structure, as must be concluded from the fact that this type of rods (always confined to the four main arms) is found in the larvæ of the more primitive forms, simple postoral and posterodorsal rods, upon the whole, occurring only quite exceptionally (*Lytechinus*, *Echinobrissus*) outside the family Echinidæ, the larvæ of which are also otherwise among the most specialized of all Echinoid-larvæ. In some cases (e. g. Temnopleurid larva, species c, fig. 22, p. 61) these rods begin as fenestrated, but terminate as simple rods. In *Evechinus chloroticus* they appear to have only two component rods.

The preoral and anterolateral rods are always simple, more or less spinous, presenting no features of special interest. The dorsal arch also affords little diversity; the long lateral processes from it, supporting lobes of the dorsal side of the body (e. g. Temnopleurid-larva, species c; *Echinometra lucunter*), are very probably homologous with the anterodorsal rods of Spatangoid-larvæ. — The primitive type of the body skeleton is, as stated above, that in which the body rod and recurrent rod unite so as to form a basket structure. This has been given up only in the Temnopleuridæ and Echinidæ, where the body rod has been more or less specially developed, and, exceptionally, in the genus *Lytechinus* of the Toxopneustidæ. A special development of the basket structure is found in the Echinometridæ, where the recurrent rod has become double, and in the Clypeastroids, where the posterior part of the "basket" often develops into a large, fenestrated plate.

The element of the Echinopluteus-skeleton displaying the greatest diversity is the posterior transverse rod, or rather the branches from its ends, the posterolateral rods. These may be simple rods, now very short, now extraordinarily long (Pl. VI, Fig. 1), or branching structures of exquisite form (e. g. Temnopleurid-larva, species a, fig. 20, p. 58; *Heliocidaris tuberculata*, fig. 21, p. 65). While it has completely disappeared in the Clypeastroid-larvæ, it has been further specialized in the Spatangoid-larvæ, carrying the unpaired posterior process, so characteristic of that larval type.

The ventral transverse rods are generally of a very uniform character in the Regularia, whereas in the Clypeastroids and Spatangoids they are somewhat specialized, being reduplicated in the former, often assuming a broad, flat shape in the latter. This apparently unimportant skeletal element has been made the starting point of an extraordinary development in *Echinopluteus transversus*, where it is transformed into a complicate

supporting apparatus for the muscular system. (Comp. e. g. fig. 34, p. 88). It is of considerable interest to trace this unusual development of a quite indifferent element into a structure of the greatest perfection.

Reduced larval forms, so common in the other classes of the Echinoderms, are only rarely met with in Echinoids, in fact were hitherto quite unknown. I have had the good fortune of discovering two most interesting cases of reduction — not counting the *Echinopluteus transversus* —, in which all the arms, excepting the postoral ones, have disappeared. One of them, the larva of *Peronella Lesueuri*, is still recognizable as an Echinopluteus, the postoral (and sometimes also the posterodorsal) arms still remaining, and a larval skeleton, rudimentary but still distinctly referable to the normal skeletal type, being developed. The vibratile band has disappeared, the larva being covered only by a uniform ciliation; only in some exceptional cases a rudimentary band is developed (p. 116; fig. 48).

In the other case, *Heliocidaris erythrogramma*, the reduction has gone so far that there is not the slightest trace of the Pluteus-shape left. This larva recalls the barrel-shaped larvæ of Comatulids and Dendrochirotes, but differs markedly from them in having only one, not very distinctly differentiated ciliated ring.

The existence in Echinoid-larvæ of a pupa-stage corresponding to that occurring in Holothurians and Ophiurans has been emphasized by Caswell Grave, who has observed transverse ciliated rings on the newly metamorphosed sea-urchin of *Mellita testudinata*. (Op. cit. Fig. 10, p. 178). I have not made any corresponding observations and shall therefore refrain from commenting on the possible existence in Echinoids in general of such a pupa-stage. Whether the *Heliocidaris erythrogramma*-larva is to be regarded as an indication in that direction I shall leave undecided.

The few Crinoid-larvæ known being all of the vermiform type there is no reason to mention them in the present connection. With the greatest expectations we may look forwards to the future discovery of some typical pelagic Crinoid-larva; the study of its relations to the other four main types of Echinoderm-larvæ will be of extreme interest. The existence of such a pelagic Pelmatozoan-larva would seem almost beyond doubt, though possibly not in any of the recent Crinoids. But these latter represent — in spite of the enormous development of the Comatulid-type — only a diminutive fraction of the whole group of the Pelmatozoa. It would hardly seem too bold to fancy that at least some of the fossil Pelmatozoans, especially of the numerous Cystideans, had truly pelagic larvæ. It is very sad that we have no hope of learning anything about them, it being in the highest degree unlikely that such larvæ should have been preserved in a fossil state. Fritsch, it is true, has described an organism



from the Lower Silurian of Bohemia, which he thinks must be a fossil Crinoid-larva ("ein Pluteus eines Crinoiden"), the "*Furca bohémica*" of Barrande<sup>1)</sup>. But provided first that it be an Echinoderm, anybody who has the slightest knowledge of Echinoderm-larvæ will see at a glance that it is quite absurd to speak of a "larva" in a case like this, where a single or double series of distinct marginal plates is represented along the whole border of the animal. But, moreover, it is certainly no Echinoderm at all. Professor O. Jaekel, with whom I have discussed this matter, informs me that he knows the "*Furca bohémica*" quite well, and states that the representation which Fritsch has given of it is quite erroneous. In fact, Professor Jaekel does not hesitate in declaring it to be identical with the organism from the Middle Cambrian (Stephen formation) of British Columbia which Walcott has described<sup>2)</sup> under the name of *Marella splendens*, and which is a Crustacean, probably allied to the Trilobites.

As regards the anatomical structure of the Echinoderm-larvæ (— leaving the reduced, barrel-shaped forms out of consideration here —) attention may be called to the fact that the ventral depression of the body, in which the mouth lies, the oral area, generally continues some way down below the upper edge of the anal area, thus forming a cavity, the lower limit of which is mostly very distinctly seen as a line passing across the anal area at about the level of the lower end of the esophagus. It is sometimes very large, as in *Ophiopluteus serratus (bimaculatus)*, sometimes also of a more complicate shape, as in the larva of *Colobocentrotus atratus*. This "suboral cavity", as I have termed it, was well figured and described by Joh. Müller in his Memoir "Über die Ophiurenlarven d. Adriatischen Meeres", p. 1, Taf. I, Fig. 1, and also Metschnikoff (Op. cit.) has carefully studied this cavity, the "subumbrella" as he names it, in the same larva, where it plays an important part during the process of metamorphosis. Also in a Spatangoid-larva he has noticed it (Taf. VIII, Fig. 12). The same structure was observed, but apparently not understood, by MacBride in the larva of *Echinocardium cordatum*; he only mentions it as "two large cavities", one on each side in "the web of skin connecting the post-oral arms." — This cavity has some connection with the question about the origin of the "amnion" of Echinoid-larvæ, and accordingly some morphological interest is attached to it.

In the epidermis of the sunk oral area is found a pair of nerve-streaks,

<sup>1)</sup> A. Fritsch. Über eine Echinodermenlarve aus dem Untersilur Böhmens. Zool. Anz. 33. 1909. p. 797.

<sup>2)</sup> Ch. D. Walcott. Cambrian Geology and Paleontology. II. No. 6. Middle Cambrian Branchiopoda, Malacostraca, Trilobita, and Merostomata. Smiths. Miscell. Coll. Vol. 57. 1912. p. 192. Pl. 25—26.

which appears to be a structure characteristic of *Auriculariæ* and *Ophioplutei*. It was discovered by Metschnikoff and made the object of a closer study especially by Semon in his paper on "Die Entwicklung der *Synapta digitata*"<sup>1)</sup>; furthermore Chun described the nervous system of *Auricularia nudibranchiata*, while it was observed by myself in *Auricularia antarctica*, all these forms agreeing very closely in regard to the shape and position of this structure. Quite recently MacBride, (Echinoderm larvæ of the British Antarctic ("Terra Nova") Expedition) gives a representation of the nervous system of *Auricularia antarctica* (Pl. I, Figs. 1—2) quite different from that given by me (Echinodermen-Larven d. deutschen Südpolar Expedition p. 81, Taf. X, Fig. 1; Taf. XI, Fig. 2). There is, however, hardly any doubt that what MacBride here represents as the larval nervous system is the edge of the atrium, which continues some way on to the oral area as a streak of thickened skin (comp. my memoir quoted above, p. 79, Taf. IX, Fig. 1), such as it was also found by Chun in *Auricularia nudibranchiata*. I do not want to deny the possibility that this structure may be of a nervous character, but that has not yet been proved, and, in any case, it is not the homologue of the nervous system of *Auricularias* in general; this latter structure is found more laterally in the oral area and is not in direct connection with the mouth<sup>2)</sup>.

In the Ophiurid-larvæ the nervous system is essentially like that of the *Auricularia*, forming a band across the oral area to each side of the mouth; for a more detailed representation of this structure in Ophiurid-larvæ I may refer to my paper, "Notes on the development of some Scandinavian Echinoderms" p. 158—160. — In Echinoid-larvæ the nervous system is

<sup>1)</sup> Jen. Zeitschr. f. Naturwiss. XXII.

<sup>2)</sup> I may take the opportunity here to object to a statement by MacBride concerning my representation of the coelomic structures of *Auricularia antarctica*. On describing the stage represented in his Fig. 2 MacBride says (Op. cit. p. 87) that "this stage corresponds with that represented in text-fig. 1 in Mortensen's latest paper, but M. has quite misunderstood it. He overlooked the rudiment of the posterior coelom altogether, and has figured a sac entirely detached from the anterior coelom as the posterior enterocoel. This sac, which lies above the junction of the stomach and intestine, has nothing to do with the coelom, but is one of the intestinal pouches characteristic of *Auricularia antarctica*." It is true that I have not observed the developmental stages of the posterior coelom (— on reexamining the material still at my disposal I do not find any such stages represented and I feel confident, therefore, in saying that I have not overlooked these stages, but they were not present in my material —). It is possible that the vesicle which I represented as the posterior coelom really is the intestinal pouch (— which I have, otherwise, not at all overlooked, stating, on p. 80, that the rectum "schwillt mehr oder weniger plötzlich an und kann bisweilen den unteren Teil des Magens ganz überdecken" —). But, anyhow, I have at least not misunderstood the anterior coelom and the hydrocoel. It must certainly be acknowledged that the representation of the internal structures of *Auric. antarctica*, given by me, means a very considerable progress beyond that given by MacBride in his first description of this larva (National Antarctic Expedition. Natural History. Vol. VI. Echinoderma. 1912), and I might perhaps suggest that the author of that description was not quite right in giving as his only comment on my representation of that larva that I had "quite misunderstood" its coelomic structures.

not of quite the same kind as in *Auriculariæ* and *Echinoplutei*. In the larva of *Echinocyamus pusillus* I have found a simicircular streak in the epidermis of the oral region, which is evidently a nervous structure (Op. cit. p. 157, fig. 5); the same structure appears to exist also in some other Clypeastroid-larvæ, and also in the larva of *Echinometra lucunter* I have observed something evidently corresponding to it (Pl. XII, Fig. 1). But it does not appear as a rule to exist in all Echinoid-larvæ, but rather as an exception. On the other hand MacBride has shown an apical nervous system of more ganglionic structure to exist in the larvæ of *Echinus esculentus* and *Echinocardium cordatum* (for references, see my paper quoted above). It will be an object of considerable interest to study the relation between these two nervous systems in Echinoid-larvæ, how far they are distributed within this larval type and whether they may occur together in one and the same larva or exclude one another.

It is a very remarkable fact that the Asteroid-larvæ do not appear to possess anything corresponding to the nervous system of the three other larval types. (Also the Crinoid-larvæ have a fairly well developed nervous system, but that is, of course, of quite another type than that of the pelagic Echinoderm-larvæ). Only a sub-epidermal network of nerve fibres and neuro-muscular cells have been observed by Gemmill in the larvæ of *Asterias rubens* and *Porania pulvillus*. This fact tends to indicate that the Bipinnaria represents a more primitive type than the other larvæ.

The intestinal organs are of a very uniform structure throughout the whole of the Echinoderm-larvæ; only a few rather unessential points may be mentioned here, viz. the existence of a small distinct intestine in the larva of *Colobocentrotus atratus* and of a kind of gizzard-like structure in the larva of *Arachnoides placenta* and, less distinctly, in some other Clypeastroid-larvæ. The main interest as to the internal structures of Echinoderm-larvæ is attached to the enterocoel and hydrocoel, and their transformations during the growth and metamorphosis of the larva. Of this, however, I have only made very few observations, it being out of the plan of the present work to pay special attention to these structures. That would have meant such an increase in the extent of the work that it was out of question merely for this reason, not to mention the time that would have been required for such a study. But, of course, it would be of the greatest interest to study these developmental processes in so many different forms of the typical larvæ as possible, this being the only way to ascertain which features are of general validity and which of only more special value. — In the present work it is only the more exceptional forms, with abbreviated development, *Peronella Lesueurii*, *Heliocidaris erythrogramma* and *Ophionereis squamulosa*, which have been made the object of

a somewhat more detailed study as regards the development and gradual transformation of the inner structures. The results acquired from the study of these objects, though they cannot claim to be of more general value, are in themselves of very great interest and throw important light on several problems connected with the developmental history of Echinoderms.

The most interesting of the facts discovered by the study of the said forms with abbreviated development would appear to be that of the amnion developing from the pharynx in *Peronella Lesueuri*, while otherwise it develops as an invagination from the ectoderm on the left side of the larva, above the hydrocoel. (In *Helicoidaris erythrogramma* it could not be decided whether it likewise develops on the left side, there being apparently no means of identifying the right and the left sides in this perfectly cylindrical larva). This may perhaps give some indication as to the way in which the amnion of Echinoid-larvæ originated. MacBride has come to the conclusion that the amniotic cavity of the Echinopluteus may be interpreted as a portion of the stomodæum which is formed separately from the rest of it<sup>1)</sup>, because in the metamorphosing larva of *Ophiolthrix fragilis* he has found the primary tubefeet protruding into the stomodæum. The fact that the amnion of *Peronella Lesueuri* does originate as an outgrowth from the pharynx would seem to lend an emphatic support to MacBride's theory. Still I would not take it as having been definitely proved as yet by these facts. *Peronella Lesueuri* is a very highly specialized type; may we then really rely upon this remarkable development of the amnion in the much reduced larva as meaning a reversion to the primitive mode of development? It is perhaps not quite safe to draw this conclusion as yet. If other similar cases were found, the conclusion would be very considerably strengthened; but this isolated, evidently very specialized case does not seem to me to afford sufficient proof. Neither does the *Ophiolthrix*-larva appear to me to be a sufficient proof of the theory. It is the only Ophiuran with a typical pelagic larva the metamorphosis of which has been adequately studied as yet. But the little we know about the metamorphosis of other Ophioplutei does not point towards the stomodæum as having generally the function of an amnion in Ophiurid-larvæ. In *Ophiopluteus bimaculatus*, so carefully studied by Joh. Müller<sup>2)</sup> and Metschnikoff<sup>3)</sup> — though not by means of sections, of course — it appears that the suboral cavity has got the function of an amniotic

<sup>1)</sup> MacBride. Textbook of Embryology. I. Invertebrata. 1914. p. 522.

<sup>2)</sup> Joh. Müller. Über die Ophiurenlarven d. Adriatischen Meeres (V. Abhandl. 1852), Taf. II—III.

<sup>3)</sup> E. Metschnikoff. Studien über die Entw. d. Echinod. u. Nemertinen. Taf. VI—VII.

cavity. Further it is a fact that the growth of the hydrocoel in Ophiurid-larvæ takes place in different ways. In the larva of *Amphiura filiformis* (*Ophiopluteus mancus*) e. g. it grows upwards over the mouth, the closing of the hydrocoel ring taking place at the lower end of the pharynx; in the larva of *Ophiura albida* (*Ophiopluteus paradoxus*) the growth proceeds in the opposite direction, the closure of the hydrocoel ring taking place above the mouth. (Comp. Pl. III, Fig. 4; Pl. IV, Fig. 28 and Pl. VI, Fig. 40 of Chadwick's Memoir on the Echinoderm-larvæ). The larva of *Ophiothrix fragilis* appears to be about intermediate between these two forms, as regards the formation of the hydrocoel ring. These facts at any rate show this much, that we must be very cautious in drawing such important conclusions from facts derived from the study of only one single form. — With this I do not mean to deny the possibility that MacBride's theory of the origin of the amnion of Echinoplutei may be right. On the contrary, it appeals to me as a very reasonable suggestion. Also a comparison with the vestibulum of Crinoid-larvæ would seem to lend support to this theory.

The fact that the hydropore is not formed in the larva of *Peronella Lesueurii* nor apparently in *Heliocidaris erythrogramma* until at a rather advanced stage of metamorphosis, may be recalled here. I would, however, not regard this fact as being of greater morphological importance, it being probably a modification caused by the exceptional conditions obtaining in these larvæ. In the same way I would not regard the unusual way in which the enterocoel develops in these forms as of essential importance from the point of view of comparative morphology.

On discussing the question of the original type of the Echinoderm-larvæ Caswell Grave<sup>1)</sup> comes to the conclusion that the larvæ with transverse ciliated rings (*Antedon*, *Cucumaria*) represent the primitive condition from which the other larvæ have been specialized "and carried far out of the path of phylogeny, as a result of their independent life. To this type of development the specialized larvæ tend to return at the time when their free-swimming life is given up." He makes an attempt to show, how the ciliated rings were useful to the free-swimming animal not only as organs of locomotion, but also as organs of feeding (comp. his textfigure II. b.). The attempt does not appeal to me as very successful, apart from the fact that it could hardly always have been, as he states, the two anterior rings that were lost when fixation on the bottom took place. It is true that larvæ of this type occur in various groups of the Echinoderms, being even apparently the rule in Comatulids and Dendrochirotes. The fact

<sup>1)</sup> Caswell Grave. On the occurrence among Echinoderms of larvæ with cilia arranged in transverse rings, with a suggestion as to their significance. Biol. Bull. V. 1903. p. 183.

that *Heliocidaris erythrogramma* has such a larva, although with only one ciliated band, might be adduced here as proving the occurrence of this larval type also in Echinoids, where it was otherwise unknown. But it is a very strong objection that in the whole class of the Asteroidea not one case of larvæ with ciliated rings is known, neither is anything corresponding to the pupa-stage known in this class, which is otherwise one of the more primitive of Echinoderms, at any rate more primitive than Ophiuroids and Echinoids. Another important fact is this, that in all the cases where larvæ with ciliated rings occur, the eggs are large and yolk-laden. This evidently means that the larvæ with ciliated rings, developing from such eggs, are modified in accordance with the fact that they have food enough in store in the yolk and therefore need not trouble with catching food. The ciliated rings of these larvæ decidedly would serve very badly as food-gatherers. If that type of larvæ were really the primitive form we should have the remarkable fact here of an organism having arisen evidently unable to subsist by its own means. The fact that the stage with the ciliated rings is never indicated in the beginning of the larval development, but always at its end in those forms which have larvæ of the typical pelagic shape, is also very hard to understand on the assumption that the form with the ciliated rings is the more primitive. Also the fact that in the viviparous *Ophionotus hexactis* the embryos develop into larvæ corresponding exactly to the generalized, primitive type of Echinoderm-larvæ, is of considerable importance in this connection: this larva decidedly needs no special adaptation to pelagic life, and it is hard to see why it should adopt this form instead of that with the ciliated rings, were it not of phylogenetic importance.

In my opinion there is then no doubt that the larva with a simple circumoral band, as it is found in the younger stages of all the four main larval types of Echinoderms, is the primitive form, and that it represents a true phylogenetic stage in the ancestry of Echinoderms — that is to say, the larva in its simplest type, the *Dipleurula*. Of course, the larvæ of recent Echinoderms, with their more or less highly specialized characters, do not represent ancestral types of the various classes of the Echinoderms, Bipinnaria of the Asterooids, Echinopluteus of the Echinoids etc. They represent special adaptations of the original pelagic ancestral form, having been modified along with the adults, so as to form groups corresponding with the natural groups of the adults, the result being that there is a larval classification exactly parallel with that of the adults. But the primitive type, the *Dipleurula* must, I have no doubt, represent the organism from which the whole of the Echinoderm stem developed.

Neither time nor space permits me to enter on a detailed discussion of the phylogeny of Echinoderms. I must content myself with stating my perfect agreement with Bather's views on this matter <sup>1)</sup>. (— I would only call attention to the difficulty pointed out already by Bury <sup>2)</sup> that no stage of fixation occurs in the embryogeny of Echinoderms, excepting the Crinoids; the fixation of Brachiolariae by means of the sucking disk is, as hinted at by Bury, evidently a secondary adaptation, which hardly counts in this connection —). Consequently I am decidedly opposed to the theories of the ancestry of Echinoderms more recently set forth by A. H. Clark <sup>3)</sup> and J. E. V. Boas <sup>4)</sup> — not to mention that of Simroth <sup>5)</sup>. In my memoir on the development of Crinoids I have objected to some few points in the theory of Clark — who maintains the barnacles to be the ancestors of Echinoderms; but otherwise I do not think this theory more worthy of a refutation than that of Simroth, deriving the Echinoderms from *Myzostoma*! My few counter-remarks to some of the interpretations of Crinoid morphology, set forth — rather emphatically — by A. H. Clark on the base of his theory, are meant as a tribute called forth by my admiration for the eminent specialist in Crinoids, not as a wish to refute his theory, which seems to me a superfluous task. Both the said theories, besides bearing evidence of most unusual conceptions of morphology, are at variance with the fundamental principle of phylogeny, that evolution goes from the lower towards the higher organization, not the inverse way (due allowance being made, of course, for the rarer cases of regressive development, as e. g. the Acoela, which is, however, only an apparent exception to the rule).

This objection does, of course, not apply to the theory of Boas, that the Echinoderms have developed from some fixed form of Coelenterates; but otherwise this theory is, in my opinion, no more acceptable than are those of A. H. Clark and Simroth. As stated above, I cannot enter on a detailed discussion of the reasons given for this theory, but must confine myself to making a few objections, which, however, would appear to suffice for proving the untenability of the theory.

One of the main facts adduced by Boas as support for his theory is this that in the Crinoids — and, mind well, not the more primitive Pelmatozoa, the Cystids, the simpler forms of which, at least, do not show any external signs of a radiate structure <sup>6)</sup> — the water-vascular system re-

<sup>1)</sup> F. A. Bather. Echinoderma, in Ray Lankester's Treatise on Zoology, Part III, 1900.

<sup>2)</sup> H. Bury. The metamorphosis of Echinoderms. Quart. Journ. Micr. Sc. 38, 1895, p. 93.

<sup>3)</sup> A. H. Clark. A Monograph of Existing Crinoids, I. U. S. Nat. Mus. Bull. 82, 1915.

<sup>4)</sup> J. E. V. Boas. Zur Auffassung der Verwandtschafts-Verhältnisse der Tiere, I, 1917.

<sup>5)</sup> H. Simroth. Über den Ursprung der Echinodermen. Verh. d. Deutsch. Zool. Ges. 1904.

<sup>6)</sup> The radiate structure of Echinoderms is regarded as requiring their derivation from "einer exquisit radiär gebauten Abteilung festsitzender Tiere" (Op. cit. p. 21).

mains in open connection with the body cavity throughout life, which is taken as a proof that the Crinoids are the most primitive of all Echinoderms<sup>1)</sup>. It would appear that the author has entirely overlooked the fact, established beyond any doubt, especially through Seeliger's researches<sup>2)</sup>, (— his results being fully confirmed by my own researches —) that the connection between the water-vascular system and the body cavity in *Antedon* is only a secondary character, arising at a rather late stage of development (in the Pentacrinoid-stage). Accordingly this is no primitive feature and cannot afford any proof of relationship with the Coelenterates.

The Crinoid-larva is regarded as the most primitive of Echinoderm-larvæ, "nähert sich viel mehr dem Coelenteraten-Larven-Typus, ist jedenfalls durchaus anderer Gestalt als die der anderen Echinodermen, und da diese Larve der ursprünglichsten Echinodermen-Abteilung angehört, hat sie bei der Beurteilung der Verwandtschaftsbeziehungen ein grösseres Interesse als die andere, aus deren Bau sich nicht auf die Abstammung der Echinodermen Schlüsse ziehen lassen". The typical pelagic, bilateral larval form "kann ich (Boas) natürlich nur als eine ganz sekundäre beurteilen. Dieselbe ist bekanntlich . . . noch nicht bei den Crinoiden ausgebildet, deren Larve mit fünf Wimperringen umzingelt ist, von denen vier allen radiären Anforderungen genügen." (Op. cit. p. 23). — I may refer to the remarks given above in criticism of the view, also expressed by Grave, that the larva with the ciliated rings is the primitive larval form of Echinoderms. Especially the structure of the *Antedon*-larva is anything but primitive, but only intelligible as a special adaptation of the simpler type of the pelagic larvæ to the conditions of the yolky eggs, as it is found likewise in other barrel-shaped larvæ developing from eggs with a rich content of yolk. On the contrary, as stated above (p. 232), there is every reason to suppose that there was also a typical bilateral larval form at least in some of the numerous fossil Pelmatozoa, should it even be proved that none of the few surviving types have such a larva. The rather bold assertion that no conclusions as regards the ancestry of Echinoderms can be drawn from the structure of the typical larvæ does not do away with the fact that all these larvæ pass through the "Dipleurula"-stage, that is to say, begin as a simple, bilateral, wormshaped organism with a segmented body cavity consisting of at least two, probably three segments, and pro-

<sup>1)</sup> From the Crinoids the Asteroids are derived and from the latter again the Ophiurids and Echinoids, the Holothurians having arisen from the Echinoids. Without entering on a discussion of this view of the genic interrelations of the classes of recent Echinoderms I would merely express my astonishment at a fancy bold enough to conceive the derivation of Asteroids from the Crinoids.

<sup>2)</sup> O. Seeliger, Studien zur Entwicklungsgeschichte der Crinoiden. Zool. Jahrb. Abt. f. Anat. u. Ontog. VI. 1893.



vided with a simple circumoral ciliated band. This fact is hardly intelligible except on the assumption that it represents the original larval type and an ancestral stage in the evolution of the Echinoderm stem. If there is any connection between Coelenterates and Echinoderms, the vestiges of it must be sought for in the structure of the *Dipleurula*, not in the Crinoids. But I fail to see how this could be found. Possibly the Ctenophora might have given rise to the *Dipleurula* —but then these latter are, in my opinion, no Coelenterates.

It is an established fact that some animal forms have a different mode of development under different biological conditions. As typical instances may be named the shrimp *Palæmonetes varians*, which has much larger eggs in Southern Europe than in Northern Europe, a corresponding rather considerable difference obtaining in the larval development, and *Musca corvina* which is recorded by Portchinski to be oviparous in Northern Russia, while in Southern Russia it is viviparous in summertime, oviparous in spring<sup>1</sup>). Such a remarkable diversity of development, for which Giard has created the name Poicilogony, was maintained by this author<sup>2</sup>) to occur also among Echinoderms, *Ophiothrix fragilis* being especially named as an instance of poicilogony. This species is stated to develop "suivant les conditions éthologiques . . . tantôt par des *Pluteus* normaux (comme dans la Méditerranée), tantôt par des *Pluteus* imparfaits tels que ceux étudiés par Apostolidès (à Roscoff), tantôt même par des embryons très condensés, incapables de nager et qui donnent une Ophiure presque sans métamorphoses (à Vimereux etc.)." (Op. cit. p. 240). This would appear to apply also to a number of other Ophiurids of the North Atlantic, since he states in a previous paper<sup>3</sup>), likewise reproduced in the "Oeuvres diverses" I. p. 509, that "presque toutes les Ophiures que j'ai observées dans la Manche sont . . . vivipares. Je citerai entre autres: l'*Ophiothrix fragilis* et l'*Ophiocoma neglecta* que j'ai plus particulièrement étudiées au point de vue de la reproduction". . . . "A un certain moment de l'année, on trouve des embryons dans toutes les Ophiures que l'on ouvre indistinctement (excepté celles qui sont infestées par les Orthonectida)."

As I have shown in my paper "On Hermaphroditism in viviparous Ophiurids" (Acta Zool. I. 1920, p. 7—8) this statement of these Ophiurids being at times of the year viviparous, while at other times they have

<sup>1</sup>) J. E. V. Boas. Kleinere carcinologische Mittheilungen. Zool. Jahrb. Abt. f. Syst. 1890.

<sup>2</sup>) A. Giard. La Poicilogonie. Congrès Internat. de Zool. Bern. 1904. Bull. Scientif. Dép. du Nord de France. 39. 1905. — Reprinted in Oeuvres diverses. I. Biologie Générale. 1911. p. 420.

<sup>3</sup>) A. Giard. Particularités de Reproduction de certains Échinodermes en Rapport avec l'Éthologie de ces animaux. Bull. Scientif. Dép. du Nord de France. IX. 1878. p. 296.

pelagic larvæ, is quite without foundation, resting, no doubt, on misinterpretations and being due to most imperfect methods of research. (The statement of the same author that these Ophiurids also are hermaphroditic is equally phantastic, as I have shown in the paper quoted above). — As for his statement that in *Ophiothrix* the larvæ now develop into the typical pluteus shape, now develop through a very imperfect larva, it rests on the researches of Apostolidès<sup>1</sup>), who expressly says (Op. cit. p. 76) that the nine tenths of the larvæ reared by him did not develop into the true larval shape but showed “une forme plus ou moins arrondie, qui continue à vivre, et dans laquelle nous avons suivi le développement complet de l’animal”. Although he says to have “des raisons de prétendre que, jusqu’à la fin du développement de l’animal, il continuera à en être ainsi” it is evident that he has simply failed to rear the larvæ beyond the stage with the posterolateral arms, the larvæ dying when they had reached this stage — in fact, he states himself that “cette forme singulière ne continuera plus à s’augmenter, mais peu à peu à se dégrader, jusqu’au moment de sa disparition.”

While thus we need not trouble with this imperfect larva with only two arms, the direct statement of Apostolidès that he has followed the complete development of the still simpler embryos cannot simply be done away with. It does, however, seem very hard to believe it to be correct — and he does not give a single figure to accompany these remarkable observations. That author moreover being anything but a first rate authority it is impossible simply to endorse his statement. It is a fact that Giard’s statement of these Ophiurids as being at times of the year viviparous, rests on misunderstood observations; it is therefore hardly too bold to suggest that Apostolidès’ statement likewise may rest on misapprehension. In any case, we cannot accept the statement, until it has been confirmed by renewed researches by a competent investigator.

It would appear that Apostolidès (Op. cit. p. 77) has also observed those incomplete larval forms in the free. I would, however, suggest that it may have been the rudimentary larval forms, *Ophiopluteus Metschnikoffi* or *O. Claparèdei*, which he has observed. But that these larvæ should also belong to *Ophiothrix*, like the typical *Ophiopluteus*, is exceedingly hard to believe. The whole question, however, very much needs reinvestigation.

As a further instance of poecilogony in Echinoderms Giard mentions *Asterina* and *Asterias*. “*Asterina cephea* habitant les mers chaudes, abandonne au hasard de la vie pélagique des oeufs qui doivent donner naissance à des larves nageuses . . . *A. gibbosa* n’est donc qu’une forme poecilogé-

<sup>1</sup>) N. Apostolidès. Anatomie et développement des Ophiures. Arch. Zool. expér. & génér. N. 1881.

nique de l'*A. cephea*. De même *Asterias Mülleri* n'est sans doute qu'une variété poecilogonique septentrionale du vulgaire *Asterias glacialis* des côtes de France." In these two cases there is, of course, no doubt as to the correctness of the observations. But the said forms are far from being only "poicilogenetic varieties" of one and the same species of *Asterina* or *Asterias*; as anybody having some systematic knowledge of these great "genera" of starfishes will agree, they are very well separated species which, on modern classification, should at least be referred to different subgenera.

In spite of the bad luck of the instances of poicilogeny among Echinoderms produced by Giard I do not pretend to maintain that poicilogeny does not exist within this animal group. In fact, we have an almost typical instance in *Asterias Mülleri*—*groenlandica*. These two forms are so closely related that they are hardly distinguishable and appear to be merely varieties of the same species. But while *A. Mülleri*, as already observed by M. Sars, hatches its eggs in a brooding cavity made by the raised arms, *A. groenlandica*, according to the beautiful observations of I. Lieberkind<sup>1)</sup> hatches its eggs within the stomach. It is unknown as yet whether there is any difference in the embryonal development of these two forms; but at any rate the breeding habits of these two forms are remarkably different.

The cases of nearly related species showing quite a different mode of development, although not to be termed directly poicilogeny, are of very considerable interest as related phenomena. Such cases were known hitherto only in the genus *Asterias*, but have been proved now to exist also within the genus *Asterina* (s. lat.) and among the sea-urchins in the genus *Helioedaris*, where *H. tuberculata* has a typical pelagic larva, *H. erythrogramma* a barrel-shaped larva showing no likeness whatever to a Pluteus. (It must be emphasized that there can be no doubt that the two said sea-urchins are really nearly related species, decidedly belonging to the same genus). In a good many cases of nearly related species one has pelagic larvæ, while the other is viviparous (*Echinocyamus pusillus* and *nutrix*, several Ophiurids). Upon the whole more extended researches will be sure to disclose many cases of dissimilar development in nearly related forms. In this connection mention must also be made of the interesting observation by Nachtsheim<sup>2)</sup> that in *Echinaster sepositus* the eggs may differ very conspicuously in size; the development, however, is the same in both larger and smaller eggs, and the larvæ developing from them differ only in size.

<sup>1)</sup> I. Lieberkind. On a starfish (*Asterias groenlandica*) which hatches its young in its stomach. Vid. Medd. D. Nat. Foren. 72. 1921.

<sup>2)</sup> H. Nachtsheim. Über die Entwicklung von *Echinaster sepositus* (Gray). Zool. Anz. XLIV. 1911. p. 601.

The observations set forth above (p. 148) tending to prove the existence of a case of true metagenesis in an Ophiuroid-larva, *Ophiopluteus opulentus*, may be recalled here. Although this is certainly quite an isolated case in Echinoderms, considerable interest is attached to it both from a morphological and a biological point of view.

The observations on the development of the various forms studied in this work convey a good impression of the great diversity obtaining, as regards the length of the time required for the development. Although I have not taken care in all cases to notice the exact time at which each stage of development was reached, still a good deal of information may be gathered from what has been noticed. It may be practical to give the facts in a tabular form.

			Young larva		Metamorphosis	
	Blastula	Gastrula	I. stage	II. stage	beginning	completed
<i>Diadema antillarum</i> .....	..	..	2 days	—	..	..
<i>Astropyga pulvinata</i> .....	..	..	1 —	..	..	..
<i>Tripneustes escutentus</i> .....	..	..	1(2) —	12 days	22 days	..
<i>Lytechinus variegatus</i> .....	6 hours	..	1 —	5 —	13 —	..
— <i>anamesus</i> .....	20 - (?less)	24 hours	2—3 —	7 —	..	..
— <i>panamensis</i> .....	..	..	1 —	..	..	..
<i>Toxopneustes pileolus</i> .....	..	24 —	2 —	..	..	..
<i>Strongylocentrotus pulcherrimus</i>	..	24 —	2 —	21 —	..	..
— <i>franciscanus</i> .....	..	24 —	2 —	..	..	..
<i>Tennopleurus toreumaticus</i> ...	..	..	22 hours	..	..	..
<i>Evechinus chloroticus</i> .....	16 hours	24 —	3 days	14 —	ca. 35 —	..
<i>Heliocidaris tuberculata</i> .....	20—	24 —	2 —	11 —	35 —	..
— <i>erythrogramma</i> ...	..	18 —	..	..	..	4—5 days
<i>Echinometra lucunter</i> .....	..	..	2 —	4 —	..	19 —
— <i>oblonga</i> .....	..	16 —	2 —	..	..	..
<i>Colobocentrotus atratus</i> .....	..	24 —	2 —	..	..	..
<i>Clypeaster japonicus</i> .....	..	14 —	3 —	11 —	..	..
<i>Arachnoides placenta</i> .....	..	16 —	ca. 1½—	2½—	3½—	..
<i>Echinarachnius excentricus</i> ...	..	..	2 —	..	8 —	..
<i>Encope micropora</i> .....	..	..	12 hours	4 —	14 —	..
<i>Mellita 6-perforata</i> .....	..	6 —	1 day	..	5 —	..
<i>Astriclypeus Manni</i> .....	..	14 —	..	3 —	6 —	13 —
<i>Peronella Lesucuri</i> .....	5—	12 —	18—20 hours	..	..	3—4 —
<i>Echinobrissus recens</i> .....	..	24 —	2 days	..	ca. 15 —	..
<i>Brissus Agassizi</i> .....	..	14 —	..	7 —	..	..
<i>Meoma grandis</i> .....	..	14 —	20 hours	..	..	..
<i>Ophiolhrix angulata</i> .....	..	18 —	1 day	..	40—45 hours	..
<i>Ophionereis squamulosa</i> .....	..	15 —	..	..	..	ca. 6 —
<i>Astropecten scoparius</i> .....	..	..	7 days (less?)	..	19—21 days	..
<i>Astrina pectinifera</i> .....	..	16 —	2 —	..	18 —	..
<i>Gymnasteria carinifera</i> .....	ca. 24 hours	2 days	5 —	..	..	..
<i>Ophidiaster Guildingii</i> .....	..	..	4 —	..	..	..
<i>Pisaster ochraceus</i> .....	24—	2 —	4 —	..	..	..
<i>Euasterias Troscheli</i> .....	24—	2—3 —	4 —	..	..	..
<i>Stichopus californicus</i> .....	24—	2 —	..	6 —	..	..

It is evident that the amount of yolk substance contained in the egg has an important bearing on the length of time required for the development. When food enough is contained in the egg for sustaining the embryo until metamorphosis is completed, the self-feeding larval stage is done away with as unnecessary and the development thus considerably shortened, e. g. *Heliocidaris erythrogramma*, *Peronella Lesueuri*, *Ophionereis squamulosa* and many other forms with abbreviated development, not mentioned in the present memoir. That also temperature has an important bearing on the time required for the development is an established fact: interesting results are sure to be obtained on studying the development of widely distributed forms in various places, where conditions are different (tropical, extratropical). The few facts known, e. g. of the development of *Peronella Lesueuri* in tropical seas, as compared with the observations given above, tend to show that the development proceeds at a conspicuously quicker rate at the higher temperature of the tropics than in the cooler climate of extratropical regions.

The said factors, yolk and temperature, cannot, however, account for all the differences. Thus e. g. of *Tripneustes esculentus* and *Lytechinus variegatus*, both living in quite shallow water in the tropics and both having small eggs, poor in yolk substance, the former takes three weeks to reach the stage of beginning metamorphosis, the latter only 13 days; or *Encope micropora* assuming the shape of a young *Pluteus* already at the age of 12 hours, while *Mellita 6-perforata*, living under similar conditions requires the double time for reaching that stage. But altogether too little is known as yet for giving a reasonable base for an attempt to find out the causes of these differences. The observations recorded here may only serve to prove that here is a problem worth studying.

In a very interesting paper on "Sea-temperature, breeding and distribution in marine animals"<sup>1)</sup> I. H. Orton comes to the result that "in those parts of the sea where temperature conditions are constant or nearly constant, and where biological conditions do not vary much, marine animals will breed continuously." He concludes that this will be the case in the tropics, founding on the statement of Semper ("Animal life", p. 110) that in the Philippines he could not detect a single species (of Invertebrates) of which he could not "at all seasons find fully grown specimens, young ones and freshly deposited eggs." This phenomenon, Orton states, "appears to be generally recognized for the tropics, but it would appear that definite systematic work on the breeding and rate of growth throughout the year

<sup>1)</sup> Journ. Mar. Biol. Assoc. United Kingdom. XII. 1920.

of a large number of animals in the tropics would still be very useful." (Op. cit. p. 355).

With the latter sentence I most heartily agree, but otherwise I must decidedly object to the statement that in the tropical seas the animals are continuously breeding — at least as regards the Echinoderms, and I cannot but wonder how Semper came to the above result. It is true that I have made only few observations, as regards this point, during my stay at the Philippines; but at any rate I found that the large *Synapta Beselii* had no ripe sexual products in February—March at Zamboanga. And it is certainly not to be assumed that the animals behave otherwise at the Philippines than elsewhere in the tropics, as regards their breeding. My observations decidedly prove that at least several of the littoral Echinoderms do not breed continuously. Thus e. g. I never found the opportunity for studying the development of *Diaulema*, until I came to Tobago, B. W. I. and there found *D. antillarum* to have ripe sexual products in the end of March; and when, about a week later on, I wanted to start a new larval culture it was impossible to find one specimen containing ripe sexual products, all were quite empty. A similar experience I had with *Echinometra van Brunti*, *Brissus obesus*, *Stichopus Kefersteini*, and in several cases I had, to my great annoyance, to give up any hope of obtaining a larval culture, because the breeding season did not coincide with my stay (e. g. *Echinoneus*). — On the other hand, I have some observations tending to show that in the tropical seas Echinoderms (some forms, at least) have more than one breeding season in the year. But for proving this definitely observations must be continued through a longer period, a stay of a few months being, of course, insufficient for such a task.

I would recall here that I have been able to prove (Die Echinoiden d. Deutschen Südpolar-Expedition, p. 71)<sup>1)</sup> that the Antarctic *Sterechinus Neumayeri* breeds at least from June to April, which fact is doubtless due to the very uniform temperature reigning in the Antarctic Sea throughout the year. This case then confirms Orton's statement that "where biological conditions do not vary much, marine animals will breed continuously." I would only object to making this a general rule; this it is certainly not, especially not in the tropics.

<sup>1)</sup> Deutsche Südpolar-Expedition. Zoologie. III. 1909.

### III. Geographical Distribution.

In my work "Die Echinodermen-Larven d. Plankton-Exped." p. 108—114 the distribution of the Echinoderm larvæ and some of the problems connected therewith were discussed at some length. Since then only very little additional information on this subject has been obtained. MacBride in 1903 published a "Report on a small collection of Echinoderm larvæ made by Mr. George Murray during the Cruise of the "Oceana" in November 1898"<sup>1)</sup>; only one species, the larva of *Luidia Sarsi*, is recorded there, from the Atlantic off S. W. Ireland (52° 1' N., 12° 27' W.). Gemmill<sup>2)</sup> has recorded some larvæ of *Luidia ciliaris* likewise from off S. W. Ireland (30—60 miles off Tearaght Island), and one single specimen of "*Brachiolaria hibernica*" from 50 Miles N. by W. of Eagle Island, W. of Ireland. In my report on "Die Echinodermen-Larven d. deutschen Südpolar-Expedition" (p. 109) a Spatangoid-larva is recorded from 10° 17' E. 28° 45' S., that is about in the mid-Atlantic between Cape and Patagonia, at a depth of nearly 5000 Meters. Apart from this highly interesting find only larvæ taken near the littoral regions are recorded in that work, as also in MacBride's reports on Echinoderm larvæ from the Antarctic Expeditions (National Antarctic Exped.; British Antarctic ("Terra Nova") Exped.). The existence of quite a considerable number of pelagic Echinoderm larvæ in the Antarctic Seas has been established herewith; but this fact, though of very considerable interest, does not concern us here. Referring still to the "*Stellosphæra mirabilis*" recorded by Koehler & Vaney from the vicinity of the Azores (ca. 36—40° N. 19—30° W.) mention has been made of, so far as I know, all records giving observations on the occurrence of Echinoderm larvæ in the open Ocean.<sup>3)</sup>

As stated in the Introduction (p. 10) I have at various occasions made efforts to bring together some more facts relating to the problem of the distribution of Echinoderm larvæ over the open Ocean. Observations made during the passage over the Indian Ocean from Aden to Singapore gave the result that, while Echinoderm larvæ were found in good numbers in the Gulf of Aden, none were observed until near the Maldives, but from there larvæ occurred the whole way across the Bay of Bengal. This would appear to indicate that larvæ do not occur in the great Arabian Sea. I would, however, not regard the negative result as conclusive, because the samples were taken there at day time. Later on samples were taken also by night, and these were invariably richer than those taken by day, in

<sup>1)</sup> Ann. & Mag. Nat. Hist. VII. Ser. XI. p. 477—78.

<sup>2)</sup> J. F. Gemmill. On a new brachiote Asteroid larva and on the advanced Bipinnaria of *Luidia ciliaris* (Philippi) Gray. Proc. R. Phys. Soc. Edinb. XIX. 1915.

<sup>3)</sup> See, however, the paper by Stanley Gardiner mentioned below (p. 251).

conformity with the well known fact that most pelagic animals avoid the strong daylight by going down in the sea, raising again to the surface at night time. I would expect that samples taken by night will prove larvæ to occur also all over the Arabian Sea. But that remains to be proved.

Besides the material of plankton samples collected for me on various cruises across the Atlantic by Messrs. Blegvad, Kramp and Fogh (comp. p. 10) I have also had the opportunity of examining some other samples likewise taken on the way to and from the West Indies, kindly placed at my disposal by Dr. Johs. Schmidt. The samples were all taken at the surface by night time. The following larvæ were obtained from these samples.

<i>Sphærechinus granularis</i> . . .	36°13' N. 33°50' W.	15/III 1911	Blegvad	Off Azores
— — — — —	36°42' - 30°36'	16/III —	—	— —
<i>Echinopluteus transversus</i> . .	32°10' - 17°20'	30/X 1911	Kramp	- Madeira
— — — — —	27°10' - 21°53'	3/XI —	—	- Canaries
— — — — —	31°22' - 14°57'	16/X 1912	Fogh	- Madeira
— — — — —	28°43' - 20°40'	22/X —	—	- Canaries
<i>Echinopluteus</i> sp. . . . .	25°40' - 24°10'	24/X —	—	— —
— — — — —	18°45' - 62°20'	19/XI 1911	Kramp	- Virgin Isl.
<i>Luidia ciliaris</i> . . . . .	36°13' - 33°50'	15/III —	(Dr. Schmidt)	- Azores
— — — — —	37°31' - 35°34'	12/V —	—	- —
— <i>Sarsi</i> (?) <sup>1)</sup> . . . . .	30°30' - 49°57'	22/II —	—	Sargasso Sea
<i>Bipinnaria</i> sp. . . . .	40°47' - 21°10'	21/III —	Blegvad	Off Azores
— — — — —	32°22' - 22°49'	26/III —	—	- —
— — — — —	20°46' - 11°16'	11/XI 1911	Kramp	Sargasso Sea
— — — — —	19°36' - 47°13'	13/XI —	—	—
— — — — —	23°15' - 58°43'	16/II 1912	—	—
— — — — —	25°16' - 55°37'	20/II —	—	—
— — — — —	24°33' - 60°12'	18/II 1913	Fogh	—
<i>Auricularia nudibranchiata</i> .	30°30' - 49°57'	22/II 1911	(Dr. Schmidt)	—
— — — — —	33°55' - 43°40'	12/III —	—	—
— — — — —	34°39' - 40°54'	13/III —	—	—
— — — — —	36°13' - 33°50'	15/III —	—	—
— — — — —	39°22' - 22°49'	20/III —	—	Off Azores
— — — — —	40°47' - 21°10'	21/III —	—	—
— — — — —	45°32' - 25°50'	21/VI —	—	—

The result is seen to be in fair accordance with that previously obtained from the study of the material collected by the Plankton-Expedition, viz. that, while in general the Echinoderm larvæ occur more numerously in the coastal waters, several specimens may be found also in mid-Ocean. This raises the interesting problem: how did they come there? Were they carried out from the coastal waters by the currents, or did they rise from the bottom?

So long as we do not know the parental origin of the larvæ found in the open sea the question cannot be answered definitely. Most probably they

<sup>1)</sup> Identification of the single specimen a little uncertain on account of the very poor preservation.



come from both sources. The question whether any deep-sea Echinoderms have truly pelagic larvæ must, after what we now know, be answered in the affirmative. *Laganum diplopora* has been directly proved to have pelagic larvæ, and it is almost certain that also *Pedicellaster 6-radialus* has pelagic larvæ (*Stellophæra mirabilis*); judging from the character of the eggs many other deep-sea forms must have pelagic larvæ (though a great percentage of them have large eggs and therefore certainly must have an abbreviated development<sup>1</sup>). On the other hand it is evident from the facts recorded that larvæ of littoral forms may be carried very far from the coasts. In this connection it is important to notice that Bipinnariæ are predominant among the larvæ found in the Sargasso-Sea (beside the large *Auricularia nudibrauchiata*); this is in good accordance with the fact that the Asterid-larvæ in general require long time for their development, much longer than do the Echinoid-larvæ. Thus there will be ample time for their being carried great distances by the currents.

The transport of the larvæ by means of the currents is, of course, of considerable zoogeographical importance. Their eventual transport across the Atlantic has some bearing on the problem of a former land connection between Africa and South America (the Archhelenis-theory)<sup>2</sup>. It is a well known fact that quite a good number of littoral Echinoderms are common to the West Indies (Brazil) and West Africa. This peculiar distribution can be accounted for only in two ways, viz. by the existence of a former land connection (or a series of islands) between the two continents along the shores of which these Echinoderms were formerly distributed, or by the transport of their larvæ across the Ocean. That the latter alternative is really possible seems undeniable from the facts made known of the occurrence of larvæ in the open Ocean. Accordingly the Archhelenis-theory is no necessity for understanding the recent distribution of the littoral Echinoderms of the tropical Atlantic. On the other hand, it must be agreed, there are many other facts, especially in the geographical distribution of land- and freshwater animals and plants, which seem to require that theory for an explanation.

The occurrence of larvæ of deep-sea forms at the surface of the ocean is another problem not very easily explained (— due allowance being made for the fact that we have as yet not definitely ascertained a single case of a larva of a deep-sea form found at the surface; we do not know

<sup>1</sup>) *Pelagothuria natatrix* has large eggs, until 1.2 mm in diameter according to Ludwig ("Albatross"-Holothurioidea, 1891, p. 119). This large size of the eggs probably means that also this form has a direct development, and we have thus the remarkable fact that this typical pelagic Holothurian has not a typical pelagic larva.

<sup>2</sup>) H. v. Thering, Archhelenis und Archinotis. Gesammelte Beiträge zu einer Geschichte der Neotropischen Region, 1907.

exactly the depth at which *Stellosphæra mirabilis* was taken, and we have not yet definitely proved *Auricularia nudibranchiata* to belong to a deep-sea Holothurian). It seems impossible that the larvæ could rise all the way by means of their ciliary movements. One cannot help suggesting that vertical currents may have something to do with the transport of the larvæ from the deeper layers towards the surface and the inverse. The existence of vertical currents is a suggestion called forth by various biological facts. Thus e. g. Prof. A. d. S. Jensen informs me that the distribution of the eggs and the young of *Reinhardtius hippoglossoides* (Walb.) in the Davis Strait seems to be explicable only on the assumption of vertical currents existing there. While the eggs and newly hatched young larvæ, with the yolk sac, are found in depths of 600—1000 Meters, the slightly older young, where the yolk sac has just been absorbed, are found at 30 Meters below the surface<sup>1)</sup>. It seems simply impossible that these young fish larvæ could have passed that great vertical distance alone by means of their own feeble swimming power. Hjort and Murray in "The depths of the Ocean" (p. 378—380) think that vertical circulation has a great influence upon the distribution of pelagic plants, and upon the whole speak of vertical circulation in the Ocean as an established fact, at least for the upper 200—300 Meters. This, however, will not suffice for explaining the ascent of the larvæ from the bottom at much greater depths. This interesting problem cannot be solved at our present state of knowledge. Upon the whole, we are hardly in possession of facts enough even for a definite formulation of the problems connected with the deep-sea larvæ. We can only see this much that continued researches will be sure to bring important results.

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<sup>1)</sup> Comp. Rapport til Indenrigsministeriet over Briggen "Tjalfe"'s praktisk-videnskabelige Fiskeriekspedition til Grønland. 1909.

## Appendix.

In a paper by D. H. Tennent on "The early influence of the spermatozoa upon the characters of Echinoid larvæ" (Papers from the Tortugas Laboratory of the Carnegie Inst. Washington. Vol. V, 1914) some observations on the early developmental stages of *Eucidaris tribuloides* (Lamk) are recorded. It is evident that the larva of this species agrees closely with that of *Eucidaris Thouarsi* (comp. p. 22, Pl. V, Figs. 1—2). In the Pluteus, 6 days old, represented in his figure 6 (p. 133) the skeleton is shown; the postoral rods are fenestrated, horizontally directed. One cannot help being struck by the resemblance with the *Echinopluteus transversus* shown by this young larva, and — in spite of the ophicephalous pedicellariæ — the conclusion seems almost unavoidable that *Echinopluteus transversus* really is the *Cidaris*-larva.

The paper is not recorded either in the "Zoological Record" or the "Bibliographia zoologica." It was therefore only per chance that I discovered it in time for mentioning this important observation by Tennent in this place.

When speaking of the phylogenetic importance of the larva of the viviparous *Ophionotus hexactis* (p. 238) I forgot to mention the larva of *Chirodota rotifera*, which, although developing within the body cavity of the mother, has also fairly distinct ciliated bands like those of the typical, free-living larvæ.<sup>1)</sup>

Attention may still be called to an interesting paper by I. Stanley Gardiner: "Notes and observations on the distribution of the larvæ of marine animals". (Ann. Mag. Nat. Hist. VII, Ser. XIV, 1904, p. 403—410), in which the problem of the importance to be ascribed to marine larvæ "in distributing species and genera from shore to shore, from one littoral zone to another" is discussed. In general the views of Stanley Gardiner are not in contradiction to those set forth in the present work, and I do not see any reason for entering on a detailed discussion thereof, the more so as I most sincerely agree with the author in the main object of

<sup>1)</sup> H. L. Clark. Development of an Apodous Holothurian (*Chirodota rotifera*). Journ. Experim. Zool. IX, 1910.

his paper "to direct attention to the subject in the hope that zoologists who are dealing with plankton will not confine their attention merely to the adult groups of the same, but will, in addition, arrange for examination of the larvæ therein in view of the distribution of the different groups of littoral animals." I would only express my astonishment at the conclusion he arrives at, viz. that "it would appear to me (Gardiner) that no results in distribution can be expected, so far as the Indo-Pacific is concerned, from Echinoderms — and probably also from Enteropneusts — other than the Crinoids," the pelagic life of which latter is considerably shorter than that of typical pelagic Echinoderm larvæ. Probably this statement is not meant so absolutely as it sounds. I also venture to think that the fear expressed by Stanley Gardiner "that in the present state of our knowledge any consideration of larval distribution is premature and must be inconclusive" has been partly removed by the present researches.

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## EXPLANATION OF THE PLATES

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Some of the figures of Ophiurid-larvæ were drawn by Mr. I. Lieberkind, who has also drawn some of the skeletal figures of these larvæ given in the text. I beg to express here my indebtedness to Mr. Lieberkind for his valuable assistance.

### Plate I.

- Fig. 1. Larva of *Echinometra lucunter* (Linn.), two weeks old, fully formed; seen from the ventral side. Drawn from life. <sup>150</sup>/<sub>1</sub>.
- 2. Larva of same species, same age; from the dorsal side. At the base of the left postoral arm is seen the beginning amniotic invagination. Drawn from life. <sup>180</sup>/<sub>1</sub>.

### Plate II.

- Fig. 1. Larva of *Tripneustes esculentus* (Leske), 17 days old; from the ventral side. Drawn from life. <sup>150</sup>/<sub>1</sub>.
- 2. Larva of same species, 22 days old; from the dorsal side. At the base of the left postoral arm is seen a small invagination, the amnion. A pedicellaria has begun to form in a groove in the posterior end. The forward direction of the ventral ciliated lobes (v. l.) is due to pressure of the larva under the cover. Drawn from life. <sup>150</sup>/<sub>1</sub>.

### Plate III.

- Fig. 1. Larva of *Lylechinus variegatus* (Lamk.), 13 days old, seen from the dorsal side. Drawn from life. The amnion has been formed and in the posterior end a pedicellaria (p) is beginning to develop. <sup>150</sup>/<sub>1</sub>.
- 2. Larva of same species, 15 days old, seen from the ventral side. Drawn of life. <sup>150</sup>/<sub>1</sub>.

### Plate IV.

- Fig. 1. Larva of *Astrichypus Manni* Verrill, 6 days old; seen from the dorsal side, amnion. Drawn from life. <sup>150</sup>/<sub>1</sub>.
- 2. Larva of *Mellita sexiesperforata* (Leske), 7 days old; seen from the dorsal side, turned slightly upwards; in beginning metamorphosis. Drawn from life. On account of the opacity of the larva the details of the body skeleton could not be discerned. <sup>200</sup>/<sub>1</sub>.

### Plate V.

- Fig. 1. Embryo of *Euclidaris Thouarsi* (Val.), 3 days old. <sup>265</sup>/<sub>1</sub>.
- 2. Young larva of same species, 6 days old, slightly restored. The skeleton dissolved. The small body to the left of the mouth probably represents part of the enterocoel. <sup>265</sup>/<sub>1</sub>.
- 3. Section of young embryo of *Phyllacanthus parvispinus* Woods, in the blastula stage. <sup>110</sup>/<sub>1</sub>.
- 4. Section of embryo in the gastrula stage of same species. <sup>150</sup>/<sub>1</sub>.
- 5. Larva of *Diadema antillarum* Phil., 5 days old; from the ventral side. Drawn from

life. <sup>220</sup>/<sub>1</sub>. The line seen across the ventral transverse rods is the lower limit of the suboral cavity.

Fig. 6. Young larva of *Astropyga pulvinata* (Lamk.), 5 days old; ventral view. Drawn from life. <sup>150</sup>/<sub>1</sub>.

- 7. Larva taken pelagically, probably belonging to *Astropyga pulvinata*. Seen in somewhat oblique side view. Some dislocation has occurred; the anal area is somewhat twisted to the left so that the side area of the larva has become too broad. The figure is slightly corrected, the postoral (p. o.) and posterodorsal (p. d.) arms being in a more upright (but unnatural) position in the specimen from which the figure has been drawn. The basal part of the left postoral rod not to be seen quite distinctly, that of the posterodorsal rod quite indistinct in the specimen. <sup>150</sup>/<sub>1</sub>, p. tr. posterior transverse rod.

#### Plate VI.

Fig. 1. Larva of Arbaciid; taken pelagically off the Azores. The postoral and posterodorsal arms broken; their length must considerably surpass that shown in the figure. <sup>29</sup>/<sub>1</sub>.

- 2. The same larva, more magnified (<sup>90</sup>/<sub>1</sub>). The larva is in beginning metamorphosis, the anterolateral and preoral arms are not broken. The large fenestrated plate at the base of the postoral (and, less developed, the posterodorsal) rods is not characteristic of the larval skeleton but is connected with the metamorphosis. p. pedicellaria; p. tr. posterior transverse rod.
- 3. Larva of *Heliocidaris tuberculata* (Lamk.), seen from the posterior end; showing the position of the ventral (v. tr.) and dorsal transverse rods (d. tr.); p. tr. posterior transverse rod; da. dorsal arch; p. o. postoral, p. d. posterodorsal arm; p. l. posterolateral lobe. <sup>225</sup>/<sub>1</sub>.
- 4. Larva of *Temnotrema sculpta* A. Ag., 20 days old. Drawn from life; ventral view. The skeleton was merely sketched in the original drawing; as it has been dissolved in the preparation, so that the sketch could not be completed, it had to be omitted in the figure. <sup>100</sup>/<sub>1</sub>.
- 5-6. Young larvae of *Holothuria* n. sp. (?), from the ventral side. Fig. 5 represents a specimen 3 days old, Fig. 6 another, 8 days old. The rectum is indiscernible. The frontal area in fig. 6 probably too narrow, due to contraction on preservation. <sup>180</sup>/<sub>1</sub>.

#### Plate VII.

Fig. 1. Larva of *Mespilia globulus* (Linn.), 15 days old; seen from above, but in such a position that the body is leaning somewhat over to the ventral side. The fact that the posterodorsal arms are narrower than the postoral arms in this figure is due only to the oblique position; in reality these four arms are of the same width. Drawn from life. <sup>110</sup>/<sub>1</sub>.

- 2. Larva of same species, ventral view; drawn from a preserved specimen. (This accounts for the narrowness of the postoral and posterodorsal arms as compared with fig. 1.) Beginning metamorphosis; two pedicellariae have appeared in the posterior end. Same age as the larva represented in fig. 1. <sup>100</sup>/<sub>1</sub>.
- 3. Larva of *Arbacia stellata* (Blv.); dorsal view. <sup>95</sup>/<sub>1</sub>.
- 4. Young larva of *Lytechinus panamensis* Mrtsn., ventral view; 5 days old. Drawn from life. <sup>150</sup>/<sub>1</sub>.
- 5. Young larva of *Lytechinus anamesus* H. L. Clark; side view; 7 days old. Drawn from life. <sup>90</sup>/<sub>1</sub>.

#### Plate VIII.

Fig. 1. Young larva of *Lytechinus variegatus* (Lamk.), 2 days old. Ventral view. Drawn from life. <sup>165</sup>/<sub>1</sub>.

- 2. Young larva of *Tripneustes esculentus* (Leske), 3 days old. Ventral view. Drawn from life. <sup>200</sup>/<sub>1</sub>.
- 3. Larva of *Lytechinus anamesus* H. L. Clark, 7 days old. Not yet fully formed. Ventral view. Drawn from life. <sup>90</sup>/<sub>1</sub>.
- 4. Larva of same species, same age as fig. 3; dorsal view. Drawn from life. <sup>90</sup>/<sub>1</sub>.

- Fig. 5. Young larva of *Tripneustes gratilla* (Linn.), 3 days old. Dorsal view. The skeleton has been dissolved.  $^{220}_1$ .
- 6. Same as Fig. 5; side view.  $^{220}_1$ , s. c. suboral cavity.
  - 7. Larva probably belonging to *Toxopneustes roseus* (Ag.). Not yet fully formed. Slightly distorted. Ventral view.  $^{110}_1$ .
  - 8. Young larva of *Toxopneustes pileolus* (Lamk.), 9 days old. Ventral view.  $^{180}_1$ .

#### Plate IX.

- Fig. 1. Young larva of *Strongylocentrotus franciscanus* (A. Ag.), 4 days old. Dorsal view.  $^{150}_1$ .
- 2. Larva of same species, 8 days old; ventral view.  $^{150}_1$ .
  - 3. — — — — — 10 days old; side view.  $^{150}_1$ .
  - 4. Fully developed larva of *Strongylocentrotus franciscanus*, taken pelagically. Drawn from a preserved specimen. The course of the ciliated band along the sides not quite distinct in the specimen.  $^{130}_1$ .
  - 5. Larva of *Strongylocentrotus pulcherrimus* (A. Ag.), 1 weeks old. Ventral view.  $^{200}_1$ .
- Figures 1—3 and 5 drawn from life.

#### Plate X.

- Fig. 1. Young larva of *Evechinus chloroticus* (Val.), 11 days old. Ventral view.  $^{110}_1$ .
- 2. More advanced larva of same species, 3 weeks old. Dorsal view.  $^{110}_1$ .
  - 3. Fully developed larva of same species; nearly 5 weeks old. Ventral view.  $^{110}_1$ .
  - 4—5. Two abnormal young larvae of *Evechinus chloroticus*.  $^{90}_1$ .
  - 6. Nearly fully developed larva of *Temnopleurus loreumaticus* (Klein); ventral view. 9 days old. Drawn from life.  $^{160}_1$ .
  - 7. Fully developed larva of *Arachnoides placentia* (L.), 7 days old. Ventral view.  $^{180}_1$ .

#### Plate XI.

- Fig. 1. Young larva of *Heliocidaris tuberculata* (Lamk.), 6 days old. Dorsal view.  $^{225}_1$ .
- 2. Fully formed larva of same species, 5 weeks old. Ventral view. In the posterior end a pedicellaria has appeared; a muscle is seen connecting the lower ends of the postoral rods. Drawn from life.  $^{150}_1$ .
  - 3. Larva of Temnopleurid, species c. Slightly restored. The true shape of the epaulets not to be ascertained.  $^{150}_1$ .
  - 4. Larva of *Echinobrissus (Oligopodia) recens* (M. Edw.), 4 days old; ventral view.  $^{105}_1$ .
  - 5. Larva of same species, 40 days old; ventral view.  $^{105}_1$ .

#### Plate XII.

- Fig. 1. Larva of *Echinometra lucunter* (Linn.), 7 days old; dorsal view. The body skeleton has begun to be absorbed. Drawn from life. Showing the nervous system (the oblique line on the anal area, at the base of the postoral arms).  $^{220}_1$ .
- 2. Larva of *Echinometra oblonga* (Blv.), 12 days old; side view. Body skeleton partly dissolved.  $^{200}_1$ .
  - 3. Larva of same species, same age; ventral view. The skeleton has been omitted in the figure, being partly dissolved so that a correct drawing of it could not be made. (Comp. fig. 2).  $^{200}_1$ .
  - 4. Larva of *Coloboentrotus atratus* (Linn.), 12 days old; side view.  $^{200}_1$ .
  - 5. Larva of same species, same age; ventral view. Skeleton dissolved. Drawing from a preserved specimen, combined with a sketch from life.  $^{200}_1$ .
  - 6. Young larva of *Temnopleurus loreumaticus*, 22 hours old; ventral view. The ciliated band rather too distinct in the figure.  $^{220}_1$ .

#### Plate XIII.

- Fig. 1. *Echinopluteus transversus*, species c. Ventral view.  $^{85}_1$ .
- 2. — — — — — a. Slightly corrected, the postoral band having been shown in what is evidently its normal place, not in the place where it is seen in the specimen, below the end of the ventral transverse rods.  $^{145}_1$ .

- Fig. 3. *Echinopluteus transversus*, species f. Ventral view. The vibratile band not distinct over the Echinoid-rudiment.  $85/1$ .
- 4. Same larva as fig. 3, in dorsal view.  $85/1$ .
  - 5. Young larva of *Mellita sexiesperforata* (Leske); 24 hours old. Ventral view.  $150/1$ .
  - 6. Larva of same species, same age; side view.  $150/1$ .

#### Plate XIV.

- Fig. 1. Young larva of *Laganum diplopora* H. L. Clark; 3 days old. Ventral view.  $200/1$ .
- 2. Embryo of *Clypeaster japonicus* Döderl.,  $2\frac{1}{4}$  days old. Showing beginning formation of the skeleton.  $180/1$ .
  - 3. Larva of same species, 11 days old. Ventral view. Drawn from life.  $145/1$ .
  - 4. Gastrula of *Echinaraehnius mirabilis* (A. Ag.), 18 hours old.  $180/1$ .
  - 5. Fully developed larva of *Echinaraehnius (Dendraster) excentricus* (Esch.), 14 days old. Ventral view. From a preserved specimen, combined with a sketch from a living specimen. Skeleton dissolved.  $105/1$ .
  - 6. Larva of same species, same age; side view. Slightly restored.  $105/1$ .
  - 7. Larva of *Encope micropora* Ag., 14 days old; ventral view. From a preserved specimen, combined with a sketch from a living specimen.  $150/1$ .

#### Plate XV.

All figures of *Peronella Lesueuri* (Val.). Figs. 1—4 drawn from life,  $85/1$ ; the rest  $180/1$ .

- Fig. 1. Embryo, five hours old, in the blastula-stage; showing irregular folding of the ectoderm.
- 2. Young larva, 17 hours old. The mouth has been formed, and the postoral arms are beginning to appear as a pair of small lateral thickenings.
  - 3. Young larva, 20 hours old; dorsal view. The postoral arms are distinct.
  - 4. Fully formed larva, 39 hours old; ventral view. The preoral lobe has been completely reduced, the mouth opening now being at the anterior edge of the body.
  - 5. Longitudinal section of an embryo, 9 hours old. A number of mesenchyme cells have been formed, but gastrulation has not yet begun.
  - 6. Longitudinal section of an embryo, 12 hours old. Gastrulation has begun.
  - 7—10. From a series of longitudinal sections of an embryo, 16 hours old; showing the shape of the entoderm. Between figs. 7 and 8 there is one section, fig. 9 following immediately after 8; there are 3 sections between figs. 9 and 10.
  - 11—13. From another series of longitudinal sections of an embryo, 16 hours old; showing the shape of the entoderm. Fig. 11 is the more dorsal of the three. In fig. 13 is seen the apical thickening.
  - 14. Longitudinal, sagittal section of an embryo, 16 hours old. The mouth (m) has begun to form.
  - 15—18. From a series of frontal, longitudinal sections of an embryo, 18—20 hours old. Fig. 15, which is the more dorsal of them, shows the widening (am.) from the lower end of the pharynx (ph.), surrounding the entoderm (ent.); this widening gradually disappears in the following figures. In fig. 18 is seen the rectum (r) in a lateral position. There are 4 sections between figs. 15 and 16, 1 between figs. 16 and 17 and 4 sections between figs. 17 and 18.
  - 19—22. From a series of sagittal longitudinal sections of an embryo, 18—20 hours old. Showing the posterior prolongation (am.) from the pharynx (ph.). Also the shape of the archenteron (ent.) appears from a comparison of these figures. Fig. 20 shows the blastoporus, which has now shifted to the ventral side, to form the anal opening (a).

#### Plate XVI.

All figures of *Peronella Lesueuri* (Val.); all  $180/1$ .

- Fig. 1. Longitudinal, frontal section of a larva 23—24 hours old. Showing the amniotic prolongation (am.) of the pharynx (ph.) continuing to the posterior end of the body. The part in the middle is the raised ventral wall of the amnion (comp. figs. 11—16):



in its posterior part the wall already has assumed an endothelial character. The spaces below the arms are the remnants of the blastocoel cavity (bl.).

- Fig. 2—4. From a series of longitudinal, frontal sections of an embryo, 32—35 hours old; fig. 2 is the more dorsal; fig. 1 the more ventral of them. The pharynx has been very much shortened and now has simply the character of the opening of the amnion. The Echinoid-rudiment has begun to form lobes, representing the young spines and primary tubefeet. In fig. 4 the curved intestine (i) is seen. The distinctly limited space to the right of it is part of the coelom (c), as is also the large, irregular space in fig. 3. In this latter figure is seen to the left below the anterior part of the amnion some nuclei, serially arranged so as to appear like a canal. This is, however, a casual arrangement of no importance and there is no real canal.
- 5. Median longitudinal sagittal section of a larva, 21—22 hours old. The amniotic prolongation of the pharynx has reached the posterior end, covering the whole of the dorsal side (comp. Pl. XV, Figs. 20—21). Its dorsal wall is beginning to assume an endothelial character, while the ventral wall has already thickened considerably. bl. blastocoel; h. hydrocoel; i. intestine.
  - 6—7. From a series of longitudinal, sagittal sections of a larva, 26—29 hours old. The amniotic opening, the former mouth, has now been transplaced to the dorsal side. There are two sections between the two figures. Below the thickened ventral wall of the amnion is seen the hydrocoel (h.), and on the ventral side the intestine (i.), the space separating them being the coelom (c.).
  - 8—9. From a series of longitudinal, sagittal sections of a larva, 32—35 hours old; fig. 8 median, fig. 9 more lateral, separated from fig. 8 by 10 sections. The two parts of the coelom seen in fig. 8 are found to be in direct connection in more lateral sections. The space in the middle probably belongs to the hydrocoel (h.?). The distinctly limited part of the coelom in fig. 9 is also seen in the adjoining section to be in direct communication with the rest of the coelom.
  - 10. Median longitudinal, sagittal section of a larva, 41—43 hours old. The amniotic opening is now entirely dorsal. The primary tubefeet are protruding into the amnion.
  - 11—13. From a series of transverse sections of a larva 18—20 hours old; fig. 11 is from the anterior end, the two lateral wings being the base of the postoral arms; figs. 12 and 13 from the middle part of the body, separated by three sections. am. amnion; bl. blastocoel; ent. entoderm; ph. pharynx; r. rectum.
  - 14—16. From a series of transverse sections of a larva, 23—21 hours old. Fig. 14 the more anterior, 16 the more posterior. In fig. 15 is seen the last trace of the blastoporus, or anal opening (a.). Figs. 14 and 15 are separated by 1 section, figs. 15 and 16 by 1 sections. The beginning folding of the ventral wall of the amnion is to be noticed. am. amnion; bl. blastocoel. The cavity in figs. 14 and 15, designated h. c., apparently represents both hydrocoel and coelom, not yet separated.
  - 17—18. From a series of transverse sections of a larva, 32—35 hours old. The young spines and primary tubefeet (t.) protruding into the amnion. The two figures are separated by 8 sections, fig. 17 being the anterior. am. amnion; c. coelom; h. hydrocoel; i. intestine.
  - 19—20. From a series of transverse sections of a larva, 41—43 hours old. Showing the pore canal (p. c.). The two figures are separated by 1 sections, fig. 19 being the more anterior.

#### Plate XVII.

All figures of *Helicoidaris erythrogramma* (Val.). All <sup>75</sup>1.

- Fig. 1. Embryo, 18 hours old, showing beginning formation of the gastrula.
- 2. Embryo, 30 hours old, in the gastrula stage.
  - 3. Embryo, 30 hours old, showing beginning differentiation of the archenteron, in the lumen of which is seen a mass of a slimy(?) substance.
  - 4. Further advanced stage in the differentiation of the archenteron, a large pouch having been formed; the hydrocoel (and enterocoel?); 30 hours old.
  - 5. Embryo, 42 hours old, showing the first indication of the amniotic invagination. The archenteron (the dark body in the middle) is connected with the blastoporus by a thin strand. The space seen above the archenteron is the hydro-enterocoel.

- Fig. 6. Embryo, 42 hours old, showing a slightly more advanced stage in the formation of the amniotic invagination and a beginning differentiation of the hydrocoel.
- 7. Embryo, 30 hours old, showing the archenteron completely separated off from the blastoporus.
  - 8. Embryo,  $2\frac{3}{4}$  days old, showing a further advanced stage of the amniotic invagination, which has formed a furrow nearly round the body. A distinct, broad ciliated band is seen round the middle of the body. The archenteron has been separated off from the blastoporus. The internal structures very indistinct in this specimen.
  - 9. Embryo,  $3\frac{3}{4}$  days old. The tubefeet of the young urchin have begun to protrude through the amniotic invagination. The internal structures not to be made out in this specimen.
  - 10. Embryo,  $3\frac{3}{4}$  days old. The primary tubefeet and the first spines (numbering 10, both together, in this specimen) are protruding through the amniotic cavity, now split open. The pigment shows a rather distinct arrangement in bands.
  - 11. Embryo,  $2\frac{3}{4}$  days old, showing the five primary tubefeet lying within the amnion.
  - 12. Embryo,  $4\frac{1}{2}$  days old. The primary tubefeet and spines have further protruded, and the oral and aboral end of the larval body are pushed up on the dorsal side of the urchin.
  - 13. Nearly metamorphosed sea-urchin; the aboral part of the larval body has been nearly completely absorbed, forming only a small prominence on the upper side. The primary tubefeet are fully extended. Embryonal spines have begun to appear also on the aboral side.
  - 14. Embryo,  $1\frac{1}{2}$  days old. The amniotic invagination has been widened so much that the primary tubefeet and the spines are assuming a circular arrangement. Only two of the tubefeet extended. The pigment forms a very prominent band above the widening of the body.

Figures 1—9 and 11 are drawn from specimens mounted in balsam and thus made transparent; figures 10 and 12—14 are drawn from specimens not thus cleared up.

### Plate XVIII.

All figures of *Heliocidaris erythrogramma* (Val.). All, except fig. 4,  $180/1$ .

- Fig. 1. Section of an embryo, 6 hours old, in a young cleavage stage. The formation of the mesenchyme has begun. The nuclei very indistinct.
- 2. Section of an embryo, 18 hours old, in a young blastula stage. The whole of the blastocoel cavity filled by mesenchymic cells, still in an embryonal condition.
  - 3. Section of an embryo, 18 hours old, in the fully formed blastula stage. The mesenchymic cells have assumed the character of a reticulum, interwoven between the large vacuoles, containing a probably fatty substance which serves as nourishment to the developing embryo.
  - 4. Part of a longitudinal section of an embryo,  $2\frac{3}{4}$  days old, showing the formation of the amniotic invagination.  $290/1$ .
  - 5. Longitudinal section of an embryo,  $2\frac{3}{4}$  days old; showing the primary tubefeet (t) protruding into the amniotic cavity (am.), which opens out through a small pore. c. enterocoel.
  - 6. Part of a section from the same series as fig. 5. The amnion is closed here. h. hydrocoel.
  - 7. Longitudinal section of an embryo, 42 hours old. Showing the hydrocoel (h) lying close towards the amniotic invagination (am), which is here still an open groove. Trace of the blastoporus is seen in the oral end; ent. entoderm.
  - 8—9. Two longitudinal sections of an embryo in metamorphosis,  $4\frac{1}{2}$  days old. In fig. 8 is seen the stone canal and its outer opening, in fig. 9 the inner opening of the stone canal into the hydrocoel. a. ampulla; c. coelom; d. dorsal; ent. entoderm. h. hydrocoel; r. reservoir of food; st. c. stone canal; v. ventral.

## Plate XIX.

- Fig. 1. *Ophiopluteus* of *Ophiothrix* species a. Misaki, 17/VI. 14.  $60/1$ .  
 - 2. — — — — c. Jolo, 20 III. 14.  $60/1$ .  
 - 3. — — — — b. Tobago, Panama. XII. 1915.  $60/1$ .  
 - 4. — — — — — — — — — —  $28/1$ .  
 - 5. — — — — — — — — — —  $13/1$ .  
 - 6. — — — — — — — — — — The young Ophiurid has been developed and dropped off, the posterolateral arms remaining in connection and still continuing the pelagic life. Tobago, Panama. XII. 1915.  $13/1$ .  
 - 7. *Ophiopluteus* of *Ophiothrix*, species d. Somewhat restored, especially the intestinal tractus. Off Jolo, 20 III. 14.  $80/1$ .

## Plate XX.

- Fig. 1. Larva of *Ophiothrix angulata* Say, var. *pocilla* H. L. Clark. Drawn from life. 40 hours old.  $200/1$ .  
 - 2. Same, P<sub>2</sub> days old. Drawn from life.  $200/1$ .  
 - 3. *Ophiopluteus opulentus*, species c. The young Ophiurid has been developed and dropped off, the posterolateral arms remaining in connection and continuing pelagic life. The arms are not represented in full length, ought to be ca. 1 cm longer by this magnification. The small swelling in the middle to be noticed.  $43/1$ .  
 - 4. Same as fig. 3, showing beginning regeneration of the larval body.  $43/1$ .  
 - 5. Same specimen as fig. 4, more magnified. Showing beginning formation of mouth, vibratile band, anterolateral (?postoral) rods.  $180/1$ .

## Plate XXI.

- Fig. 1. *Ophiopluteus costatus*, species a.  $90/1$ .  
 - 2. — — — — b.  $60/1$ .  
 - 3. — — — — *opulentus*, species a. Slightly restored.  $85/1$ .

## Plate XXII.

- Fig. 1. *Ophiopluteus retrospinus*, species a. The nervous system is distinctly seen.  $80/1$ .  
 - 2. — — — — b. Nervous system only partly distinct.  $90/1$ .  
 - 3. — — — — *opulentus*, — — c.  $43/1$ .

## Plate XXIII.

- Fig. 1. *Ophiopluteus fulcitus*, species a.  $62/1$ .  
 - 2. — — — — b.  $115/1$ .  
 - 3. — — — — c.  $116/1$ .

## Plate XXIV.

- Fig. 1. *Ophiopluteus fulcitus*, species a.  $115/1$ .  
 - 2. — — — — *undulatus*, species c.  $90/1$ .  
 - 3. — — — — a; in metamorphosis.  $10/1$ .

The details of the skeletal plates of the young Ophiurid could not be given quite accurately by this magnification. The first ventral plate has appeared; in four of the interradii is seen an unpaired plate, which evidently represents the mouth-shield. The preoral band was not very distinct and is perhaps not quite correctly represented.

## Plate XXV.

- Fig. 1. *Ophiopluteus undulatus*, species a. Slightly restored.  $90/1$ .  
 - 2. — — — — b. Slightly restored.  $90/1$ . The three inner arm-pairs probably still longer than represented. The widening on the ends not distinct, drawn only from analogy with the other species of this type. The shape of the preoral band perhaps not quite correct; the situation distinct only on one side.

## Plate XXVI.

- Fig. 1. *Ophiopluteus arcifer*, species a.  $^{85}/_1$ .  
 - 2. — — — b.  $^{80}/_1$ .  
 - 3. — — — c.  $^{80}/_1$ .

## Plate XXVII.

- Fig. 1. *Ophiopluteus formosus*, species a.  $^{95}/_1$ .  
 - 2. — — — b. Slightly restored.  $^{60}/_1$ .  
 - 3. — — — *similis*.  $^{43}/_1$ .

## Plate XXVIII.

- Fig. 1. *Ophiopluteus serratus*.  $^{60}/_1$ .  
 - 2. — — —, beginning metamorphosis.  $^{60}/_1$ .

## Plate XXIX.

- Fig. 1. *Ophiopluteus pusillus*, species a.  $^{115}/_1$ .  
 - 2. — — — b.  $^{115}/_1$ .  
 - 3. — — —; in metamorphosis.  $^{115}/_1$ .  
 The remnants of the vibratile band to be noticed.  
 - 4. *Ophiopluteus pusillus*, species c.  $^{105}/_1$ .  
 - 5. — — — d.  $^{105}/_1$ .  
 - 6. — — — *diegensis*.  $^{105}/_1$ . The small spots in the posterior part of the body are pigment cells.

## Plate XXX.

- Fig. 1. *Ophiopluteus* of *Ophiocoma*, species c. slightly restored.  $^{115}/_1$ .  
 - 2. — — — *formosus*, species a. in metamorphosis.  $^{95}/_1$ .  
 - 3. — — — *monacanthus*.  $^{60}/_1$ .  
 - 4. — — —, in side view, somewhat distorted.  $^{60}/_1$ .

## Plate XXXI.

- Fig. 1. Larva of *Ophionereis squamulosa* Koehler; 45 hours old. Drawn from life. Ventral view.  $^{120}/_1$ .  
 - 2. Same larva, same age. Dorsal view. The 6 primary plates and three of the terminal plates have appeared; the oral skeleton has not yet appeared in this specimen. c. b. ciliated band; hp. hydropore; pr. t. primary tentacle; tf. <sub>2</sub> second pair of tubefeet.  $^{215}/_1$ .  
 - 3. Same larva,  $2\frac{1}{2}$  days old; from the ventral side. The mouth opening has been formed. Letters as in fig. 2; further st. c. stone canal; b. t. buccal tentacles.  $^{215}/_1$ .  
 - 4. Same larva, 6 days old; the metamorphosis nearly completed, but the anterior end of the larval body and traces of the ciliated bands (cb.) are still distinctly visible. The first ventral plate (v.) and the first side plate with its spine have been formed. The mouth shields have not yet appeared. t. terminal plate.  $^{215}/_1$ .  
 - 5. Longitudinal, frontal, section of larva of *Ophionereis squamulosa*, 26 hours old; e. c. enterocoel; h. hydrocoel; st. stomach.  $^{180}/_1$ .  
 - 6. Larva of same species, 26 hours old; drawn from a cleared up specimen. The hydrocoel is in a more advanced stage than in Fig. 5, showing the five radial canals. The enterocoel is indistinct. st. stomach.  $^{180}/_1$ .  
 - 7. Cleavage stage of *Amphiura vivipara*.  $^{110}/_1$ .  
 - 8. Further advanced stage of the same; the nuclei have arranged themselves in a layer along the surface so as to form the ectoderm.  $^{110}/_1$ .  
 - 9. Young embryo of *Amphiura vivipara*, showing the arms curved over the dorsal side, in the skin of which the primary plates are observed, irregularly arranged.  $^{80}/_1$ .

## Plate XXXII.

All figures of *Ophionotus hexactis* (E. A. Smith).

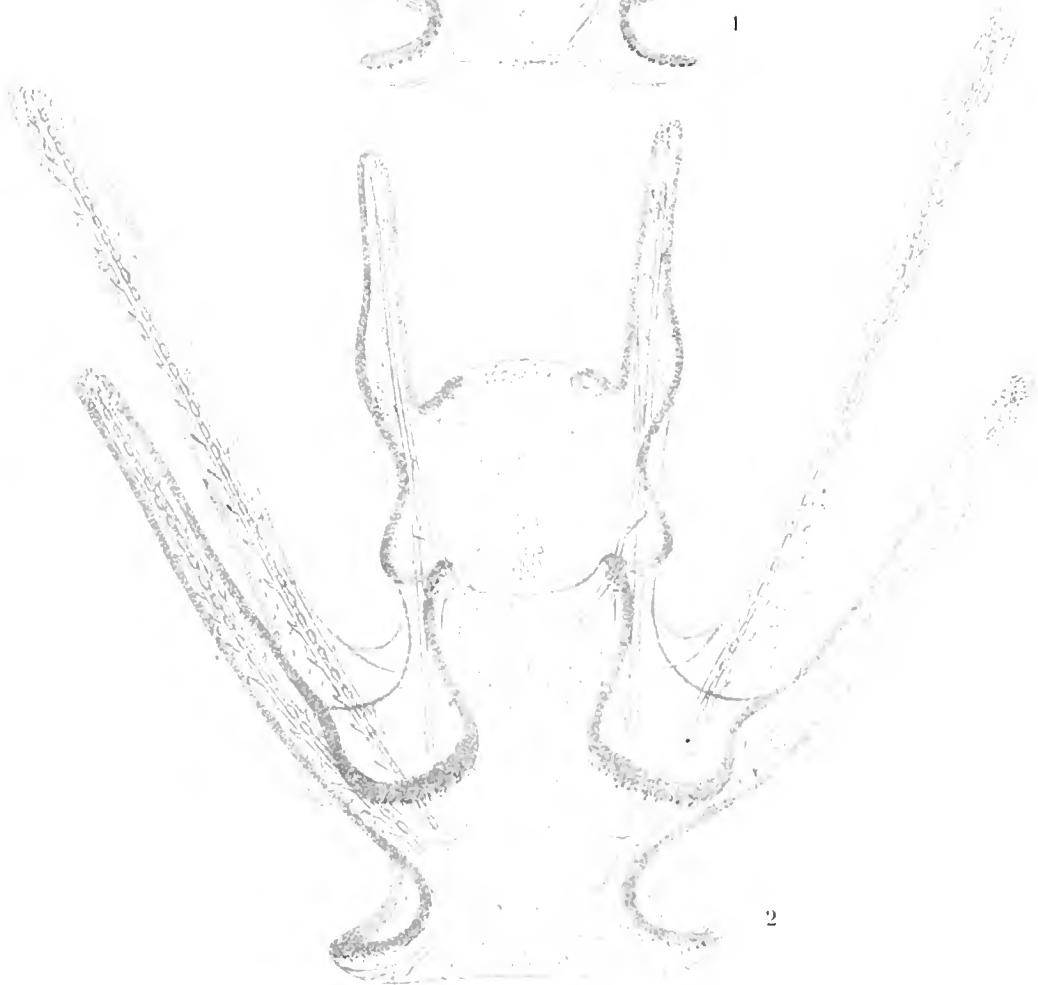
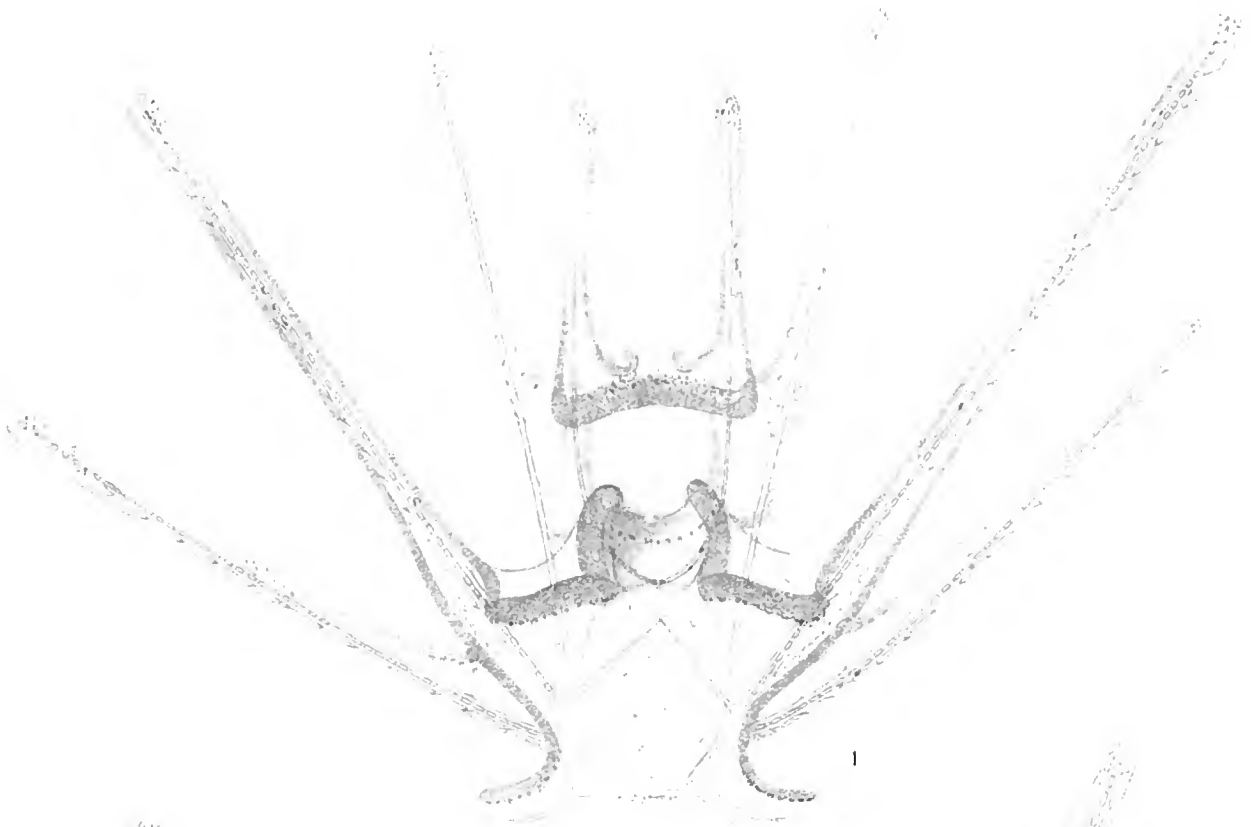
- Fig. 1—2. Young larva with a right hydrocoel. 1 from the ventral side, 2 in side view.  $^{150}/_1$ .

- Fig. 3. Fully formed larva; the hydrocoel has formed the primary lobes. The rudimentary skeleton (sk.) is seen. <sup>150</sup>/<sub>1</sub>.
- 4. Larva in a slightly less advanced stage, with a right hydrocoel. <sup>150</sup>/<sub>1</sub>.
  - 5. Fully formed, normal larva. The round hole seen in the stomach is the entrance to the rectum, which is seen here directly from above. <sup>150</sup>/<sub>1</sub>.
  - 6. Fully formed larva, in side view. The oral lobe is bent somewhat forwards so as to cover the oral region.
  - 7. Abnormal larva. <sup>150</sup>/<sub>1</sub>.
  - 8. The young Ophiuran lying within the ovarian sac, on the wall of which are seen two small, nearly absorbed eggs (e.). <sup>60</sup>/<sub>1</sub>.
  - 9. An ovary, attached to the genital rhachis; a trabecule of connective tissue is proceeding from the ovary. <sup>85</sup>/<sub>1</sub>.  
a. c. anterior coelom; e. egg; h. hydrocoel; m. mouth; n. nerv(?); p. c. posterior coelom; r. rectum; rh. rhachis; sk. skeleton; st. stomach; tr. trabecule.

### Plate XXXIII.

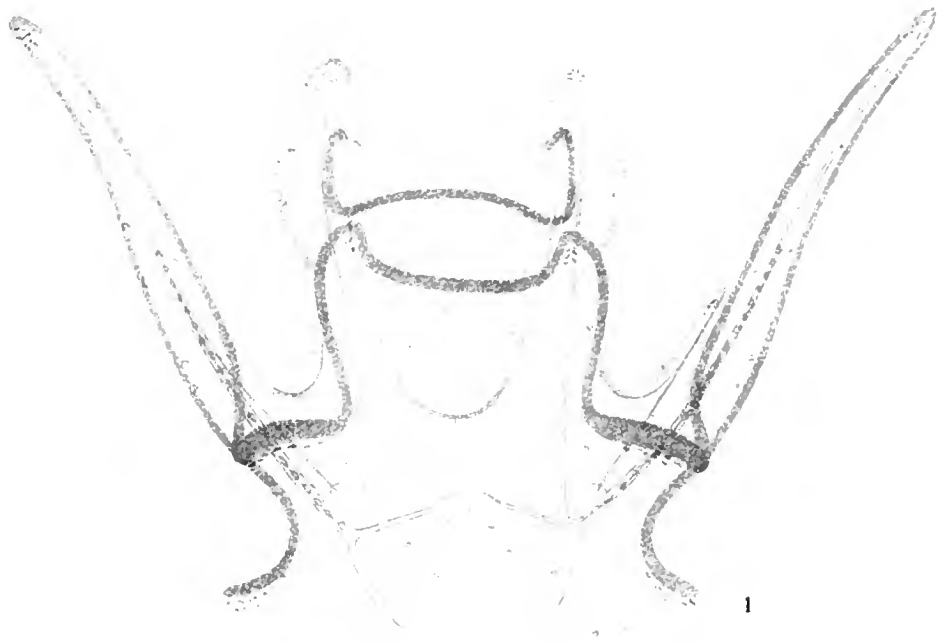
- Fig. 1. Larva of *Asterina pectinifera* (M. Tr.); 18 days old. Drawn from life. <sup>100</sup>/<sub>1</sub>.
- 2. Fully formed larva of same species; same age. Drawn from life. <sup>100</sup>/<sub>1</sub>.
  - 3. Larva of *Astropecten scoparius* M. Tr., 7 days old. s. c. suboral cavity. <sup>85</sup>/<sub>1</sub>.
  - 4. Larva of same species, 19 days old. Side view. <sup>85</sup>/<sub>1</sub>.
  - 5. Larva of same species, in metamorphosis. 19—21 days old. <sup>85</sup>/<sub>1</sub>.
  - 6. Larva of *Gymnasteria carinifera* (Lamk); 26 days old. <sup>150</sup>/<sub>1</sub>.
  - 7. *Bipinnaria* sp. from the Red Sea. <sup>60</sup>/<sub>1</sub>.
  - 8. Larva of *Stichopus californicus* (Stimps.), 6 days old. Drawn from life. <sup>75</sup>/<sub>1</sub>.
  - 9. Larva of same species, same age; side view. Drawn from life. <sup>75</sup>/<sub>1</sub>.
-



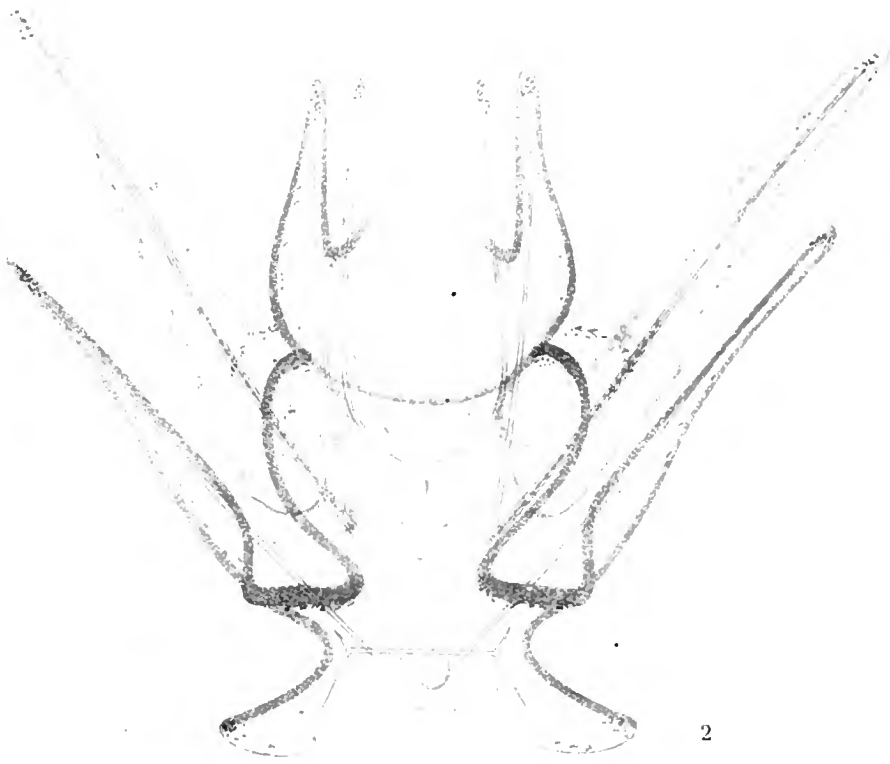






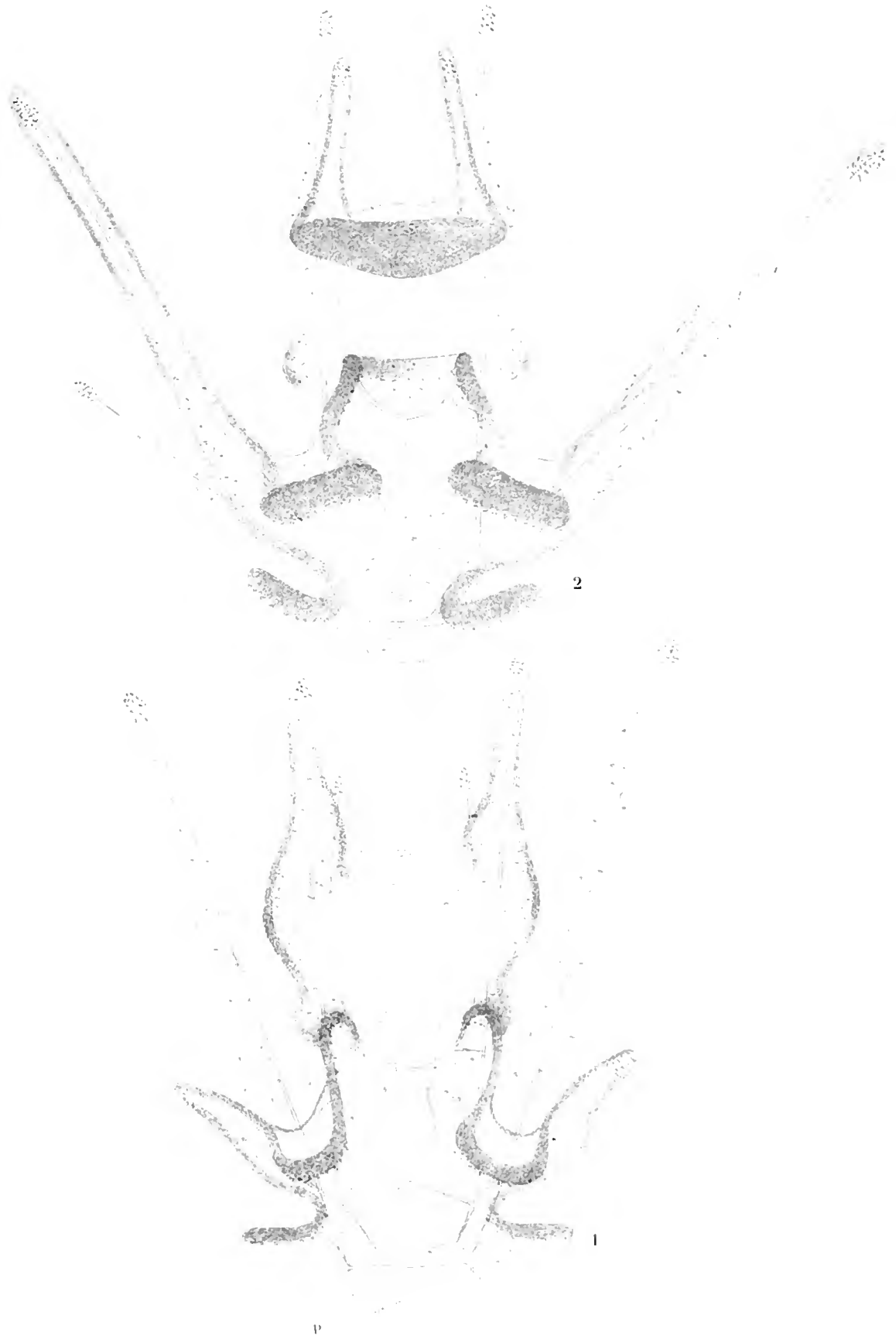


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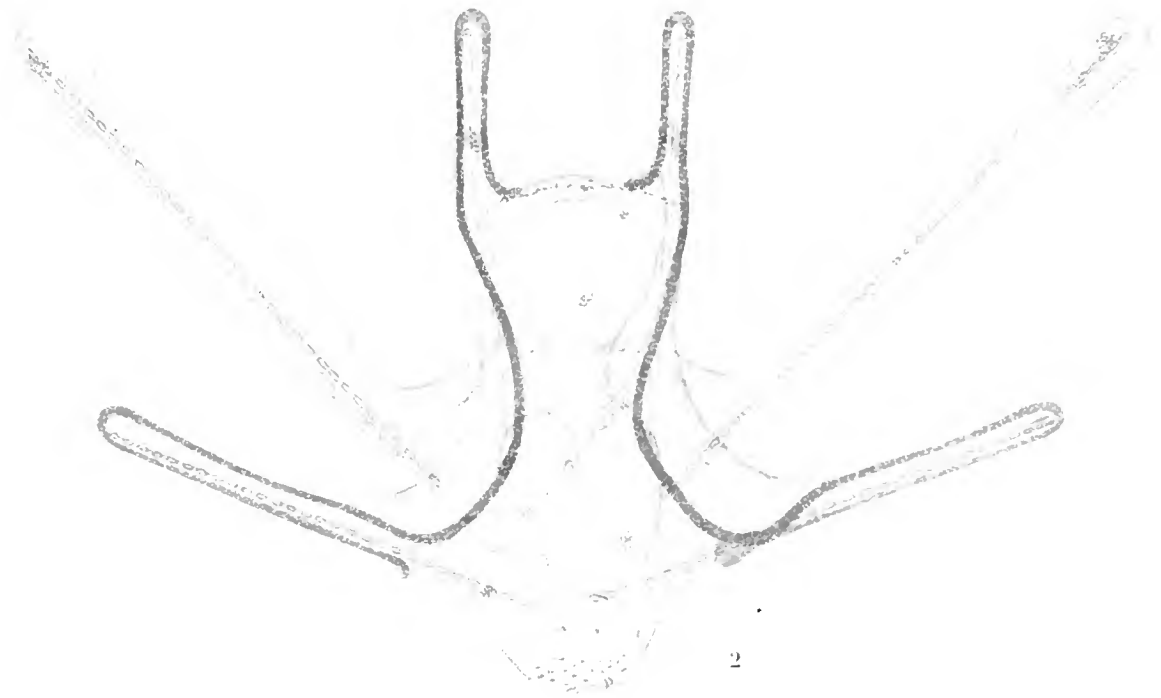
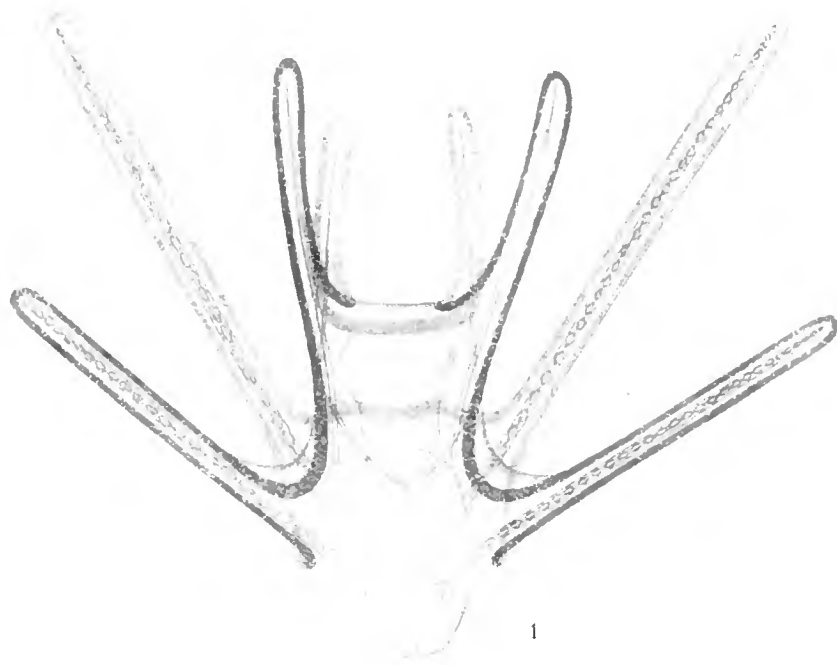


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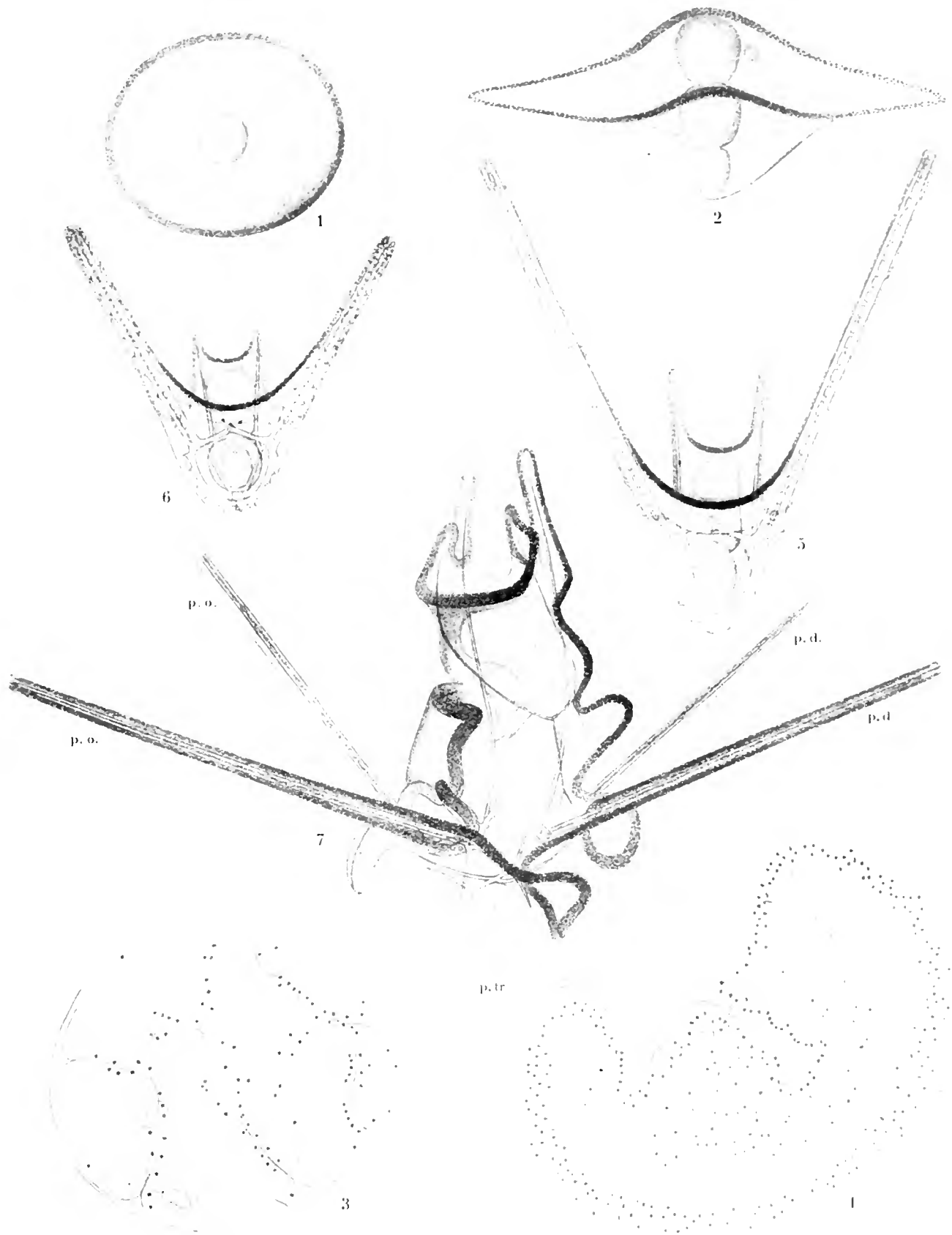






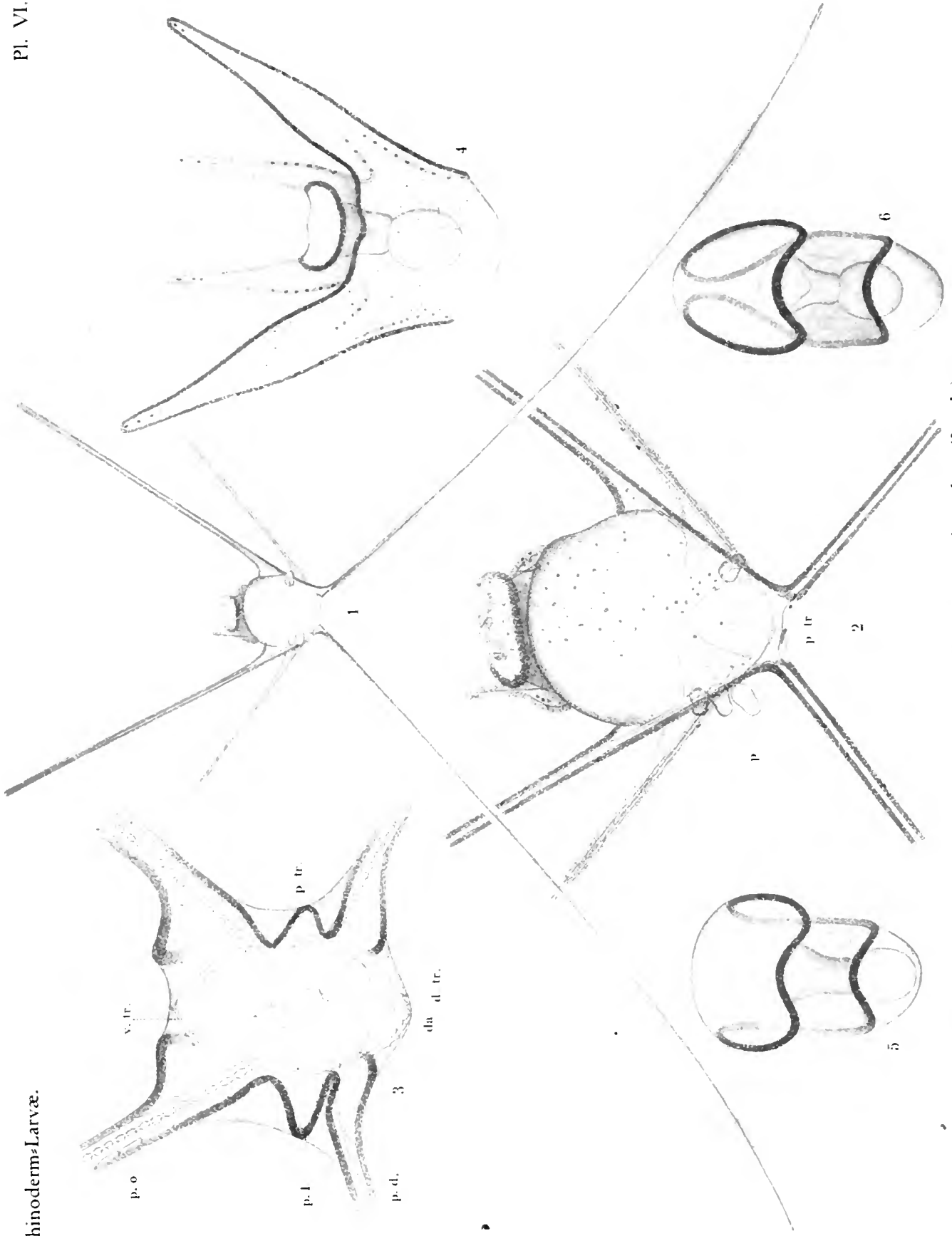
1. *Astriclypeus manni* Verr., 2. *Mellita 6-perforata* (Leske).





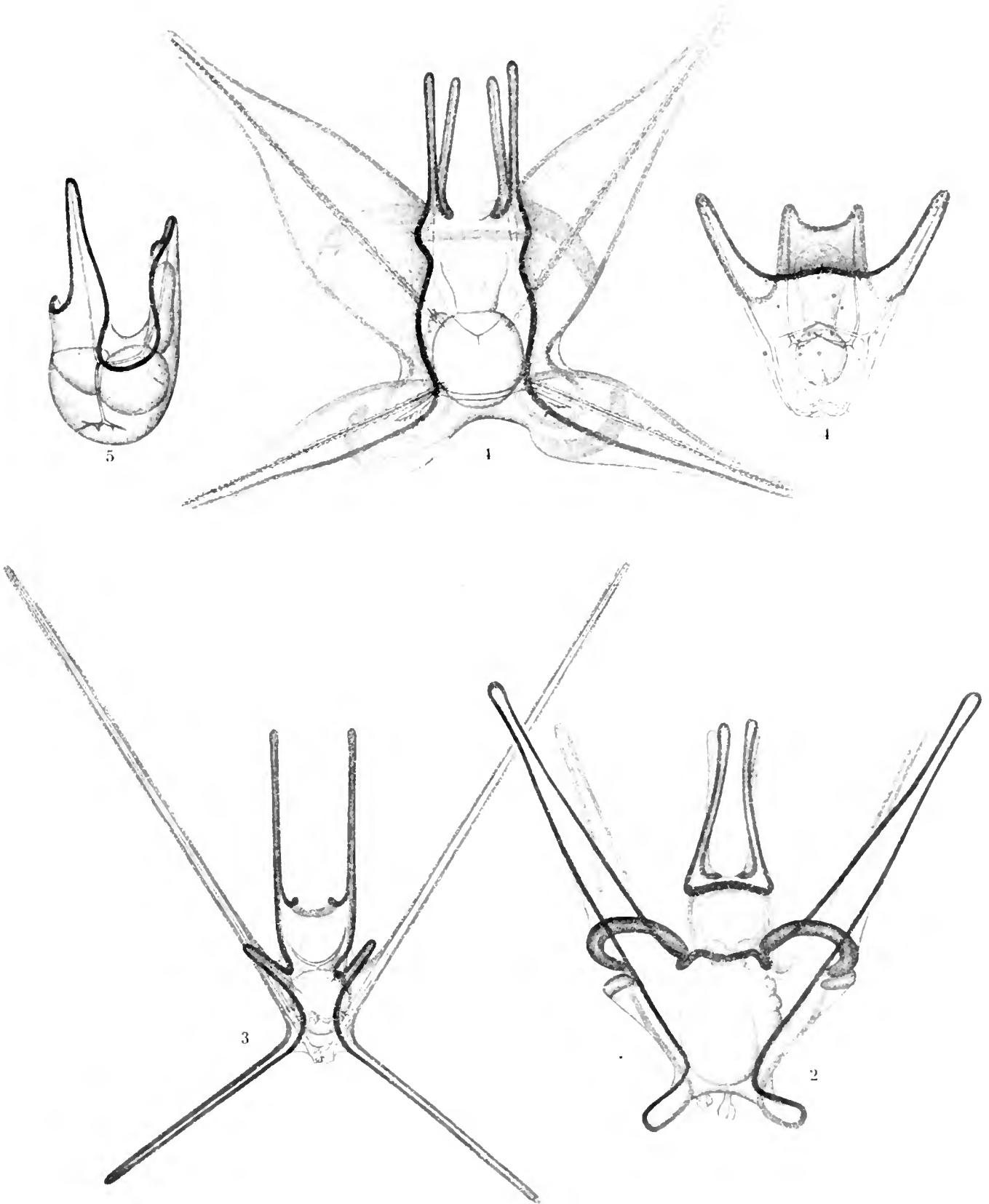






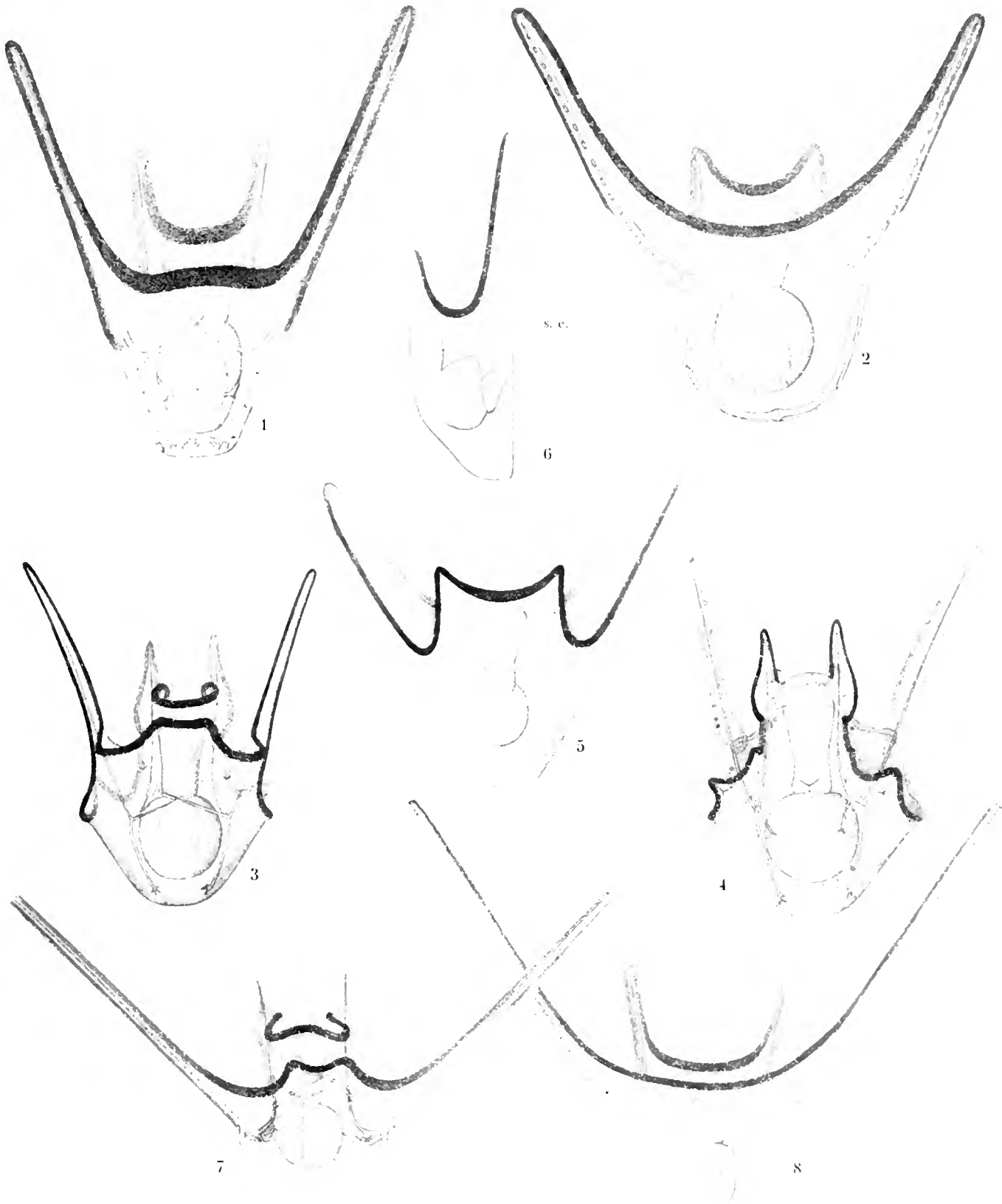
1—2. *Arbacia* sp.; 3. *Heliocidaris tuberculata* (Lamk.);  
4. *Temnotrema sculpta* A. Ag. 5—6. *Holothuria* n. sp. (?).





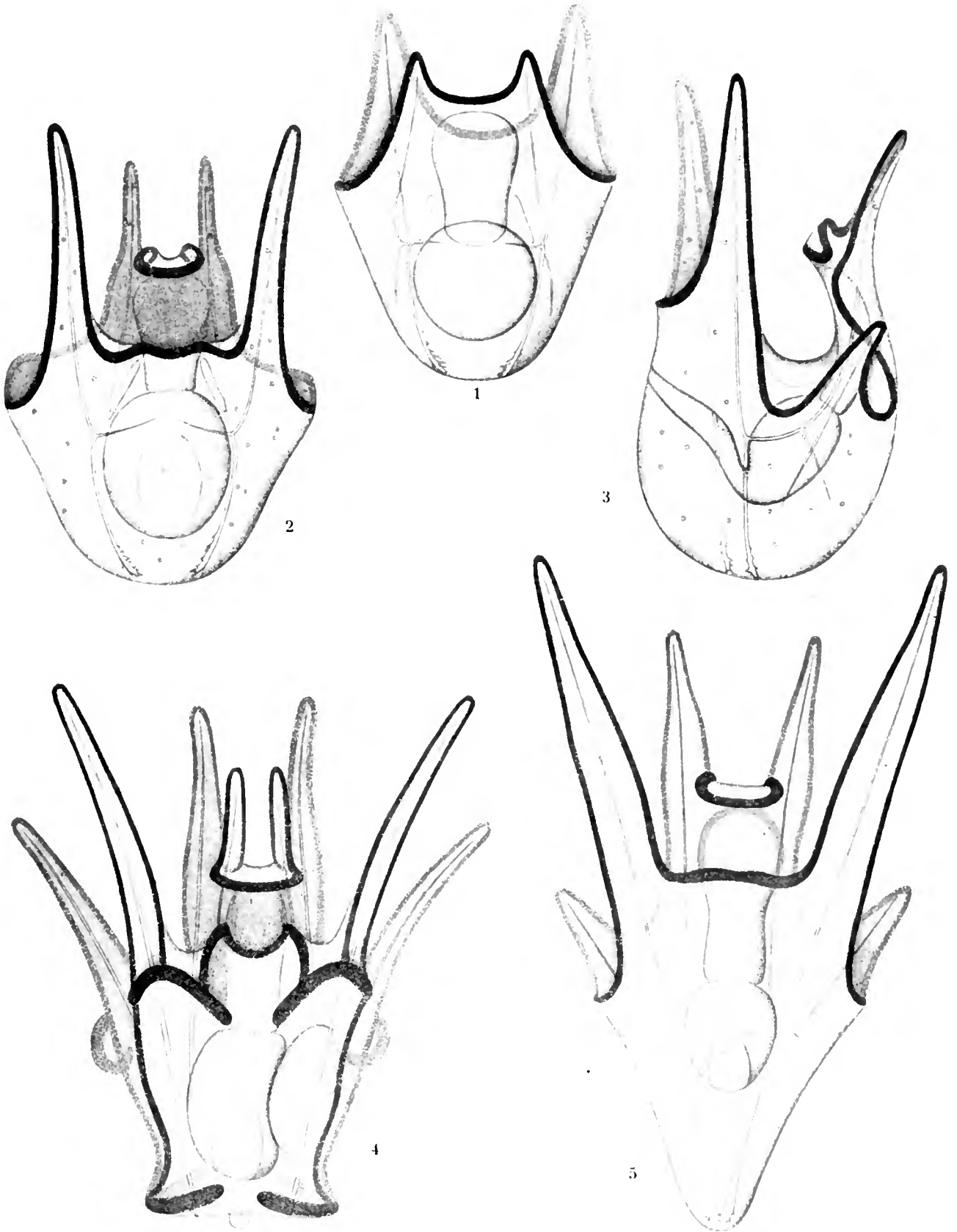
1—2. *Mespilia globulus* (Linn.);  
3. *Arbacia stellata* (Blv.); 4. *Lytechinus panamensis* Mrtsn.;  
5. *Lytech. anamesus* H. L. Clark.





1. *Lytechinus variegatus* (Lamk.); 2. *Tripneustes esculentus* (Leske);  
 3—4. *Lytechinus anamesus* H. L. Clark; 5—6. *Tripneustes gratilla* (Linn.);  
 7. *Toxopneustes roseus* A. Ag. (?); 8. *Toxopneustes pileolus* (Lamk.).

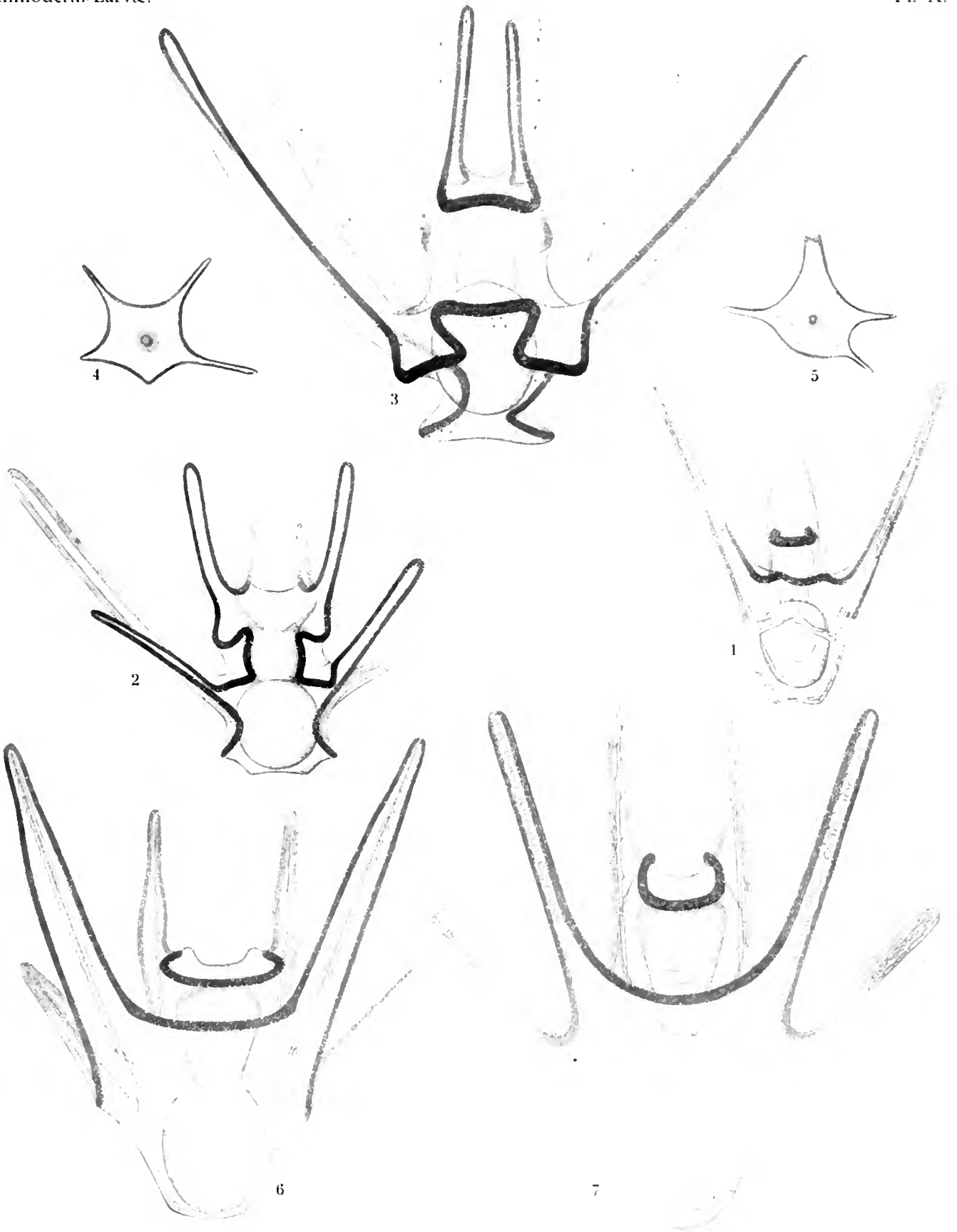




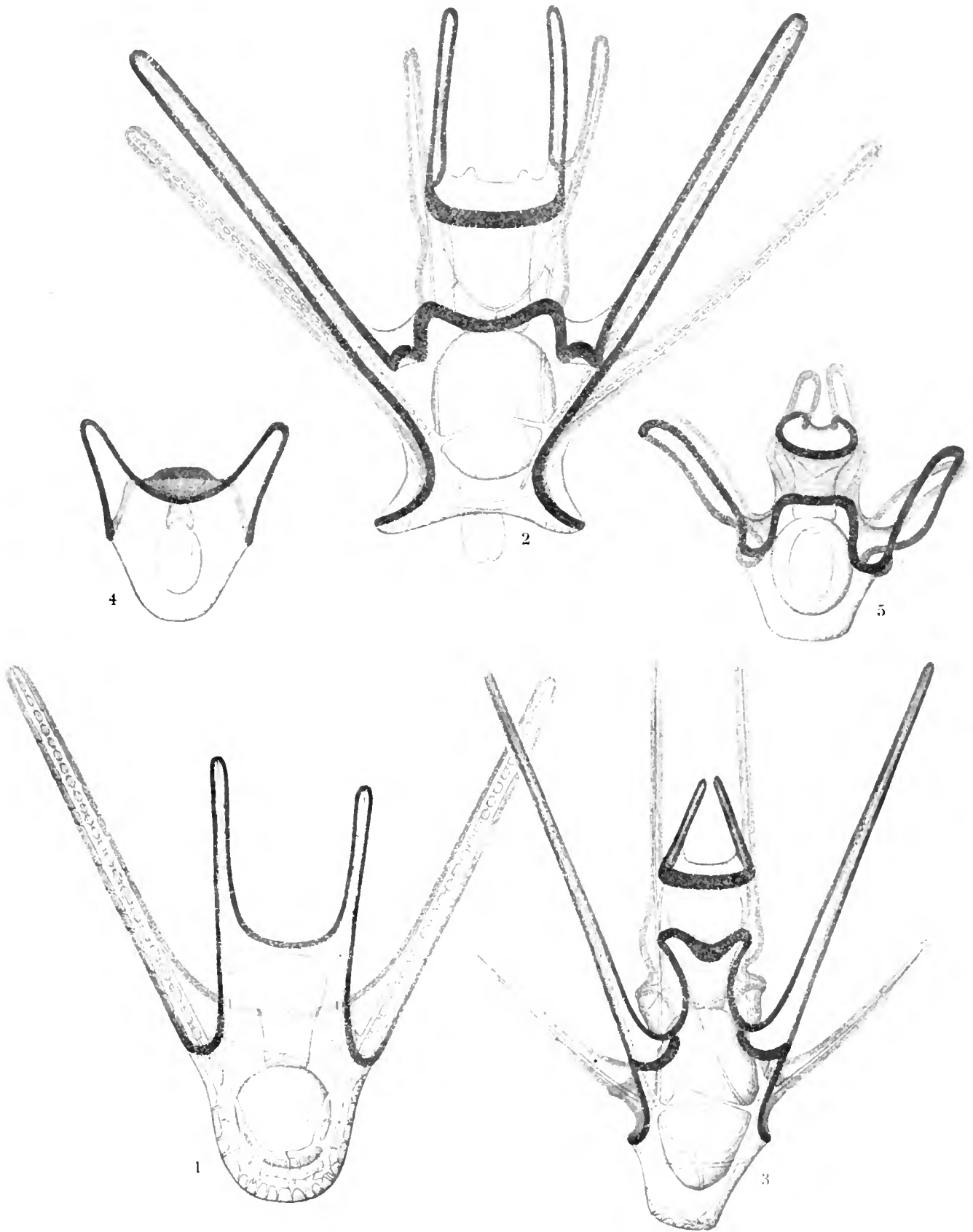
1—4. *Strongylocentrotus franciscanus* (A. Ag.);  
5. *Str. pulcherrimus* (A. Ag.).





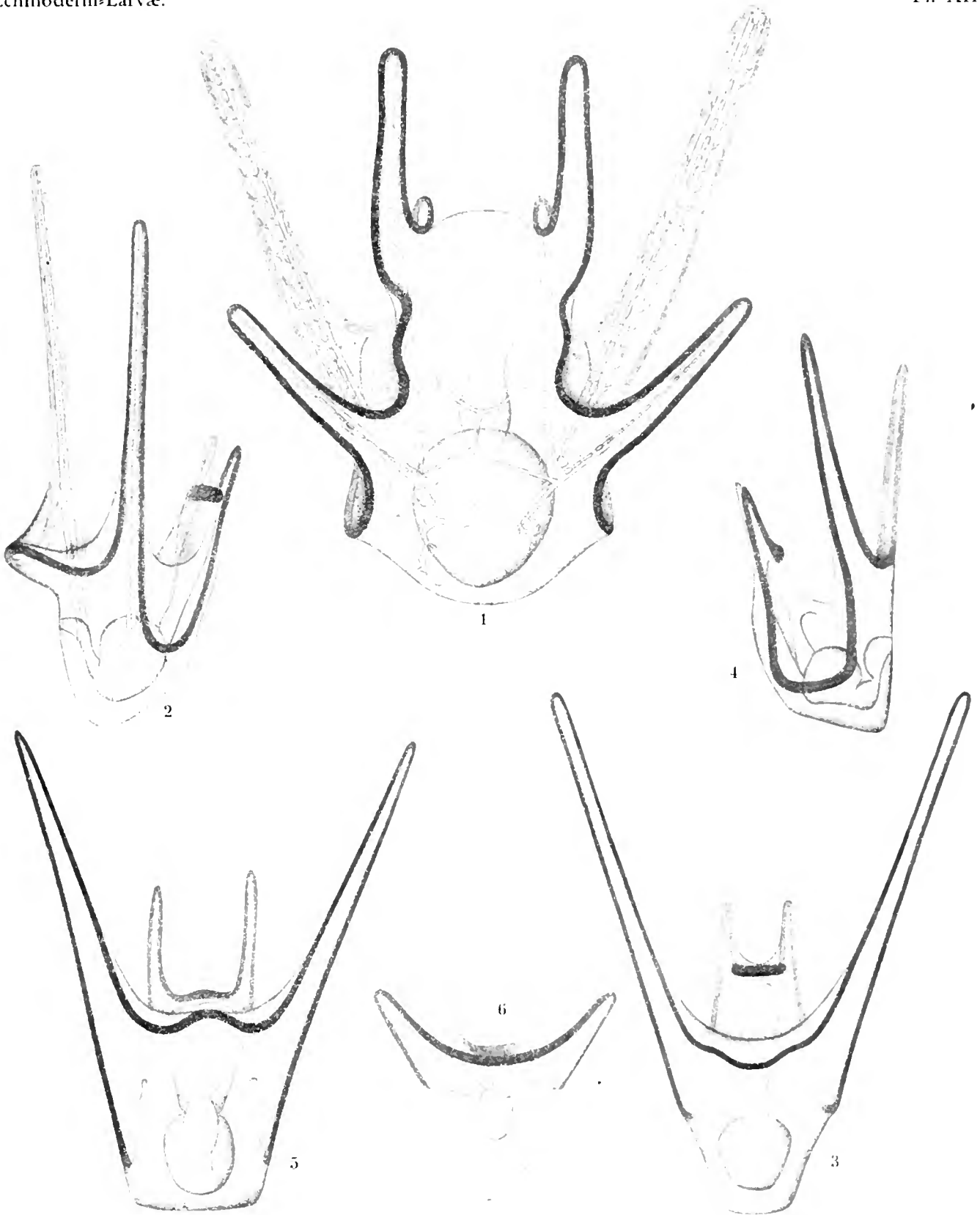






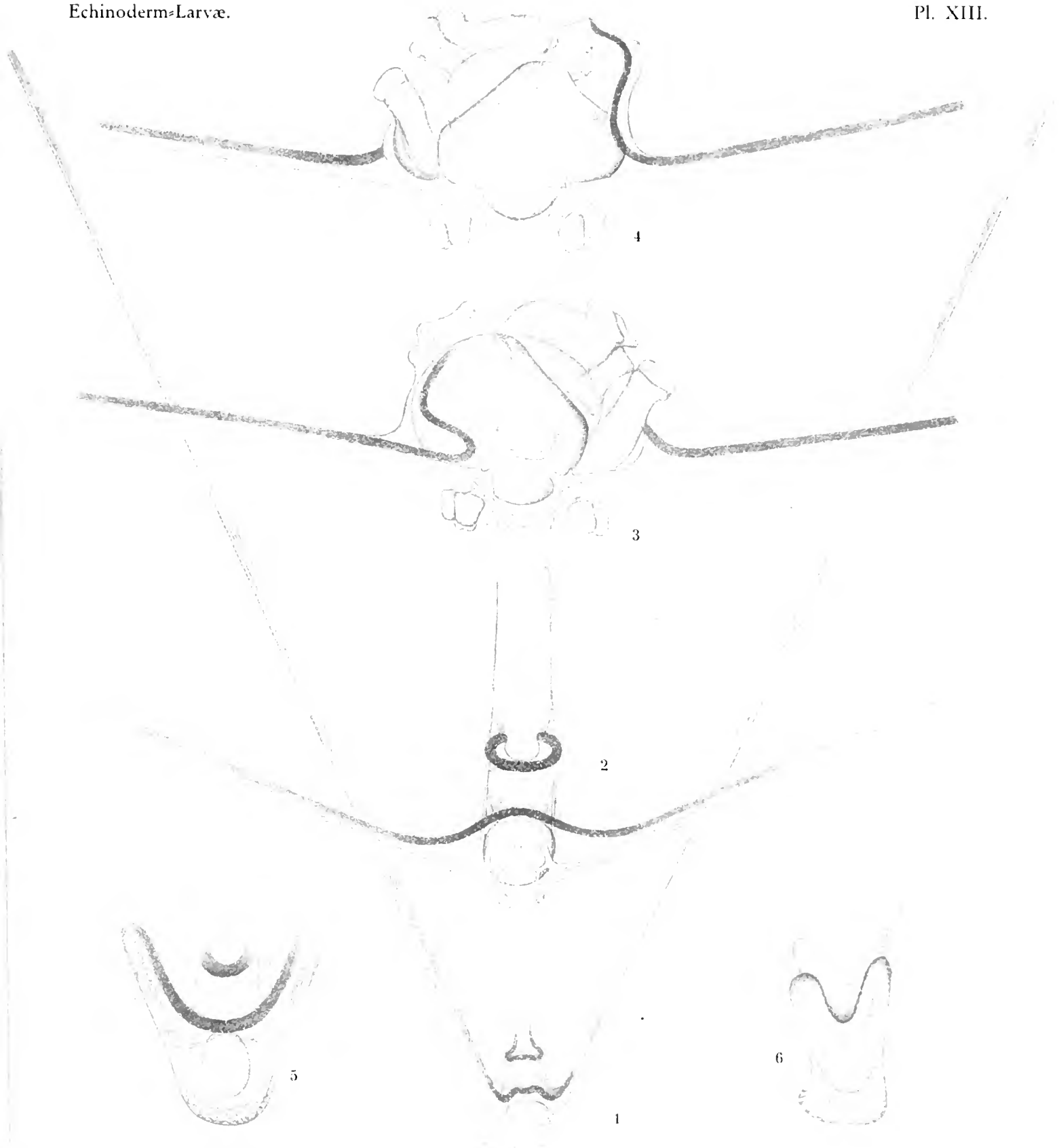
1—2. *Heliocidaris tuberculata* (Lamk.);  
3. *Echinopluteus* of *Temnopleurid*, sp. c.;  
4—5. *Echinobrissus recens* (M. Edw.).





1. *Echinometra lucunter* (Linn.);  
2—3. *Echinometra oblonga* (Blv.); 4—5. *Colobocentrotus atratus* (Linn.);  
6. *Tennopleurus toreumaticus* (Klein).

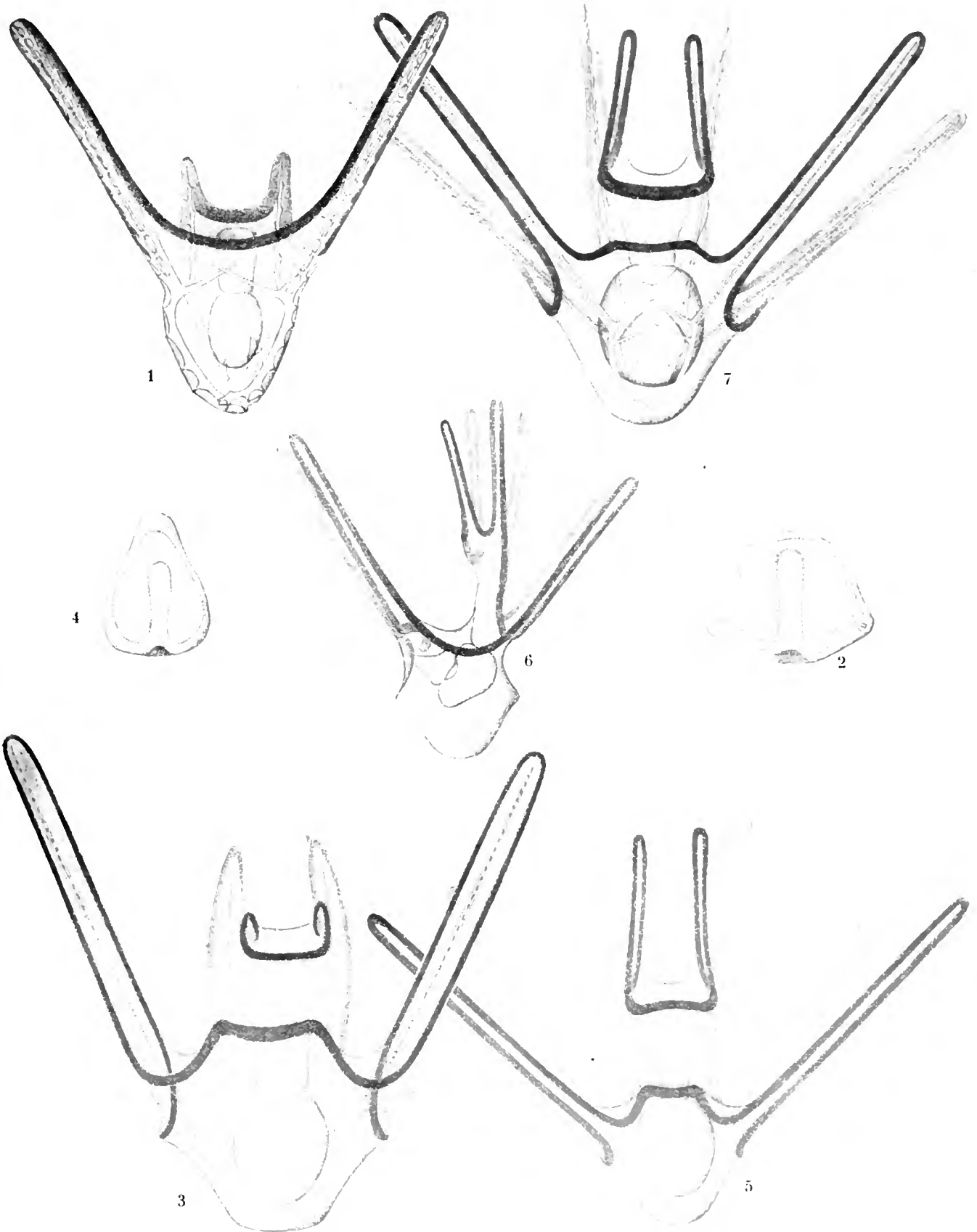




1—4. *Echinopluteus transversus*, species a, c, f.  
5—6. *Mellita 6-perforata* (Leske).







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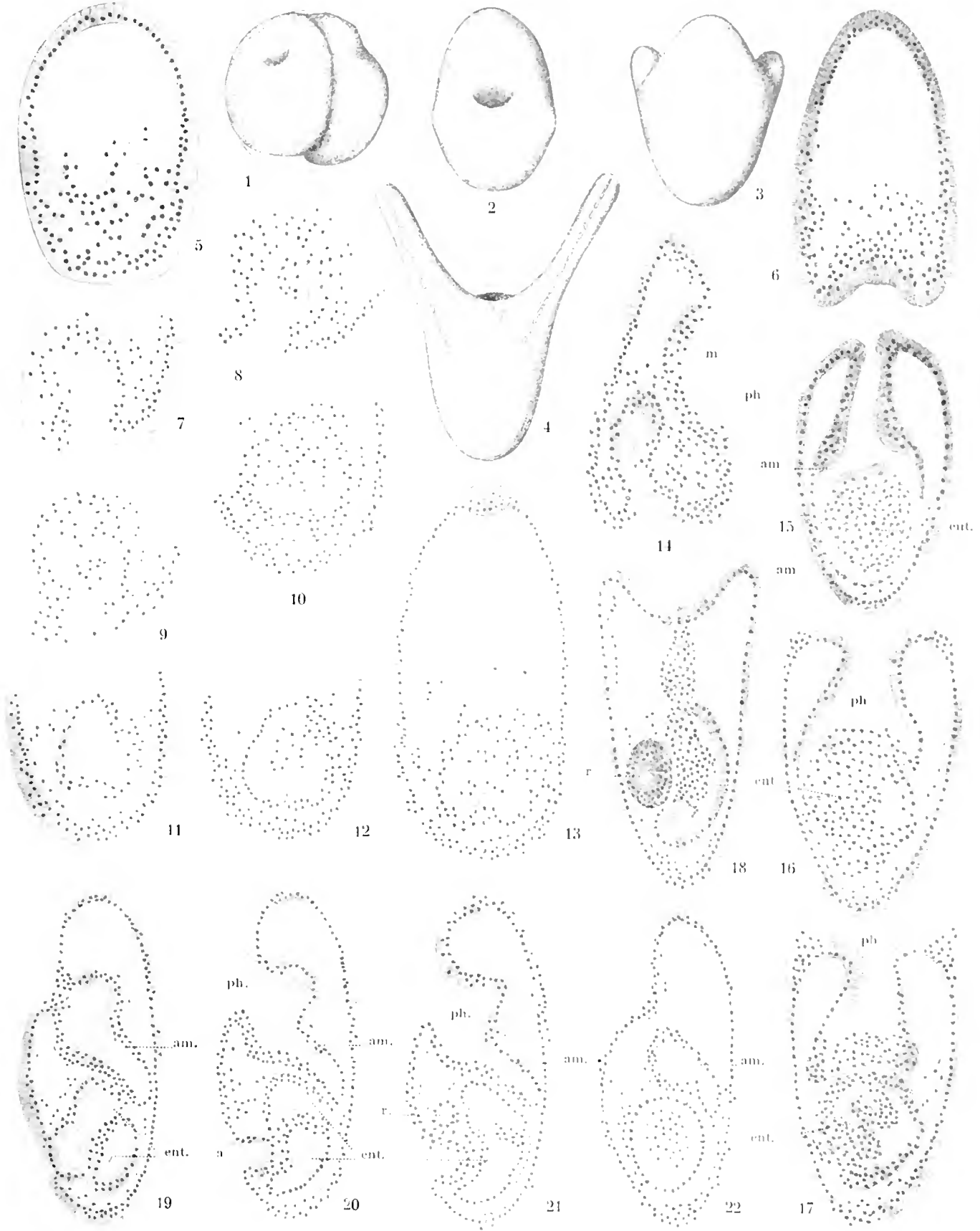
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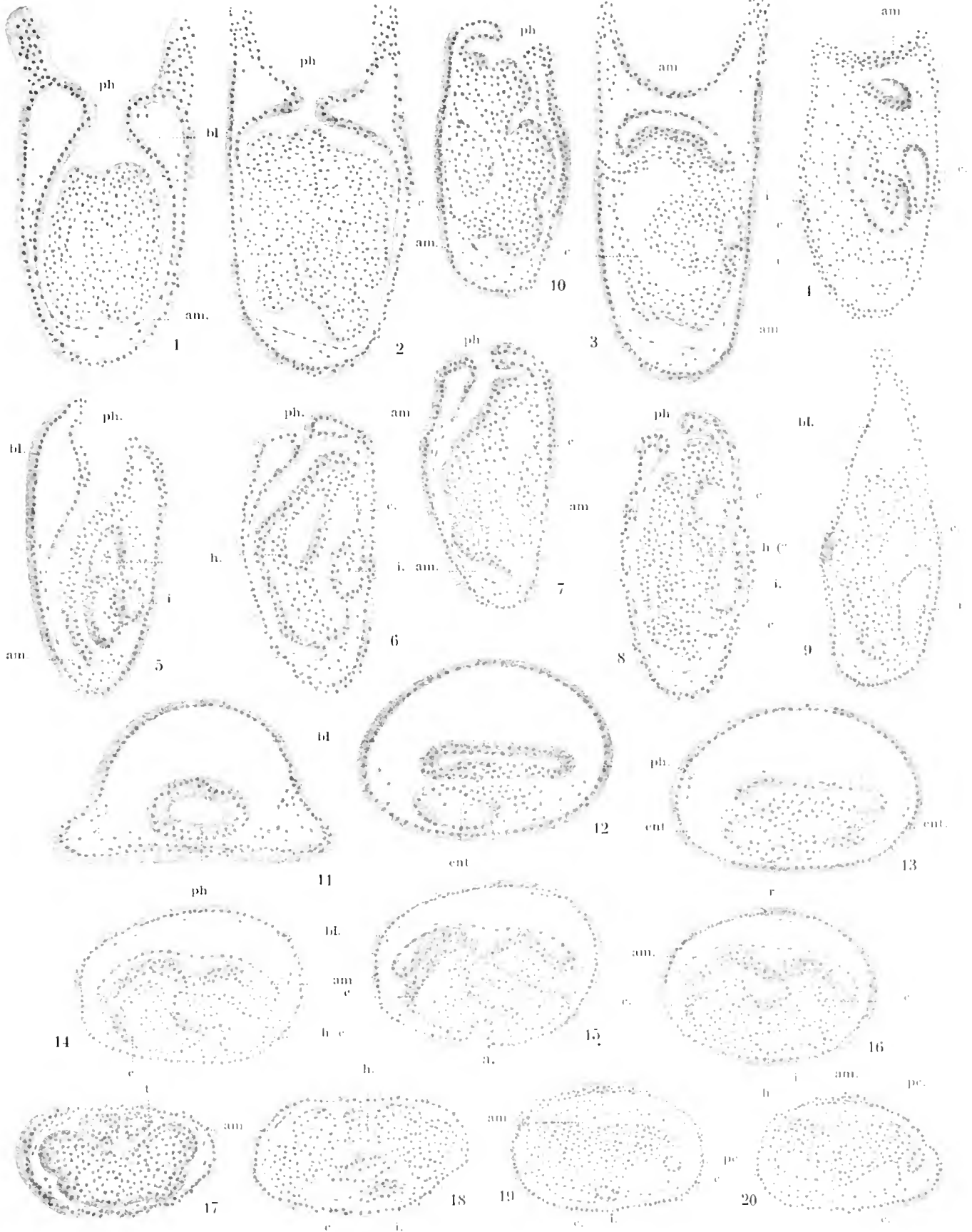
1. *Laganum diplopora* H. L. Clark;  
2-3. *Clypeaster japonicus* Döderlein; 4. *Echinarachnius mirabilis* (A. Ag.);  
5-6. *Echinarachnius excentricus* (Esch.); 7. *Encope micropora* Ag.



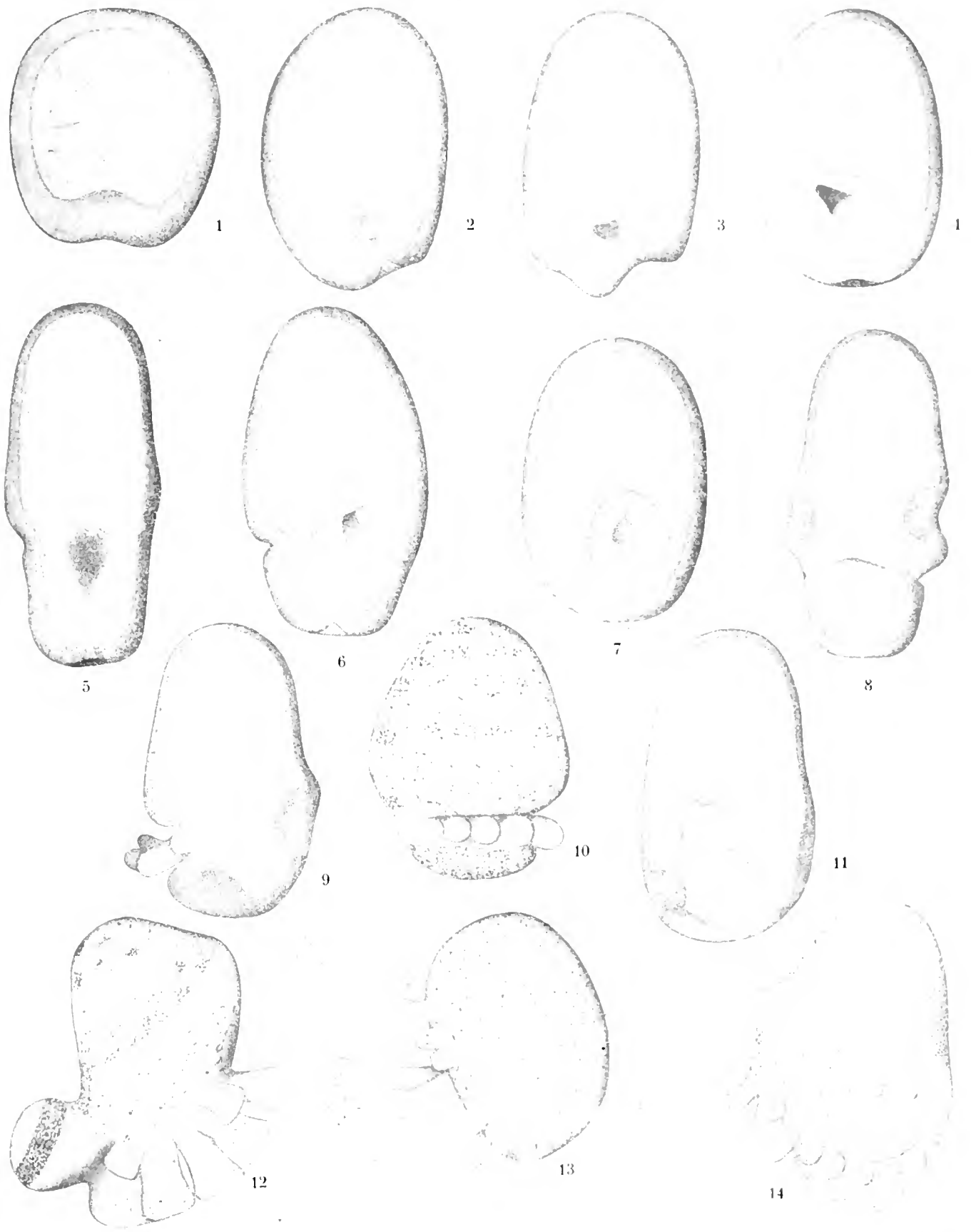


Th. Mortensen del.



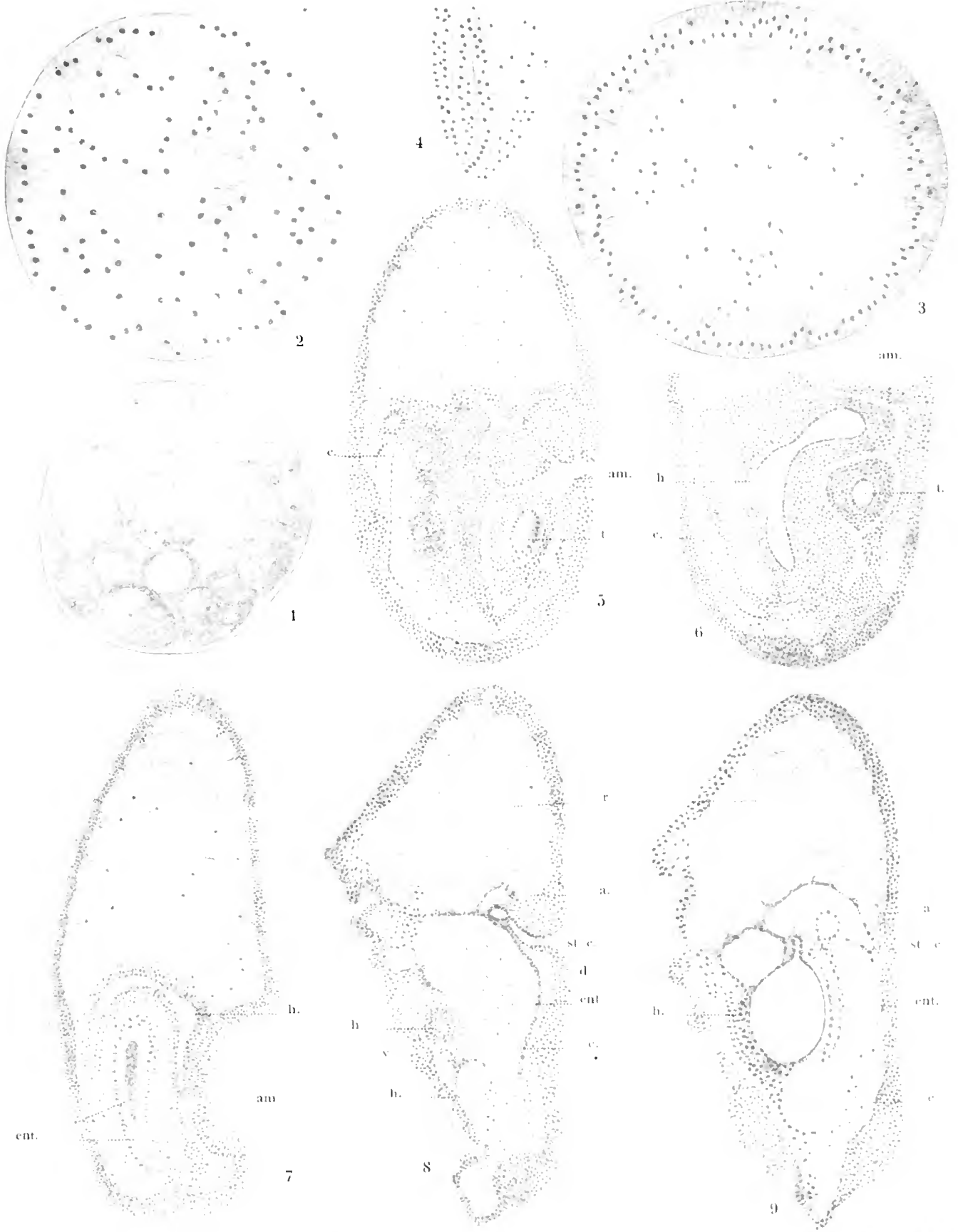




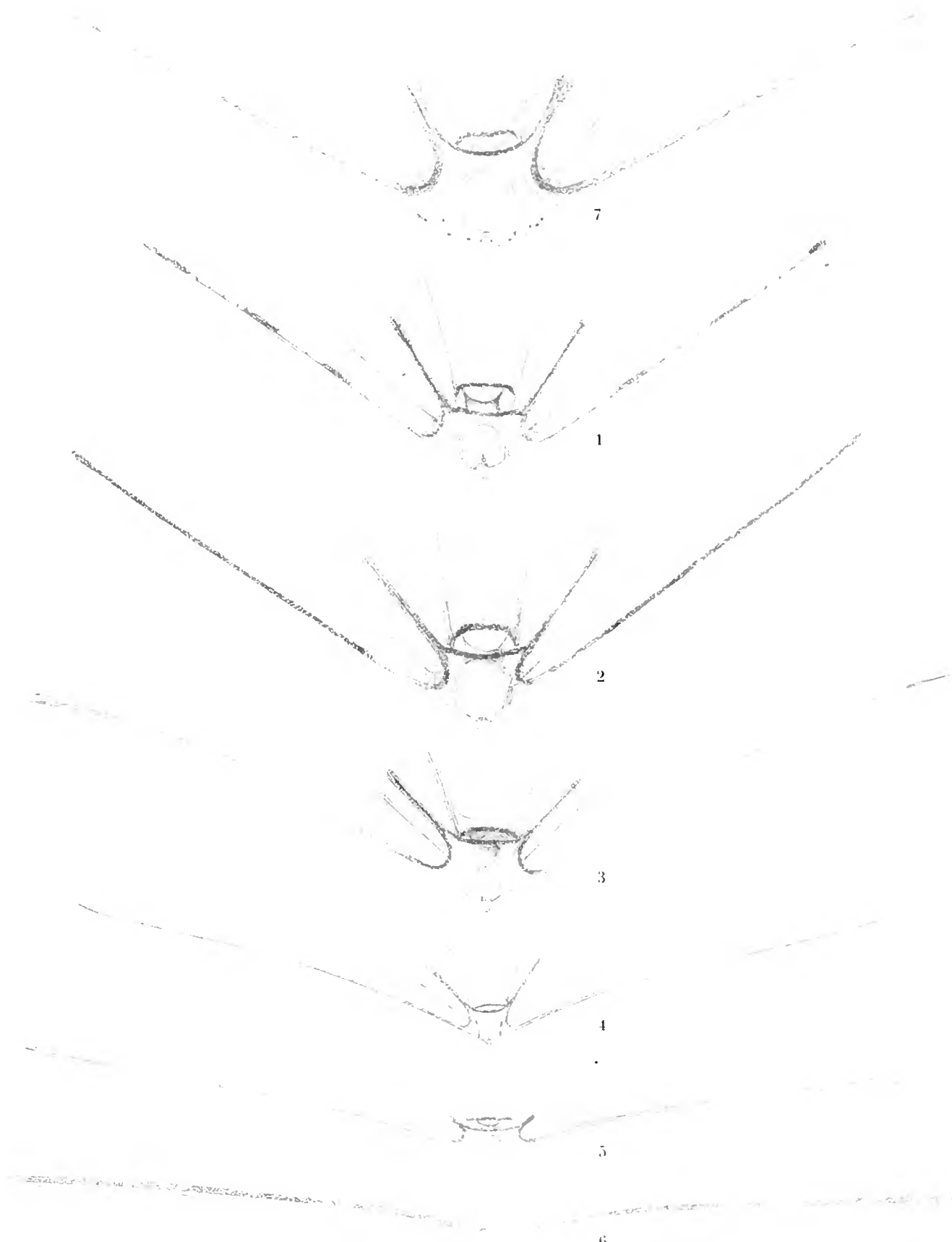




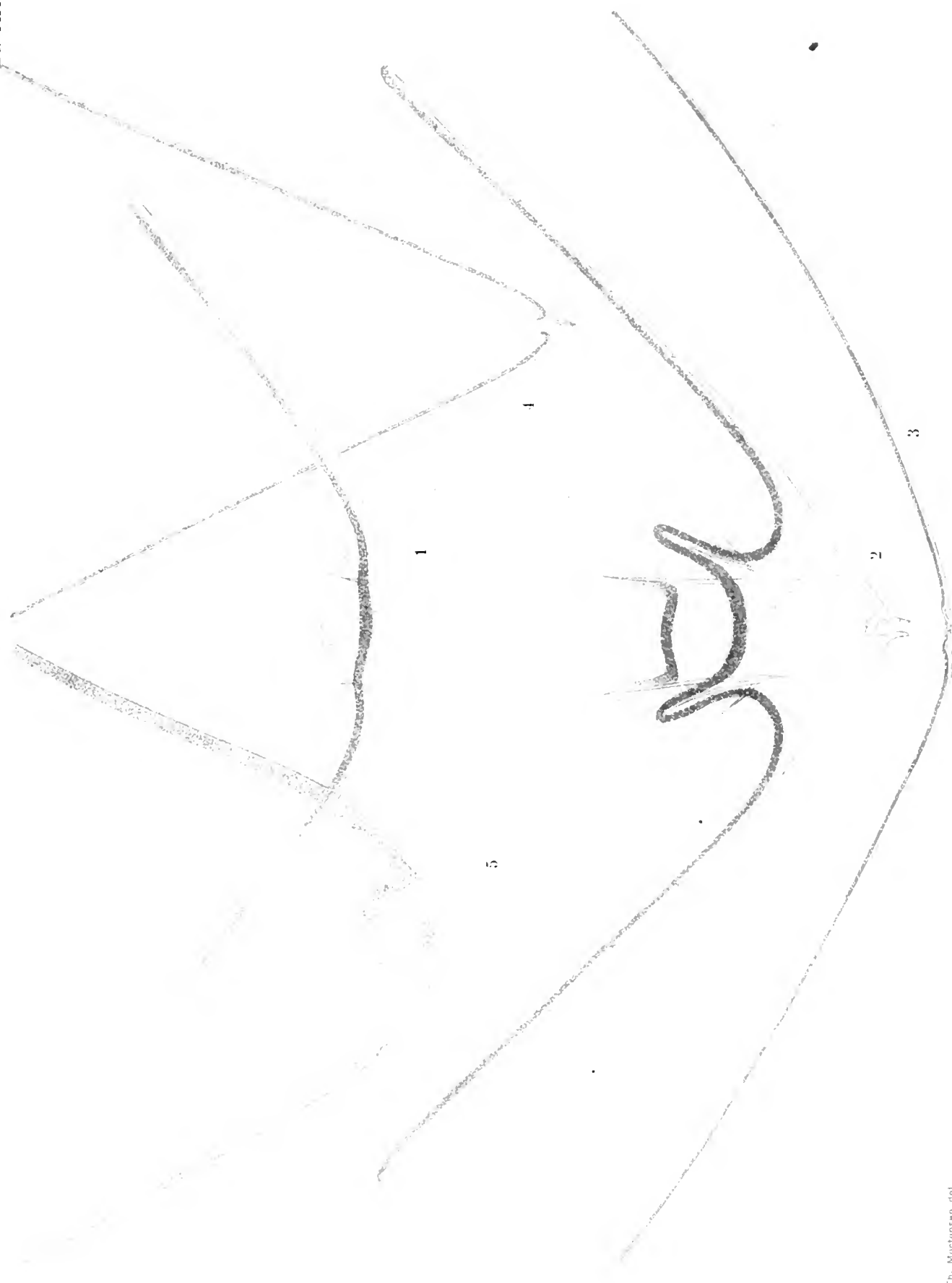




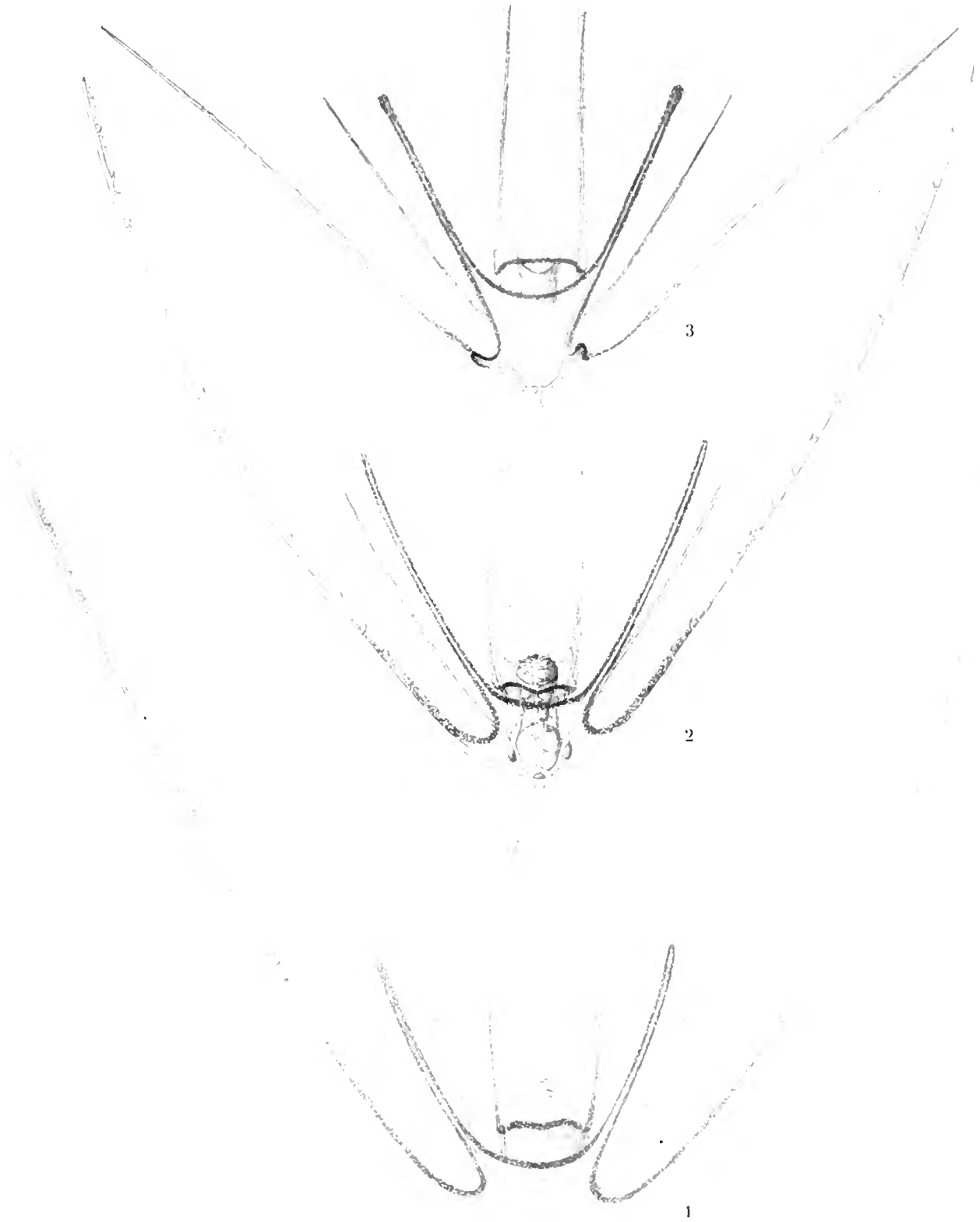








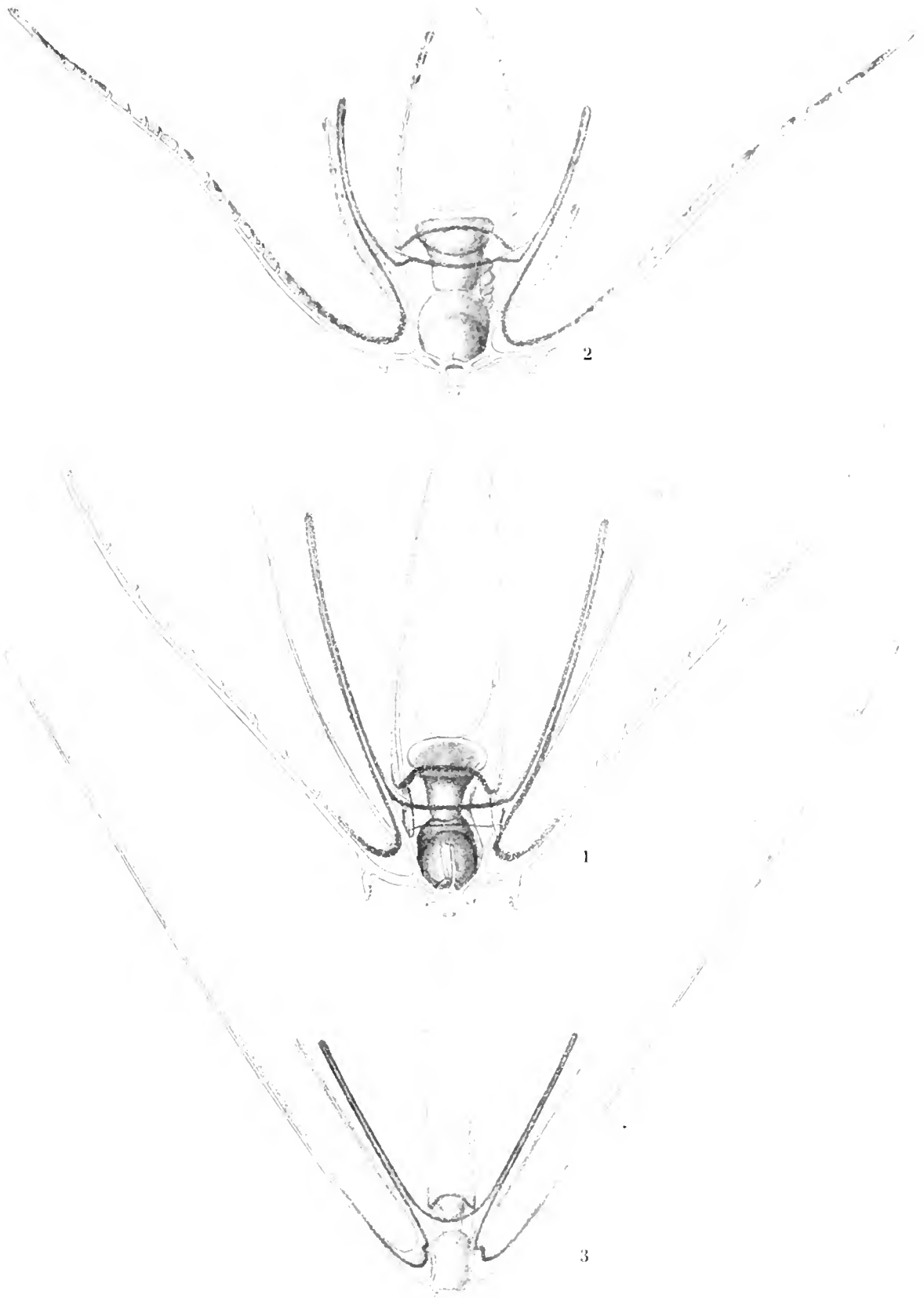




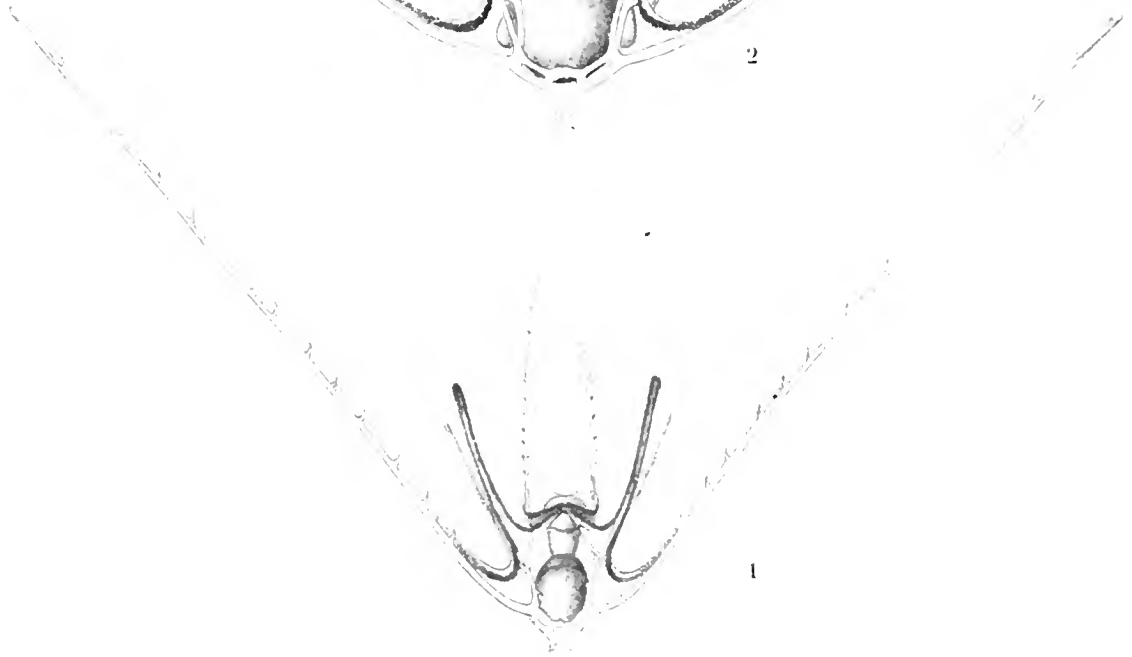
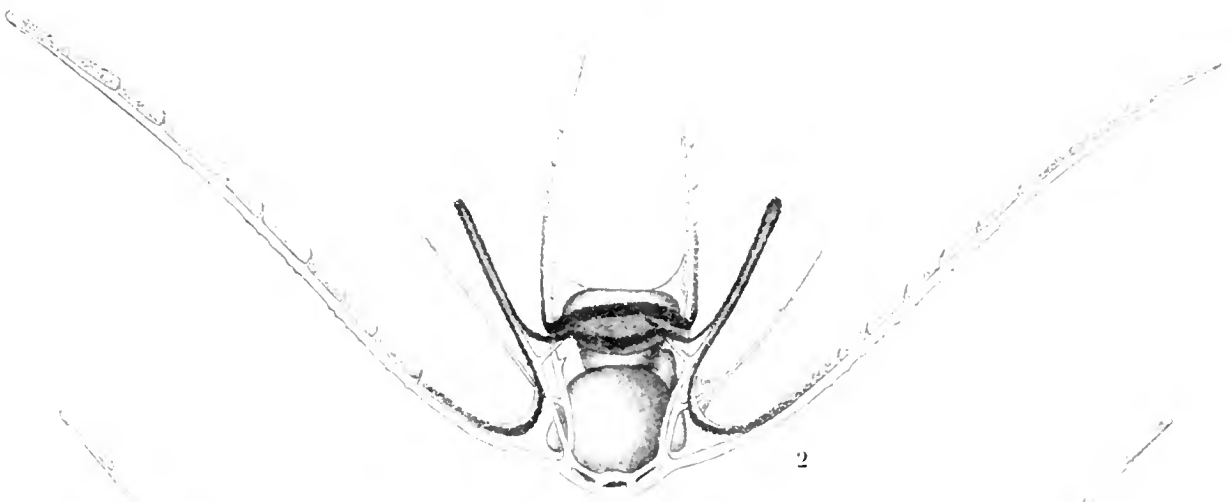
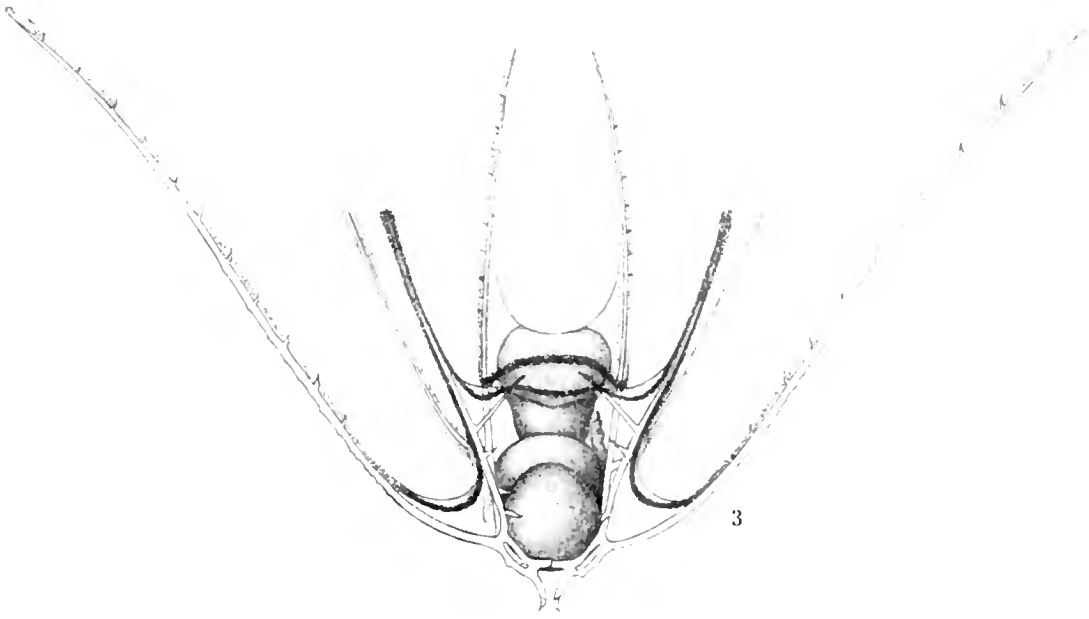
1-2. *Ophiopluteus costatus*, sp. a-b.; 3. *Ophiopl. opulentus*, sp. a.



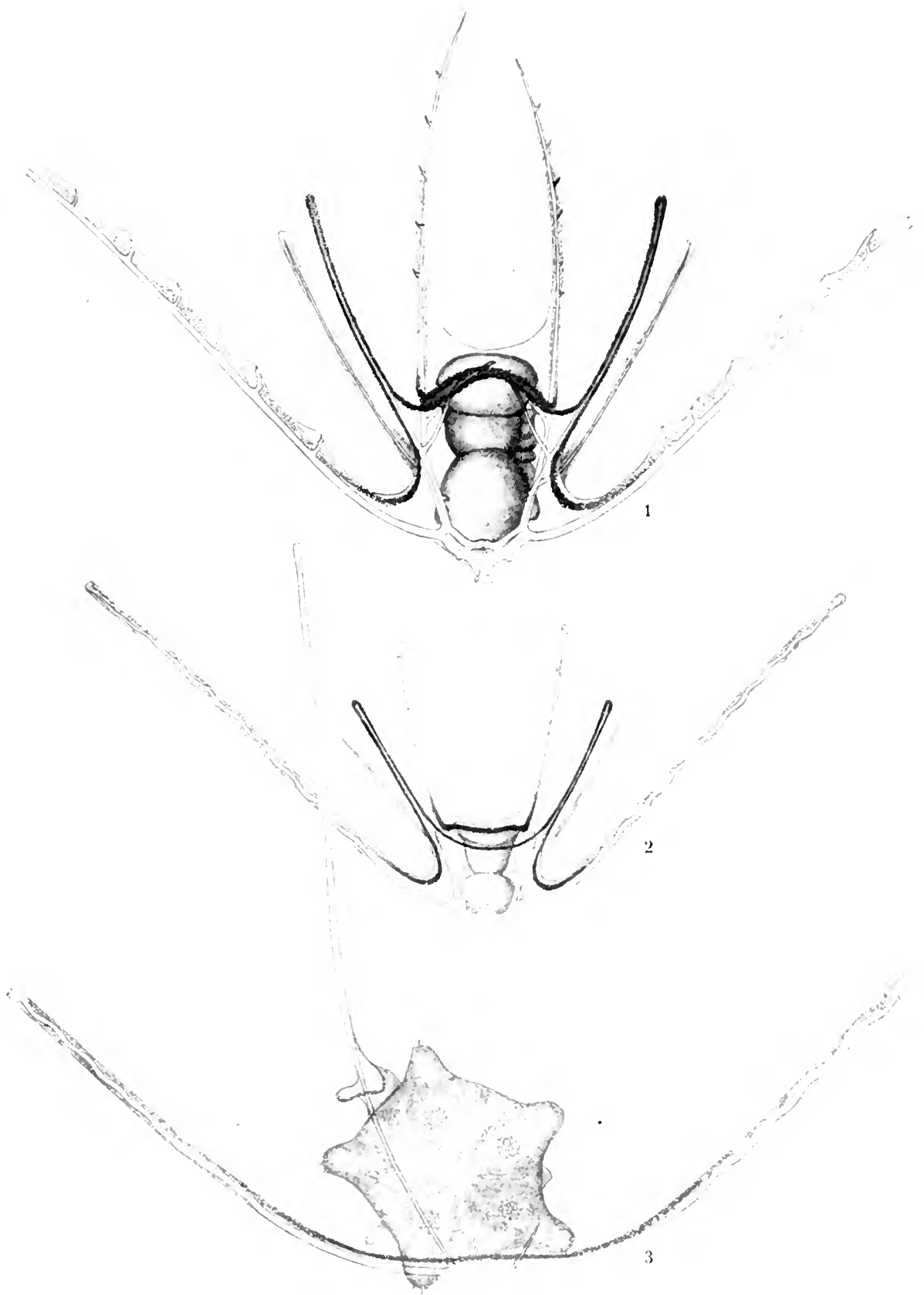






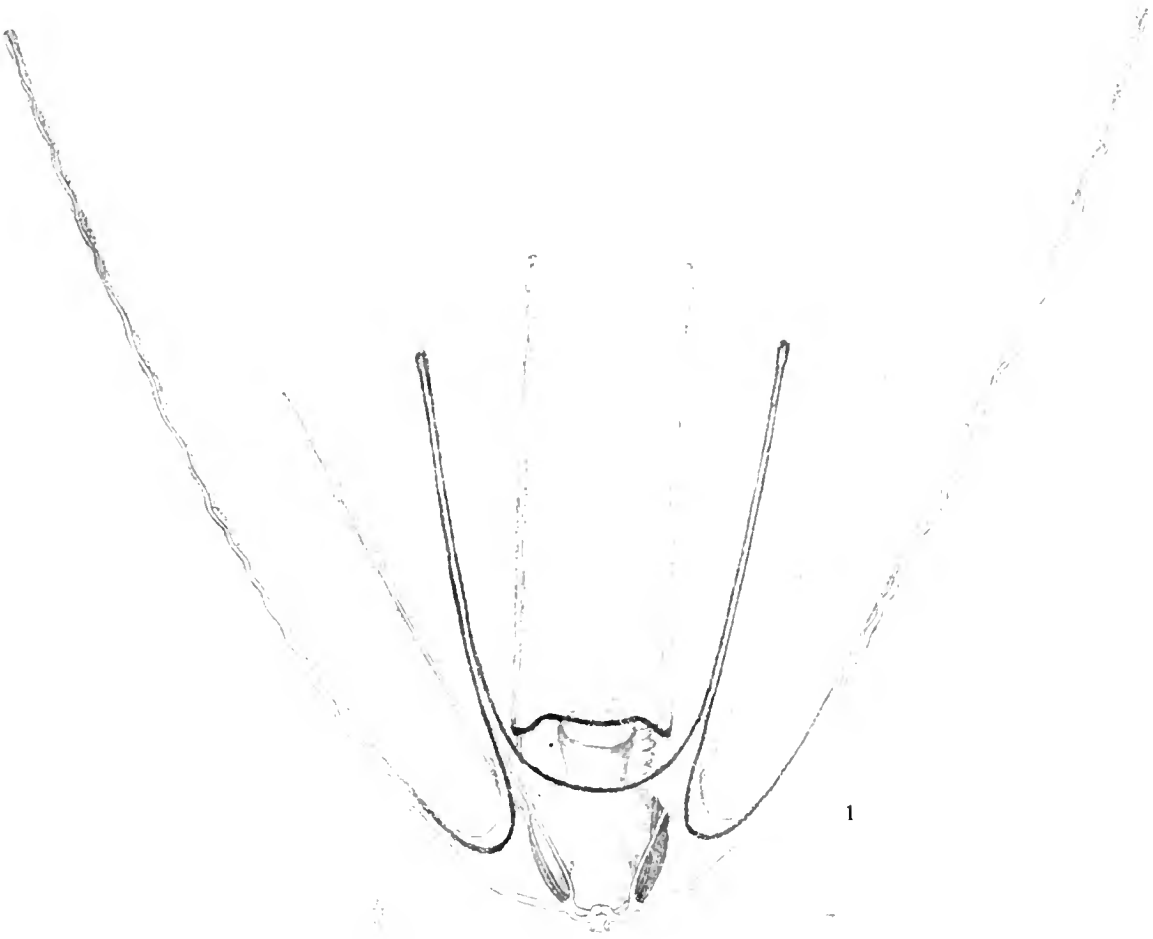




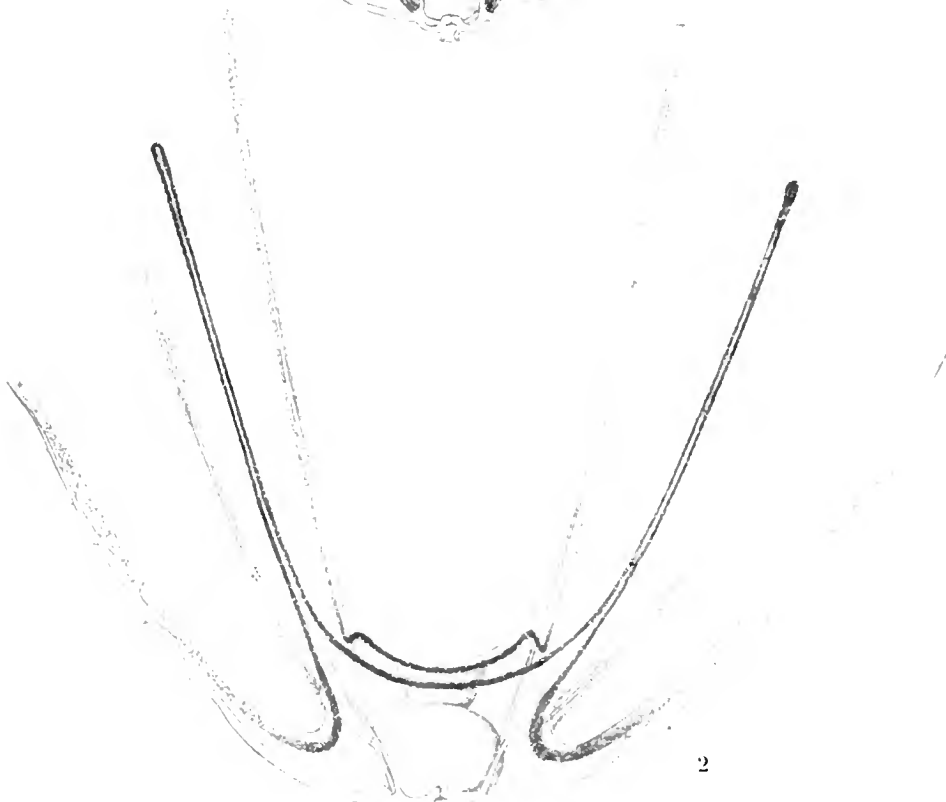


1. *Ophiopluteus fulcitus*, sp. n. 2-3. *Ophiopl. undulatus*, sp. n.





1

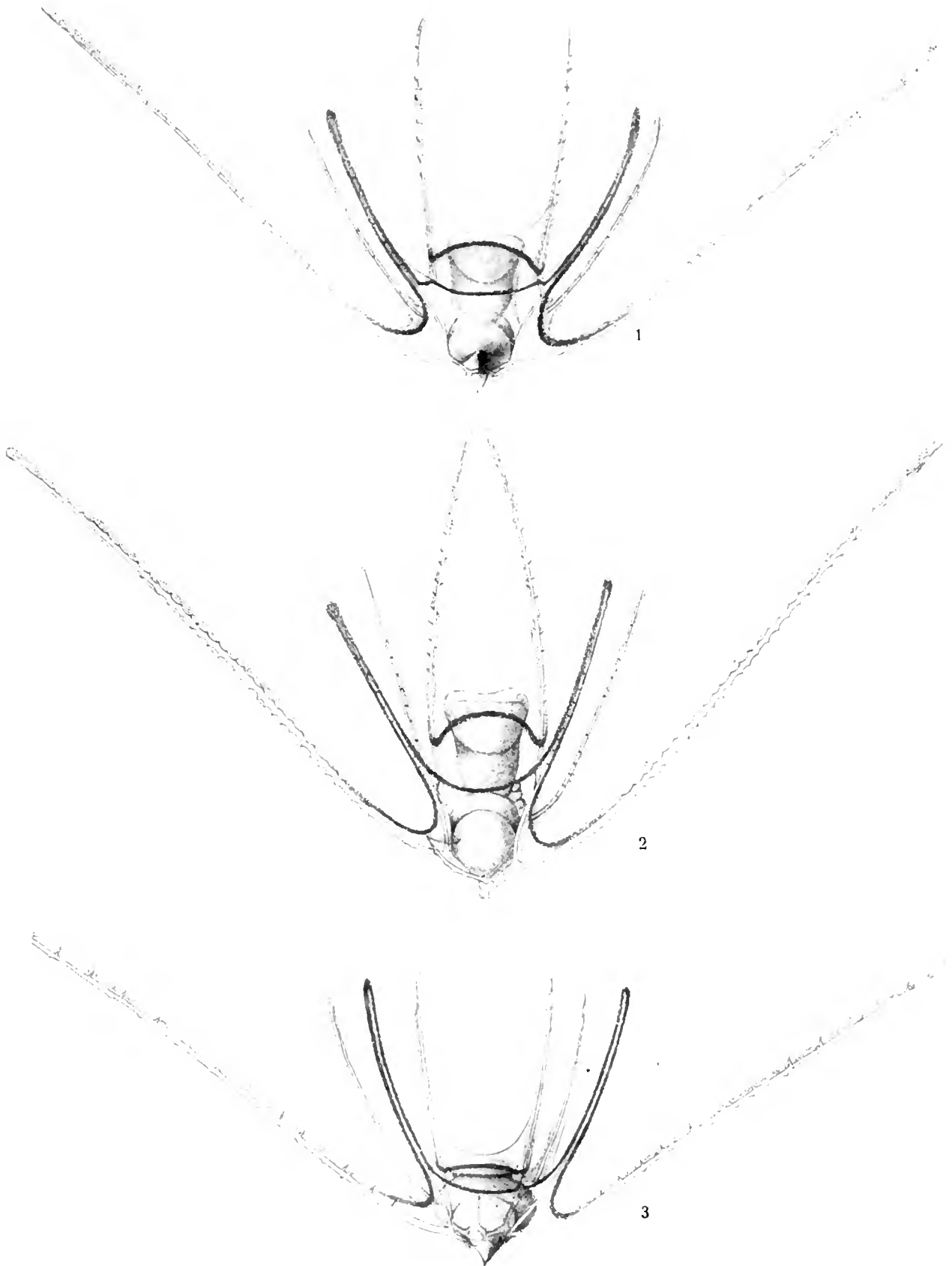


2

*Ophiopluteus undulatus*, species a-b.

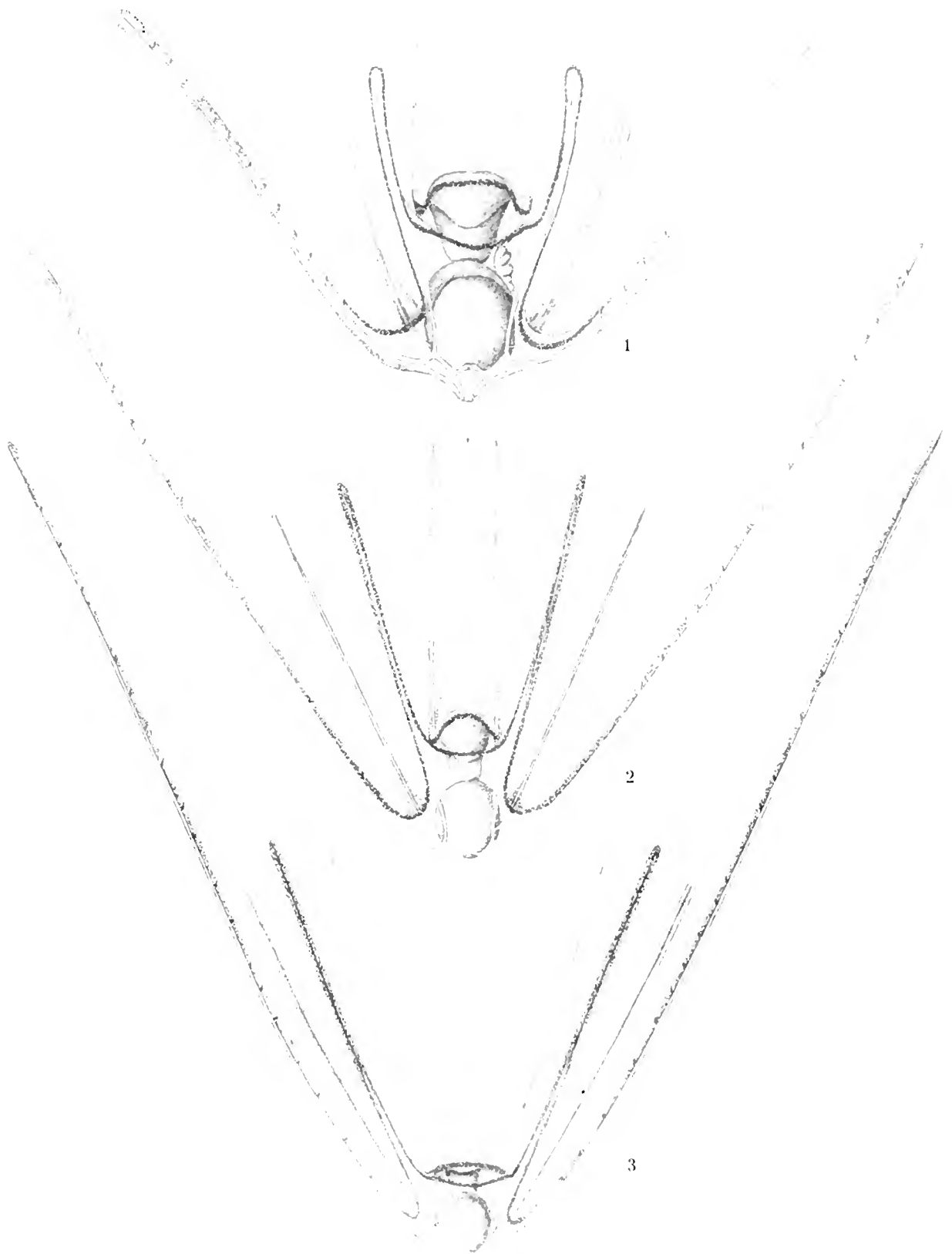






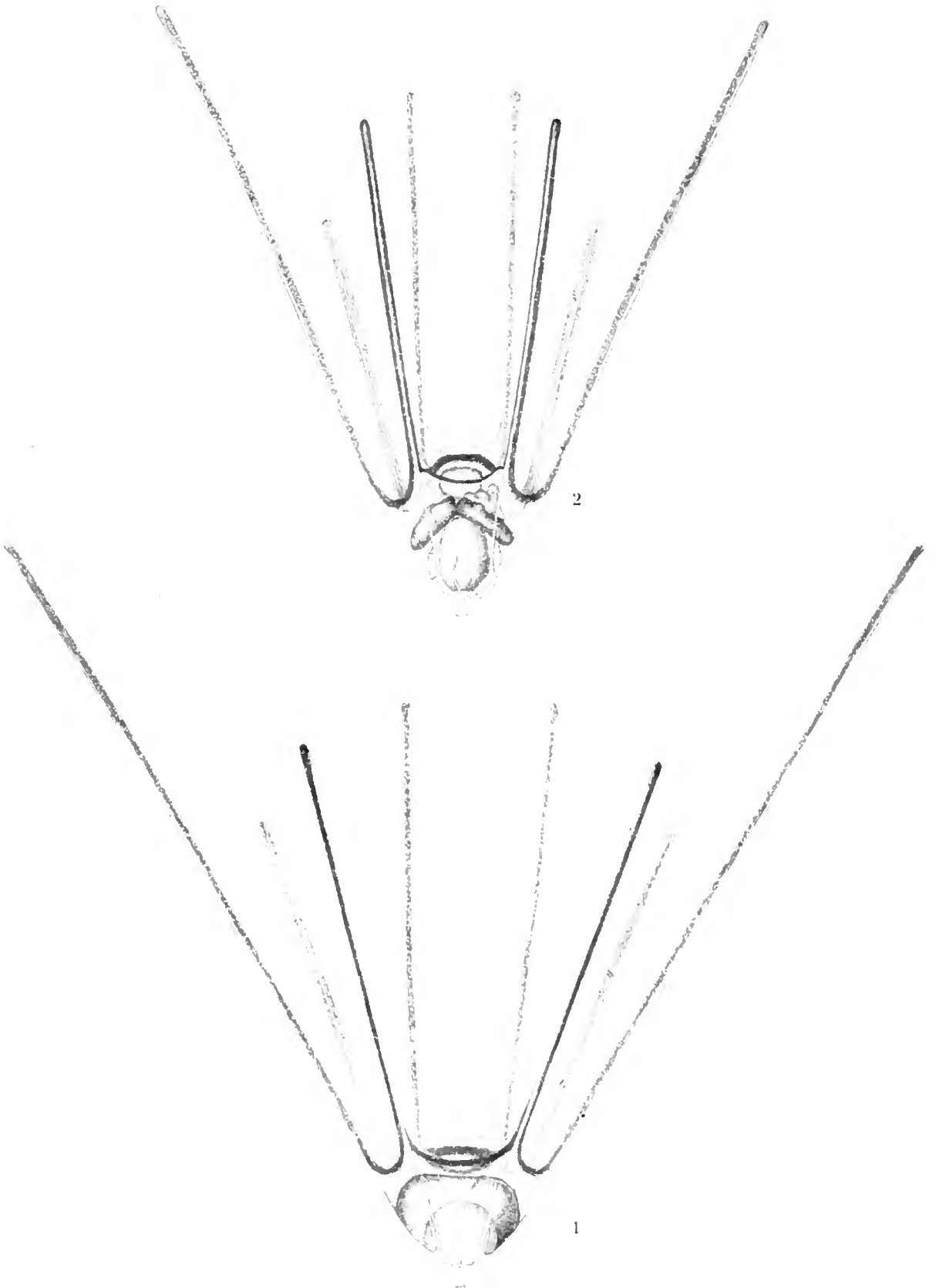
Ophiopluteus arcifer, species a—c.



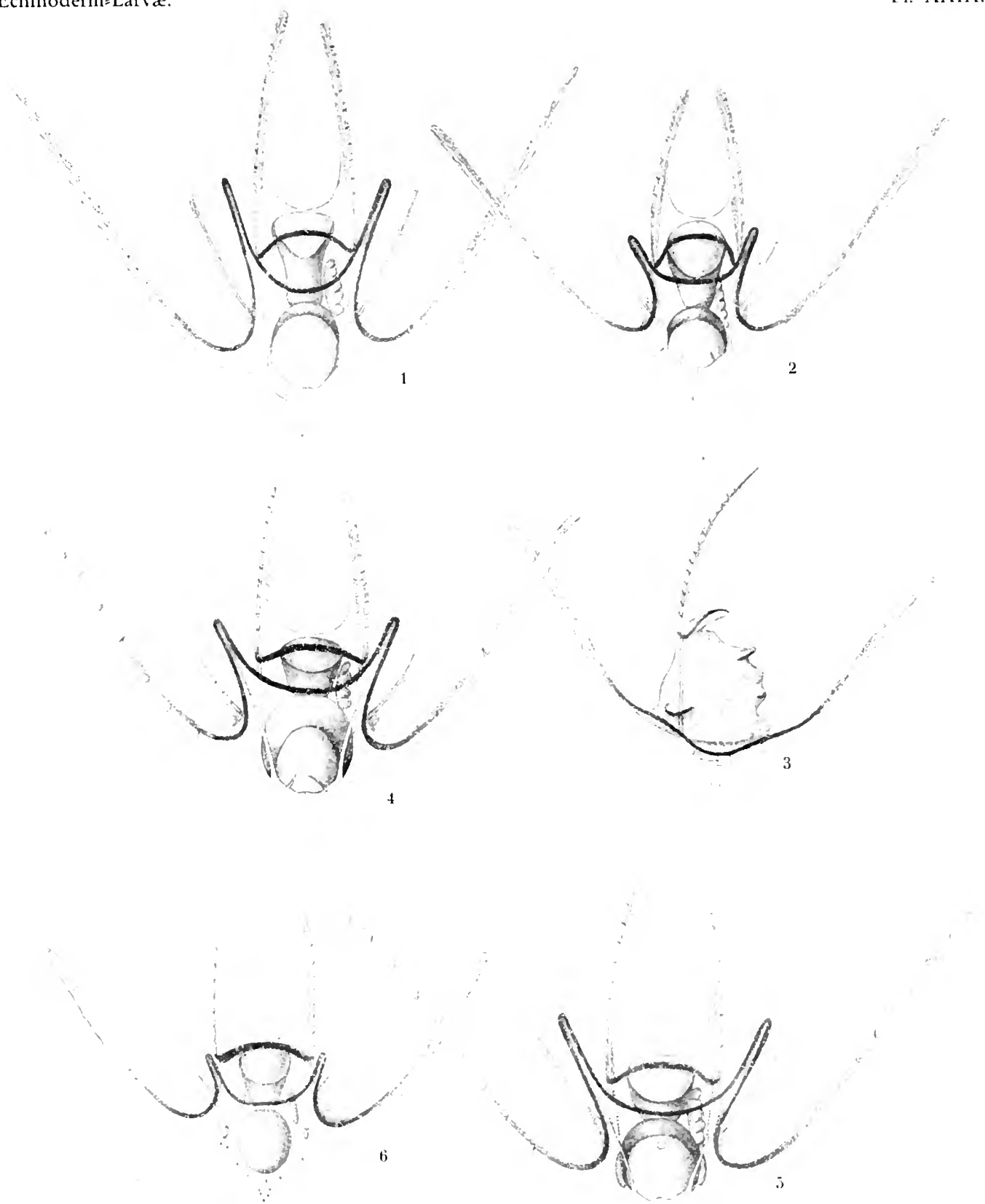


1—2. *Ophiopluteus formosus*, sp. a—b; 3. *Ophiopl.* similis.





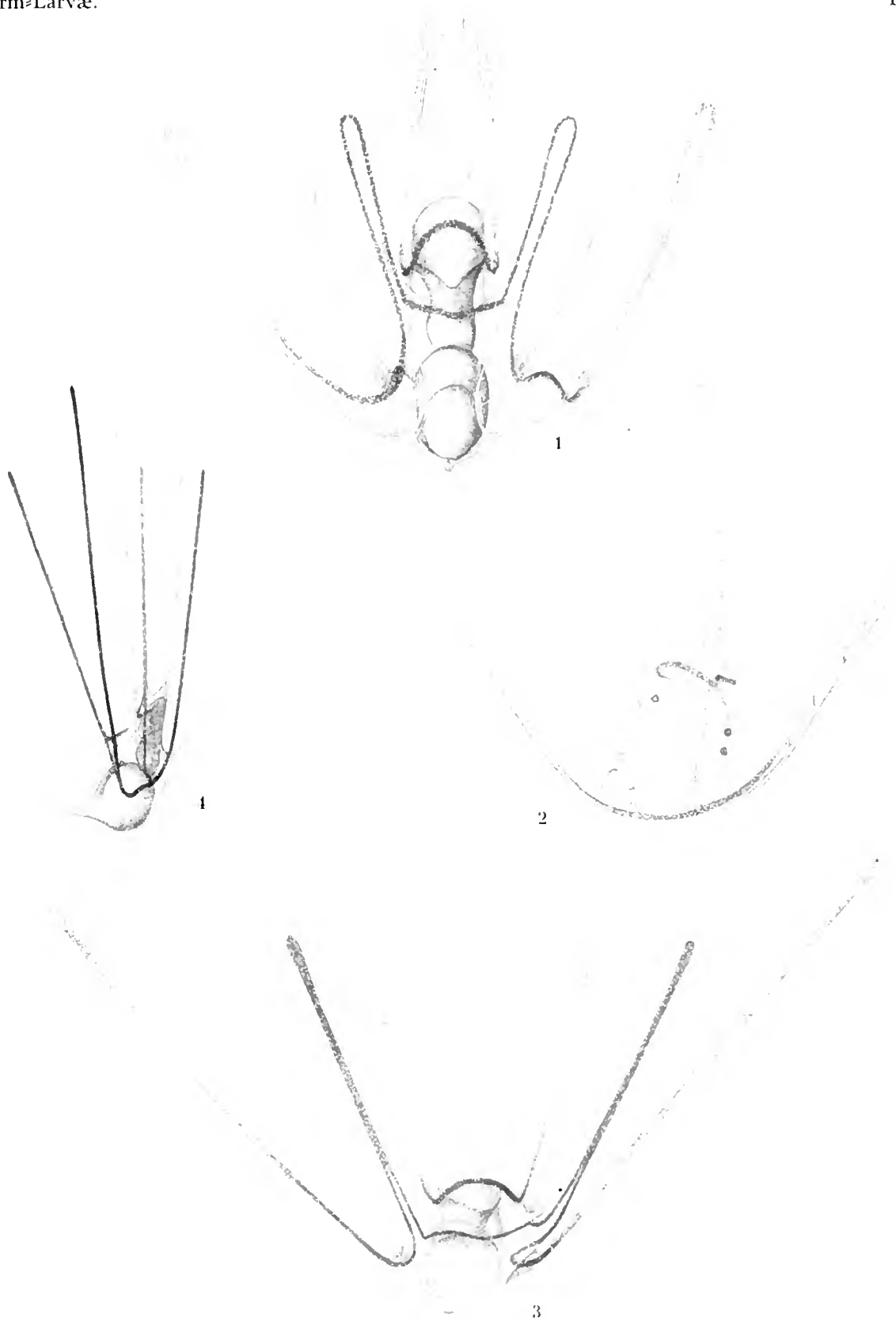




1-5. *Ophiopluteus pusillus*, sp. a-d; 6. *Ophiopl. diegensis*.

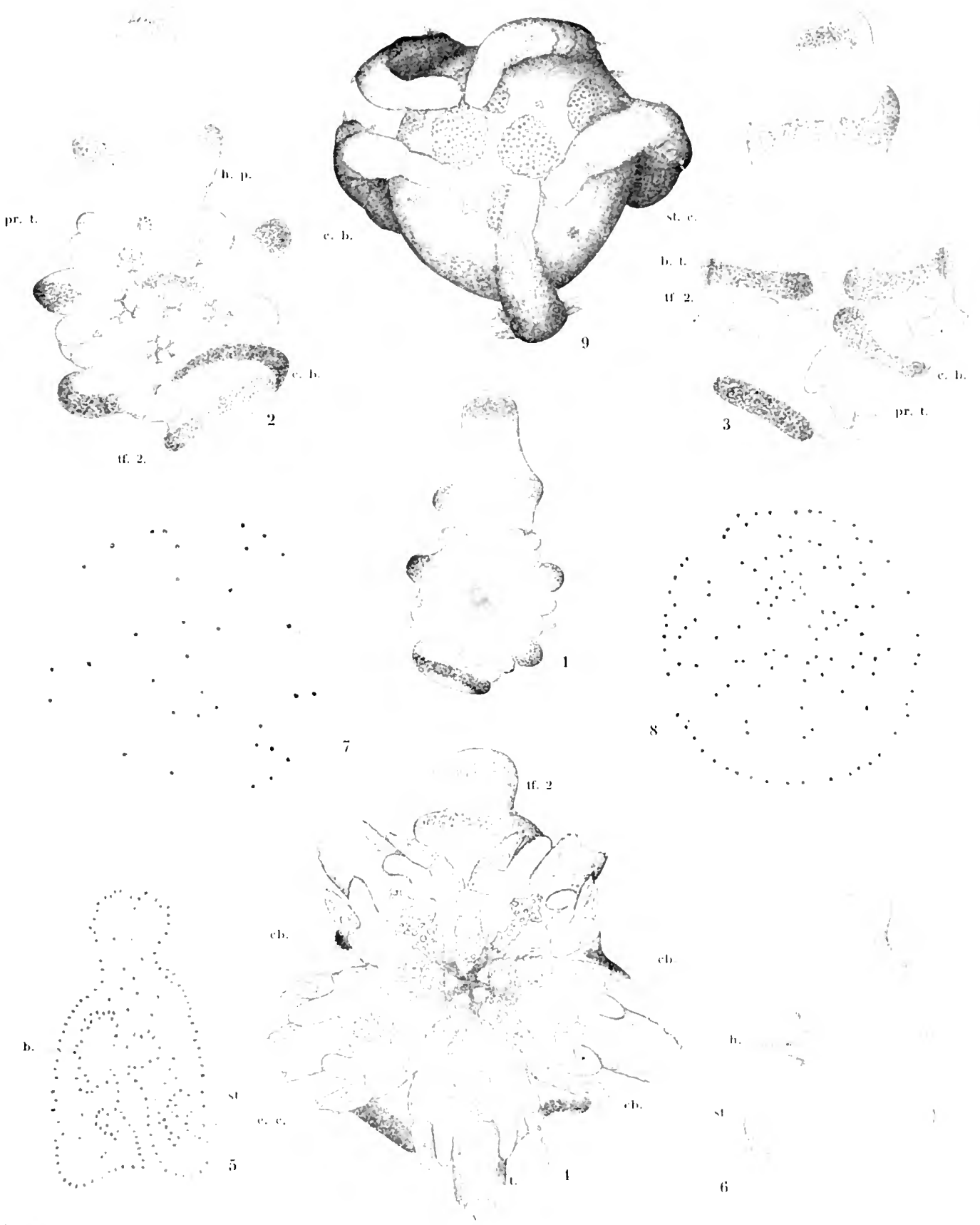






1. *Ophiopluteus* of *Ophiocoma*, sp. c; 2. *Ophiopl. formosus*, sp. a.  
3-4. *Ophiopl. monacanthus*.



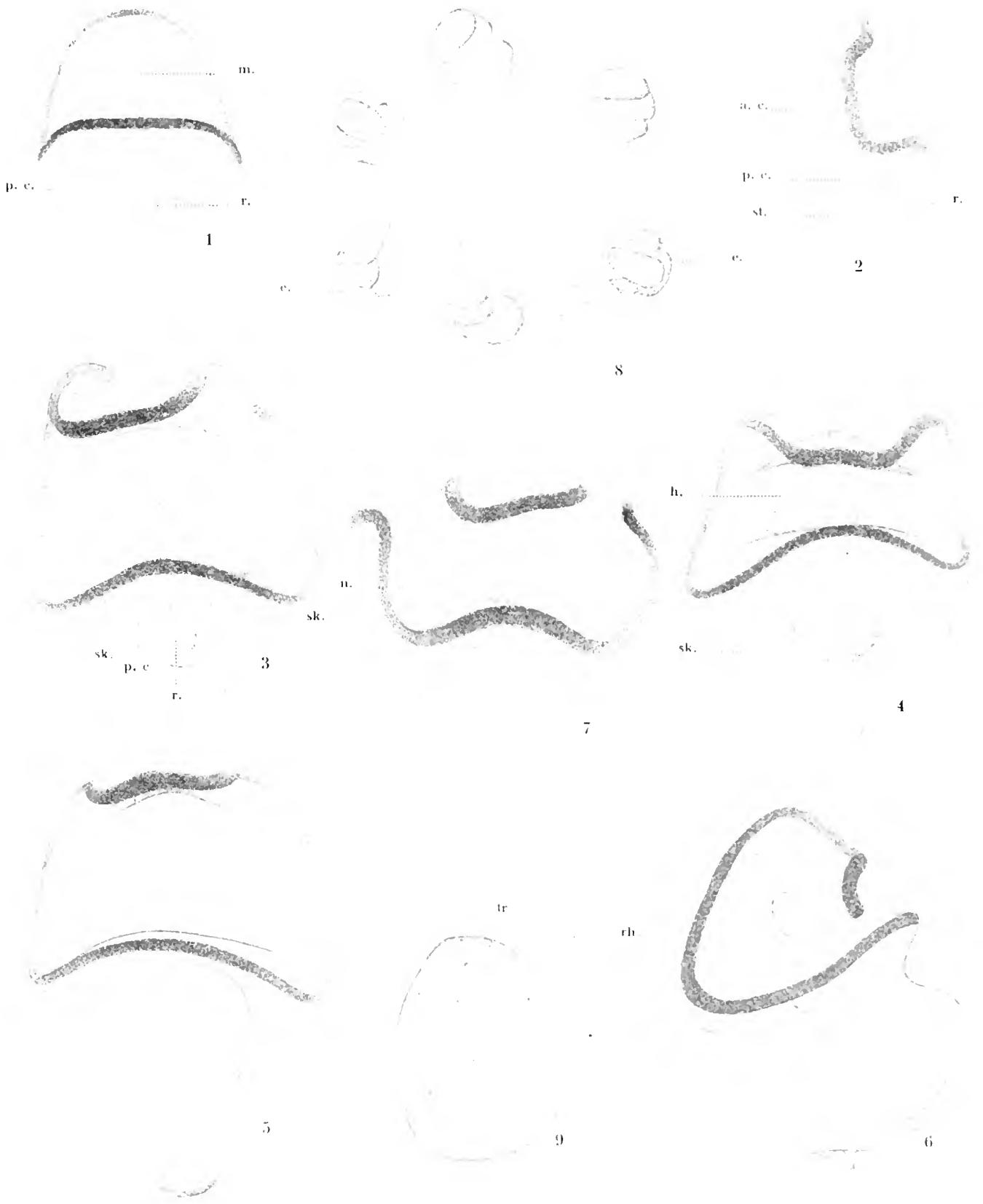


Th. Mortensen del.

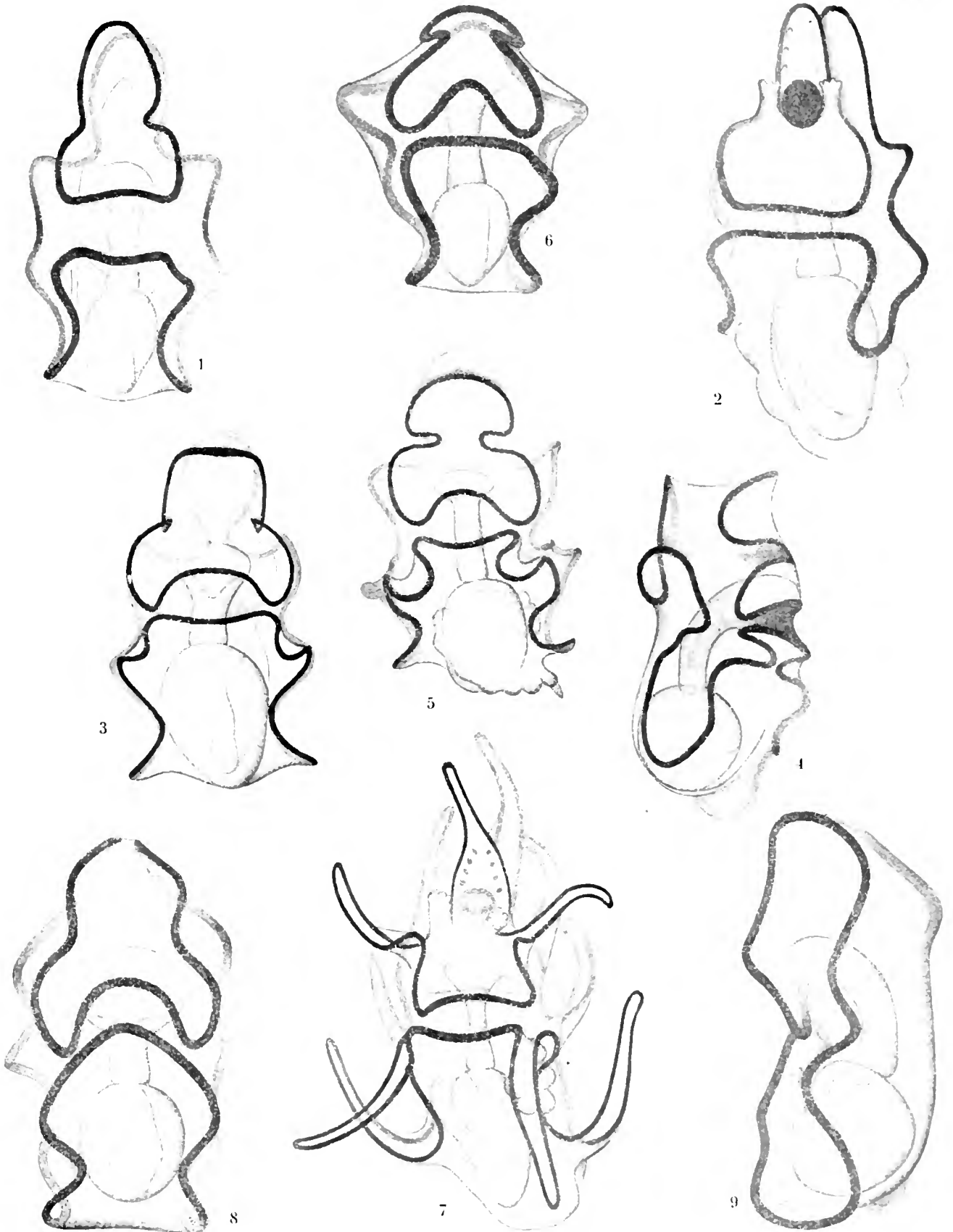
Dansk. Papir. Anst.

1—6. *Ophionereis squamulosa* Kochler; 7—9. *Amphiura vivipara* H. L. Clark.









1-2. *Asterina pectinifera* (M. Tr.);  
 3-5. *Astropecten scoparius* (M. Tr.) 6. *Gymnasteria carinifera* (Lank.);  
 7. *Bipinnaria* sp.; 8-9. *Stichopus californicus* (Stimps.).











