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The Development of the Calcareous Test of Echinocardium cordatum

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VI. *The Development of the Calcareous Test of* Echinocardium Cordatum.

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Communicated by Prof. E. W. MACBRIDE, *F.R.S.*

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INTRODUCTION.

The most important stages were obtained through the agency of Dr. TH. MORTENSEN, of Copenhagen, who kindly sent to Prof. E. W. MACBRIDE, F.R.S., a tube containing a very large number of small urchins belonging to the species *Echinocardium cordatum*. These specimens, which represented all stages from metamorphosis (one specimen—an imago*—still had large pieces of larval spicules attached to it) up to urchins measuring slightly over 2 mm. in length exclusive of the spines, were dredged from locality 56° 33′ N., 1° 47′ E., at a depth of 89 metres, on 12th July, 1905. Prof. MACBRIDE handed over this material to the writer, suggesting that it might be of interest to work out the early post-larval development of the skeleton.

* The term "imago" is used throughout this paper to designate the stage immediately after the metamorphosis of the larva.

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On examining the youngest stage—the imago referred to above—it was found practically impossible to determine how many plates went to form the test, as the sutures, though present, could not be made out. Other investigators appear to have met with the same difficulty—*e.g.*, THÉEL (1892) does not appear to have analysed successfully the skeleton of the imago of the Clypeastroid *Echinocyamus pusillus*, although he describes the development of the permanent skeleton laid down in the larva in considerable detail.

Since nothing is known of the skeleton of an irregular urchin at metamorphosis, it was deemed advisable to study its development in the Echinopluteus. The only way to do this was to attempt to rear the larvæ in the laboratory. Consequently, on 12th May, 1925, a considerable number of adult urchins were obtained, packed in sea-weed and ice, from Plymouth. Artificial fertilisations were made immediately after the arrival of the material, but, as the breeding season was practically over, only one culture proved successful. The ova obtained from three other females started to divide, but broke down after a time. The successful culture was small, but the larvæ were carefully looked after, thinned out into fresh culture-jars after a few days, and kept well supplied with food (the diatom *Nitzschia*). The majority of the plutei were healthy and perfectly normal. Quite a large number had metamorphosed by 2nd June—*i.e.*, towards the end of the third week—and the rest metamorphosed during the fourth week. Although the imagines lived for a short time after metamorphosis, the majority died off when they had reached the stage shown in fig. 16. A number reached the stage shown in fig. 17—*i.e.*, when the buccal plates begin to appear in the peristome. The largest specimen died when the test measured 1 mm. in length (exclusive of the spines). The absence of proper food at the stage when the young urchin begins to feed is probably the reason for this.

Specimens measuring 2–5 mm. in length were obtained from Lowestoft, and older stages from Plymouth. The material, in all cases, was fixed in 70 per cent. alcohol.

The illustrations are, for the most part, camera lucida drawings, the sutures, in many cases, being filled in under crossed nicols.

The writer is deeply indebted to Prof. E. W. MACBRIDE, F.R.S., for his interest and encouragement throughout; also to H. GRAHAM CANNON, D.Sc., for advice respecting a number of the illustrations, as well as for reading through the manuscript.

PREVIOUS WORK.*

Prior to 1914 very little was known of the early development of a Spatangoid, although several larvæ had been described and figured much earlier. In that year a complete

* In a letter to the writer, received after the present paper had been finished, Dr. TH. MORTENSEN kindly called attention to a number of observations on young irregular urchins included in two of his systematic memoirs. Stages in the post-embryonal development of *Brisaster fragalis* are described in 'The Danish Ingolf Expedition—Echinoidea,' 1907, pp. 111–114, Plate XIII. The smallest specimen found measured 2 mm. in length. In a later memoir (MORTENSEN, 1910, pp. 75–83) young stages of *Abatus cavernosus*, found in the deepened petals of the adult, are described. Dr. MORTENSEN identified genital 5 in the young *Abatus*, and also suggested that it might remain as the posterior plate of the adult periproct.

account of the external features of the development of *Echinocardium cordatum* was given by MacBride. Later (1918) the same author published an account of the development of the internal organs, thus furnishing the first complete account of the development of a Spatangoid up to and a little beyond the metamorphosis. The development of the calcareous skeleton (apart from the purely larval skeleton) has, however, remained untouched up to the present. In a recent paper Barrois (1924, Plate IX, figs. 15, 16, 17, 18) gave a number of figures showing the positions which the inter-ambulacra occupy in the larva. But as it was not his purpose to deal with the skeletal development, nothing was added to the subject. In his figures it is sometimes difficult to distinguish between developing plates and developing spines. The latter are never shown above the actual plates to which they belong.

Of the other species of Echinoids which have been studied, the Clypeastroid *Echinocyamus pusillus* (Théel, 1892) approaches most nearly to a Spatangoid in development. But although Théel, in his excellent paper, described the external features of the larval development and worked out the development of such calcareous elements as spines, sphæridia, and teeth in detail, he does not seem to have succeeded in analysing the composition of the test at metamorphosis.

Of the post-larval development of a Spatangoid very little is known. Lovén (1874) deals with the *adult* skeleton in great detail, while Hawkins (1920) has also studied the plating of the ambulacra very minutely. Lovén (1874, Plate III, fig. 32) figures the peristome and a number of the surrounding plates for a young *Brissopsis lyrifera*, and gives three figures (Plate III, figs. 33–35) of *Echinocardium flavescens* showing the transition of the peristome from a pentagon to the reniform contour of the adult. In a later paper (1883, Plate XIV) the same author figures a young specimen of *Abatus cavernosus* measuring 2·3 mm., and also a few stages in the post-embryonal development of *Echinocardium flavescens* (Plate XV): in the earliest stage the periproct is already completely surrounded by the posterior inter-ambulacrum. The figures of "Pedicels of Spatangidæ, Echinidæ, . . ." (Plates VIII–XI) are excellent, the prehensile tube-foot of the adult *E. cordatum* being shown in fig. 120, Plate XI. In addition to the works referred to by the writer in a previous paper (Gordon, 1926), Westergren's work on the development of the test of *Echinoneus cyclostomus* (1911) may be noted. As specimens under 4 mm. in diameter were not available, the early post-larval development was not dealt with, and, in the smallest specimen figured, the periproct was already infra-marginal (*i.e.*, in the adult position).

In the present paper the development of the test has been worked out from its earliest appearance in the Echinopluteus, and the test of the imago successfully analysed. The whole of the post-larval development is here described for the first time.

Methods.

(*a*) *For studying the Development of the Permanent Skeleton laid down in the Pluteus.*

Previous workers, such as Müller (1846), Théel (1892) and MacBride (1914), have given excellent figures of the developing urchin as it appears in the larva at various stages. There was no need, therefore, to repeat this in the present paper; it was only essential to determine the order in which the various skeletal elements appear, together with the number and arrangement of these. Although the methods employed in the study of the Echinopluteus of *Echinus miliaris* (Gordon, 1926) were at first employed, it soon became evident that certain modifications would be necessary. In the regular urchin all the skeletal elements (the genital plates excepted) are laid down in the "echinus-rudiment" which, even in advanced Echinoplutei, is confined to the left side. Once the prepared specimens are mounted and properly orientated, the skeletal elements can readily be examined. In the Spatangoid also, the rudiment is at first situated on the left side of the larva. As development proceeds, however, the ambulatory surface spreads round on to the dorsal and ventral surfaces of the larva, so as to occupy about three-quarters of the circumference of the pluteus at metamorphosis (*see* MacBride, 1914, p. 481; also 1918, figs. 10*a* and 10*b*, Plate 19). Thus, once the larva is mounted, examination of the developing plates becomes difficult, as only a comparatively small number are visible at a time, and the body of the Echinopluteus is too thick to allow of certain areas being brought into focus. If the larvæ are macerated until the necessary transparency is obtained, the plates become displaced.

After maceration overnight in a cold 4 per cent. solution of sodium hydroxide, the specimens were examined (before mounting) in a watch-glass, either in pure distilled water or in glycerin, a high compensating eyepiece being used to give the desired magnification. The specimens could thus be rotated as required, and the number of plates, spines, etc., in each area ascertained. Rough drawings of the type shown in fig. 2 were made of the entire skeleton, and notes taken. Then, after mounting, such plates as were visible were examined in detail.

The individual plates are at first quite separate from each other, but as they increase in size they come into contact to form an apparently continuous meshwork. In advanced Echinoplutei it therefore becomes a matter of the utmost difficulty to determine the number of plates present, especially in the ambulacra. The number of inter-ambulacral plates can be ascertained with certainty because each plate bears a primary spine; (some of the plates may have more than one spine, but these additional ones are always much smaller than the primary ones). Examination under crossed nicols does not help, as at this stage the calcite, though anisotropic, is too openly meshed and the spines are too crowded together. A number of the advanced plutei were macerated for only a short time (2–3 hours) in the 4 per cent. sodium hydroxide solution, and then transferred to distilled water, dehydrated in the usual way, cleared in xylol, and mounted in canada balsam. But examination under high power failed to reveal the sutures, especially in the ventral (oral) aspect. By accident it was found that, if an advanced Echinopluteus is treated rather too long in the sodium hydroxide solution, the specimen swells up somewhat when transferred to distilled water and the individual plates are thus beautifully separated from each other. The complete skeleton can then be analysed with absolute certainty, but the specimen has to be sacrificed, as the plates become displaced in the process of mounting.

(*b*) *For studying the Post-Larval Development.*

The actual imago presents the same difficulty as the advanced Echinopluteus, but when treated in the same way the plates separate slightly, and are easily counted. In slightly older urchins, however, examination under crossed nicols is very satisfactory provided whole mounts are not used. A number of young urchins were mounted entire, and from two of these figs. 7 and 16 were obtained. The sutures in such specimens can only be made out with difficulty, if at all, even when the composition of the test is known, because the thickness of the specimen and the presence of the digestive tract render examination under a high power or with crossed nicols difficult. As the urchin increases in size and commences to feed, the alimentary canal is generally full of sand-grains and the spines become more and more numerous, so that, although the individual plates become more compact and the sutures are in reality more pronounced, yet little can be made of whole mounts.

The following method was tried and found successful. The specimens were tinged with eosin in absolute alcohol, embedded and orientated in paraffin wax in the usual way. Once the block had thoroughly cooled, half the test (either the dorsal or the ventral half) was cut away by hand. It was found, in the case of all except the very smallest specimens, that by means of a fine scalpel the wax within the test could, with a little care, be slackened and removed entire, taking with it all the viscera. The wax was then dissolved away in xylol, and many of the specimens—especially the ventral halves, where the spines are so arranged as to leave the ambulacra quite exposed and the tube-feet can be examined—were then mounted in canada balsam. But on the dorsal halves the spines are numerous, and bend backward in such a way as to obscure the test almost entirely, especially in the neighbourhood of the genital and ocular plates. To remove these spines, therefore, was essential, although how to do so without damaging the plates was a problem. After the wax had been dissolved away the specimens were transferred to absolute alcohol, passed down through the various grades of alcohol to distilled water, and then treated with a 4 per cent. sodium hydroxide solution. Maceration was allowed to proceed until the spines moved on agitating the liquid slightly. (Experience showed that if the spines were allowed to drop off in the sodium hydroxide bath, the test collapsed during manipulation before it could be mounted.) The specimen was then placed in distilled water, and the spines nipped off with two fine needles. One needle was inserted beneath a backwardly directed spine, the latter being raised right over and brought into contact with the second needle, when it became detached from its tubercle.

If the test be subjected accidentally to pressure the sutures may give way, but with a little care a complete half of the test, denuded of all spines and showing no trace of gut, can be obtained in this way. Should it be thought inadvisable to remove all the short fasciolar spines (especially those in the neighbourhood of the apical system of plates), they may be left adhering to the test until it has been placed on a slide and covered with canada balsam: the small spines will then come off quite easily, as they will adhere to a needle if it is passed gently over them. In specimens prepared in this way it is possible to detect the primordia of developing plates, if not quite at the commencement at least very near to it, and when examined under crossed nicols, the individual plates can be made out quite distinctly. When the skeletal parts of the tube-feet were required, maceration was allowed to proceed only until the tube-feet became quite transparent when cleared in xylol, and most of the spines were left on the specimens.

A few of the larger specimens measuring 10–15 mm. in length were stained and carefully etched with concentrated hydrochloric acid to show up the sutures in the modified petal. This method is preferable to examination under crossed nicols when the test becomes sufficiently thick to allow of slight etching.

The Development of the Permanent Skeleton in the Echinopluteus.

Soon after the Echinopluteus has reached the stage figured by MacBride (1914, fig. 9, Plate 33)—*i.e.*, when all the twelve larval arms have been acquired and the aboral spike is still relatively long (figs. 3 and 4)—calcification commences in the "echinus-rudiment." Just as is the case in the larva of *Echinocyamus pusillus* (Théel, 1892), plates are laid down at first only in the inter-ambulacra. One of the earliest stages found shows, in inter-ambulacra **1**, **2**, **3** and **4**, four developing plates arranged as shown in fig. 1, a. This arrangement, though transient, recalls that found in the inter-ambulacra of the regular urchin *Echinus miliaris* (Gordon, 1926, text-fig. 3). In that form, however, no more plates appear in the inter-ambulacra until after metamorphosis (Gordon, 1926, fig. 16). The unpaired inter-ambulacrum (No. **5**) has already six plates (fig. 1, b), of which the third in column *b* is larger and more advanced than the others. In addition to these plates, a number of calcareous granules are present: these are, in all probability, the primordia of the spines, which develop above the inter-ambulacral plates, and of additional plates.

As development proceeds these inter-ambulacral plates increase in size, and in course of time two or three additional plates are laid down. The first (unpaired) plate in each inter-ambulacrum develops much more slowly than the others, and no spine is formed above (external to) it for a considerable time, while a primary spine is formed above the succeeding plates. These spines develop in exactly the same way as the typical spines of *Echinus miliaris* (Gordon, 1926, pp. 268–72). The inter-ambulacral plates are very openly meshed in the centre, becoming more closely reticulate round the periphery. From the centre of the original triradiate spicule a vertical process arises which forms the greater part of the tubercle in the manner described for *E. miliaris*. In *Echinocardium*, however, a small ring of solid calcite is formed on the summit of the developing tubercle (see also Théel, 1892, Plate VII, fig. 98) : this fits into the socket (acetabulum) of the spine. The descending processes from the main body of the tubercle are met by upgrowths from the plate itself, and the large central meshes already referred to are situated directly under the tubercle.

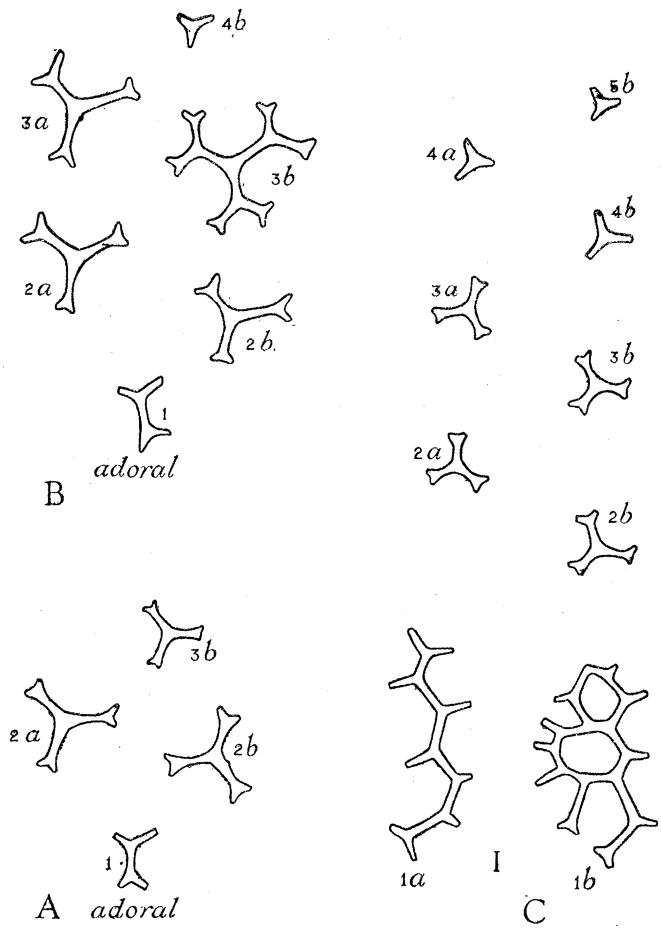

Fig. 1.—A. An early stage in the development of inter-ambulacrum **1**; only four plates have as yet appeared. B. Inter-ambulacrum **5** from the same Echinopluteus. C. Ambulacrum **I** from a later larva showing four plates in column *a*, five in column *b*.

In the unpaired inter-ambulacrum only one more plate is laid down, making a total of seven. Of these, the three next the peristome (the unpaired one and plates *2a* and *2b*) do not differ appreciably from the corresponding plates in other areas. The remaining four, however, grow very rapidly and are larger than any of the others in the Echinopluteus, plate *3b* being particularly large (see fig. 2). In addition to the primary spine a number of others (three, four, or even five) are formed later on each plate round the periphery (see fig. 2). These small spines develop in exactly the same way as the primary ones to begin with, but after metamorphosis at least twelve of these, three on each plate, become clavate at their extremities. These are the short spines belonging to the sub-anal fasciole (figs. 7 and 16, *s. a. fasc.*).

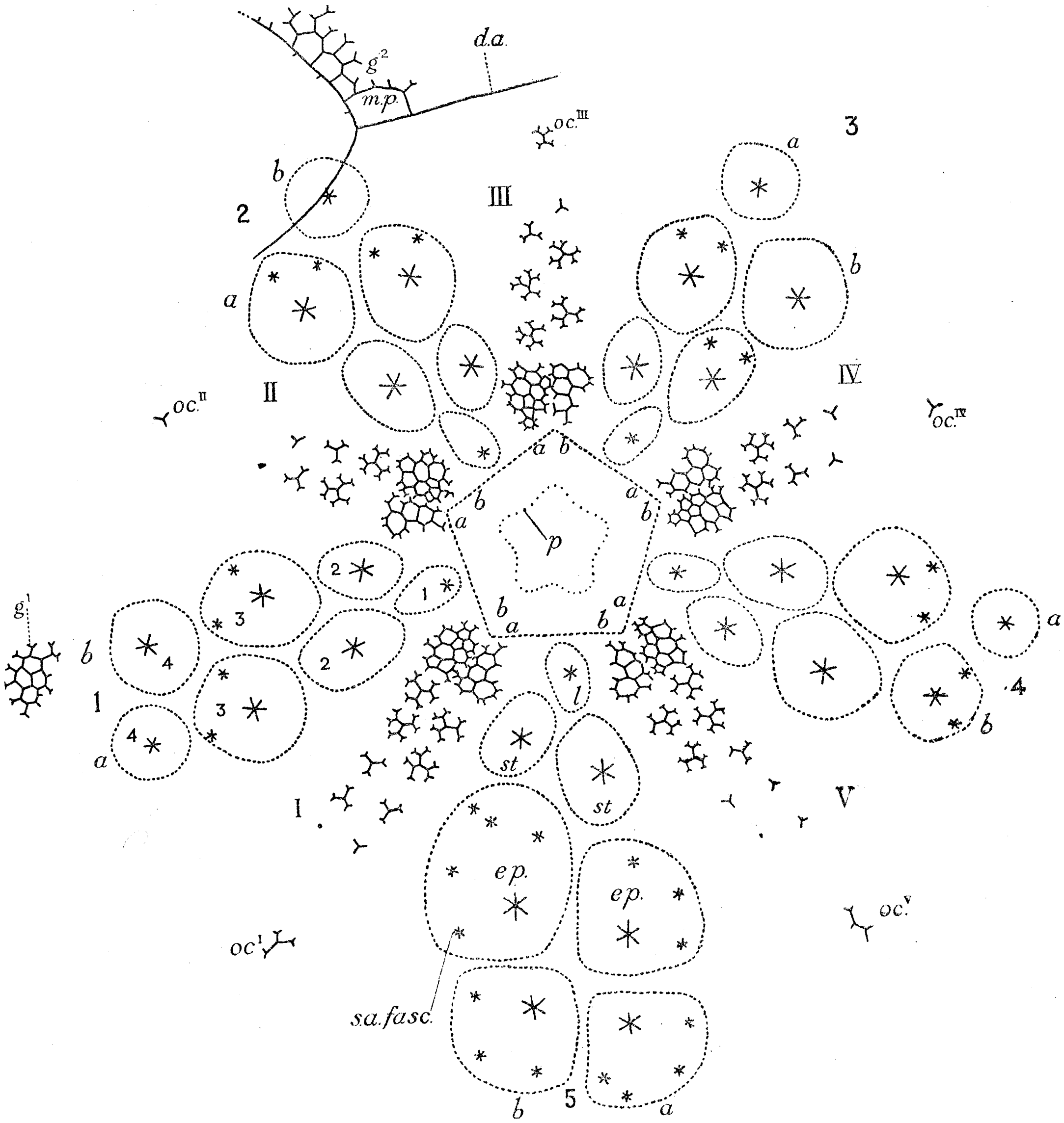

FIG. 2.—A diagram of the complete test from a late Echinopluteus. The ambulacra are built up from a camera lucida drawing while the inter-ambulacra are indicated by dotted lines. **I–V**, ambulacra; **1–5** inter-ambulacra; *a* and *b* the two columns of plates in each area. The method of numbering the inter-ambulacral plates is shown in area **1**; six-rayed stars indicate the positions of the spines; oc^{I}–oc^{V}, ocular plates; *p* represents the outline of the peristome when the plates are in their proper relative positions (*i.e.* when they articulate with each other); *s. a. fasc.*, sub-anal fasciole; g^1 and g^2, genitals **1** and **2**; *d. a.*, dorsal arch; *m. p.*, madreporic pore; *l.*, labrum; *st.*, sternal plate; *ep.*, episternal plate.

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Of the other inter-ambulacra, areas **1** and **4** develop somewhat more rapidly than areas **2** and **3**, the former each possessing, at metamorphosis, seven plates, with perhaps a hint of an eighth, while the latter have each only six, with, occasionally, a hint of a seventh (see fig. 2). In each of the four areas two of the plates acquire a pair of small secondary spines in addition to the primary ones. As a rule these are situated on plates *3a* and *3b* of areas **1** and **2** ; *3a* and *2b* of area **3** ; *3a* and *4b* of area **4**.

Meanwhile calcification has been proceeding in the ambulacra. Just after the stage shown in fig. 1, A and B, a pair of plates is laid down in each ambulacrum. Whether one series precedes the other or not has not been determined, for, as plate-formation is rapid, no specimen showed only one plate in each area. The plates in the two series can, however, be distinguished from each other because they soon assume a somewhat different shape (see fig. 1, C). The plates in the series **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* all resemble plate *a* shown in the figure, those in the series **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* being similar to plate *b*. Soon afterwards new plates arise successively in each column. That these are formed in rapid succession is clear from fig. 1, C, but those in the second series (the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series) appear slightly in advance of the corresponding plates in the other series. From this it is reasonable to suppose that, in the case of the first pair of plates, the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* would be the first to be laid down. A sphæridium is formed above each of the first plates in the series **I***b*, **II***b*, **III***a*, **IV***b*, **V***a*. These do not appear until a comparatively late stage, and are formed simultaneously with the small spine which appears on the unpaired inter-ambulacral plate (fig. 2). As might be expected, the development of the sphæridium is the same in *Echinocardium* and in *Echinus miliaris*, but whereas in the latter the base of the sphæridium is very irregular (GORDON, 1926, fig. 10), it is quite regular in all the sphæridia examined in the former species (*i.e.*, it is always a six-rayed star). Why the base should be quite regular and normal in the one species and greatly reduced in the other it would be difficult to say.

It has already been stated that inter-ambulacrum **5** is larger than the others, while inter-ambulacra **1** and **4** are also slightly in advance of the remaining two. Correlated with this, more plates are laid down in ambulacra **I** and **V** than in ambulacra **II** and **IV** (see fig. 2). The number of plates in the anterior ambulacrum varies slightly. Sometimes it is as low as that in areas **II** and **IV**, sometimes as high as that in areas **I** and **V**, and in others it is intermediate between that of the two foregoing sets, as the following table shows :—

TABLE I.

Ambulacrum.	**I.**		**II.**		**III.**		**IV.**		**V.**	
Column.	*a.*	*b.*	*a.*	*b.*	*a.*	*b.*	*a.*	*b.*	*a.*	*b.*
No. of plates in—										
Pluteus A.	5	6	4	4	4	4	4	4	6	5
Pluteus B.	5	5	4	4	5	5	4	4	5	5
Imago C.	6	6	5	5	6	5	5	5	6	6

In *Echinocardium* the primary tube-foot is, from the first, a mere nodule, while in *Echinus miliaris* it is at first well developed and capable of much extension, only becoming reduced to a nodule a short time after metamorphosis. In *Echinus* also the ocular plates appear very early, and are indeed the first skeletal elements to appear in the "echinus-rudiment." In *Echinocardium*, on the other hand, the oculars do not appear until quite late, the first traces being found when there are at least five plates in each column of ambulacra **I** and **V**.

While the skeletal elements are being laid down in the "echinus-rudiment," the madreporic plate (genital **2**) is being formed around the water-pore. This plate, as is the case in regular urchins, arises as a proliferation of part of the dorsal arch. A short time before the ocular plates make their appearance, another genital plate (genital **1**) is laid down on the right side of the larva, being situated a short distance from plates *4a* and *4b* of inter-ambulacrum **I** (see fig. 2). These are the only genital plates that are present at metamorphosis.

Fig. 2 is a diagrammatic representation of the plates present in an advanced Echinopluteus, just before the ambulacral plates join up with each other to give the appearance of a continuous meshwork. The number and relative positions of the spines on the inter-ambulacral plates are represented diagrammatically; a large six-rayed star denotes a well-developed primary spine, smaller stars denote less advanced primary spines, and very small ones represent small secondary spines.

The peristome is bounded by fifteen plates, two in each ambulacrum and one in each inter-ambulacrum, the last projecting somewhat nearer the centre than the two others. The number of ambulacral plates in each area has been given in the preceding table (Table 1, pluteus A). The two anterior inter-ambulacra (**2** and **3**) have each only six plates, while the remaining three have each seven. Plates *3a*, *4a*, *3b*, *4b* of inter-ambulacrum **5** are very well developed, plate *3b* having five secondary spines, plate *4a* having four, and the remaining two each three. In all the inter-ambulacra except area **3** the plates in column *b* are laid down slightly in advance of the corresponding plates in column *a*; in area **3** the reverse is the case. The ocular plates are situated some distance from the last-formed ambulacral plates; genital **1** is near the aboral plates of area **1**; genital **2** consists of a number of open meshes around the posterior end of the dorsal arch (*d. a.*).

By the time metamorphosis is reached, the number of ambulacral plates has increased to that given for imago C in the preceding table, and each plate consists of a few open meshes. The ocular plates are also somewhat more advanced, and an additional plate is generally present in inter-ambulacra **2** and **4**. The plates, as they increase in size, grow out to meet each other, and in the late larva it is almost impossible to make out the sutures unless the method described on p. 259 be adopted. As the "echinus-rudiment" increases in size it spreads round from the left side of the Echinopluteus on to both the dorsal and ventral surfaces of the larva. A note on the position of some of the inter-ambulacral areas relative to the larval spicules may be useful.

The buccal membrane or peristome of the developing urchin is always situated on the left side of the larva. Inter-ambulacrum **2** grows round on to the dorsal surface so that

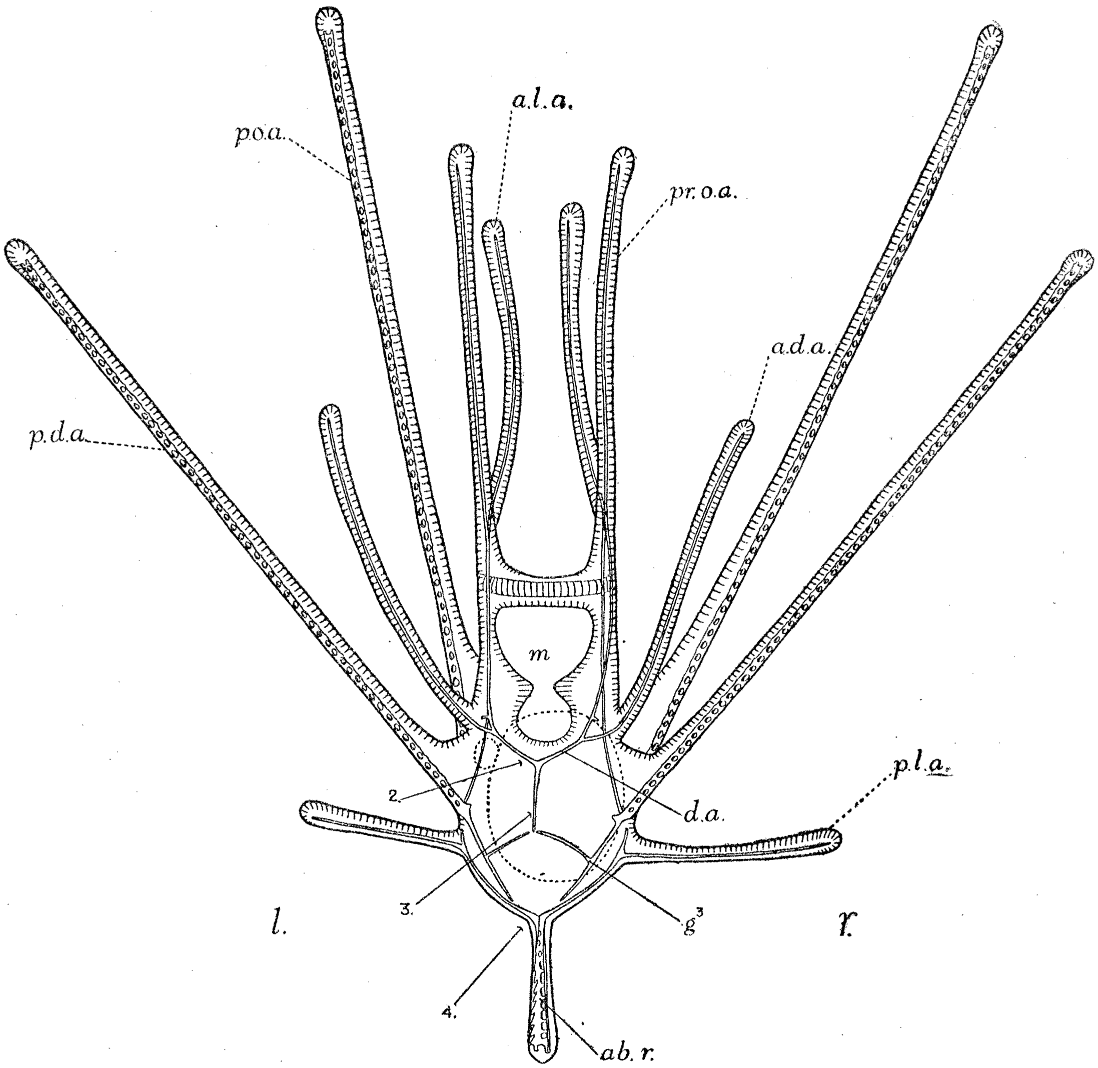


FIG. 3.—Dorsal aspect of an Echinopluteus, to show the larval spicules. *l.*, left side, *r.*, right side, of larva; *p. d. a.*, postero-dorsal arm; *p. o. a.*, post-oral arm; *pr. o. a.*, pre-oral arm; *a. l. a.*, antero-lateral arm; *a. d. a.*, antero-dorsal arm; *d. a.*, dorsal arch; *p. l. a.*, postero-lateral arm; *ab. r.*, aboral rod; 2, 3 and 4 indicate the positions of the apical plates of inter-ambulacra **2**, **3** and **4**, respectively in the late larva; g^3 indicates the posterior extension of the right postero-dorsal rod, part of which later gives rise to genital **3**. The outlines of the stomach and of the small "echinus-rudiment" are indicated by broken lines. *m.*, mouth.

Outline drawn from a mounted specimen under camera lucida. 1 × 135.

plate *4b* is laid down over the posterior end of the left arm of the dorsal arch (see fig. 3, **2**.) This arm extends anteriorly to support the left pre-oral arm (*pr. o. a.*), giving off a side branch to support the left antero-dorsal arm (*a. d. a.*). In *Echinocardium* the median arm of the dorsal arch is long (*d. a.*, figs. 3 and 6), and plates *4a* and *4b* of inter-ambulacrum **3** are laid down near the posterior extremity of this rod (fig. 3, **3**). Inter-ambulacrum **4** (fig. 3, **4**) extends posteriorly along the left side of the Echinopluteus, the last two plates (*4a* and *4b*) being situated near the dwindling remnant of the aboral rod (*ab. r.*). The aboral rod undergoes resorption during the development of the

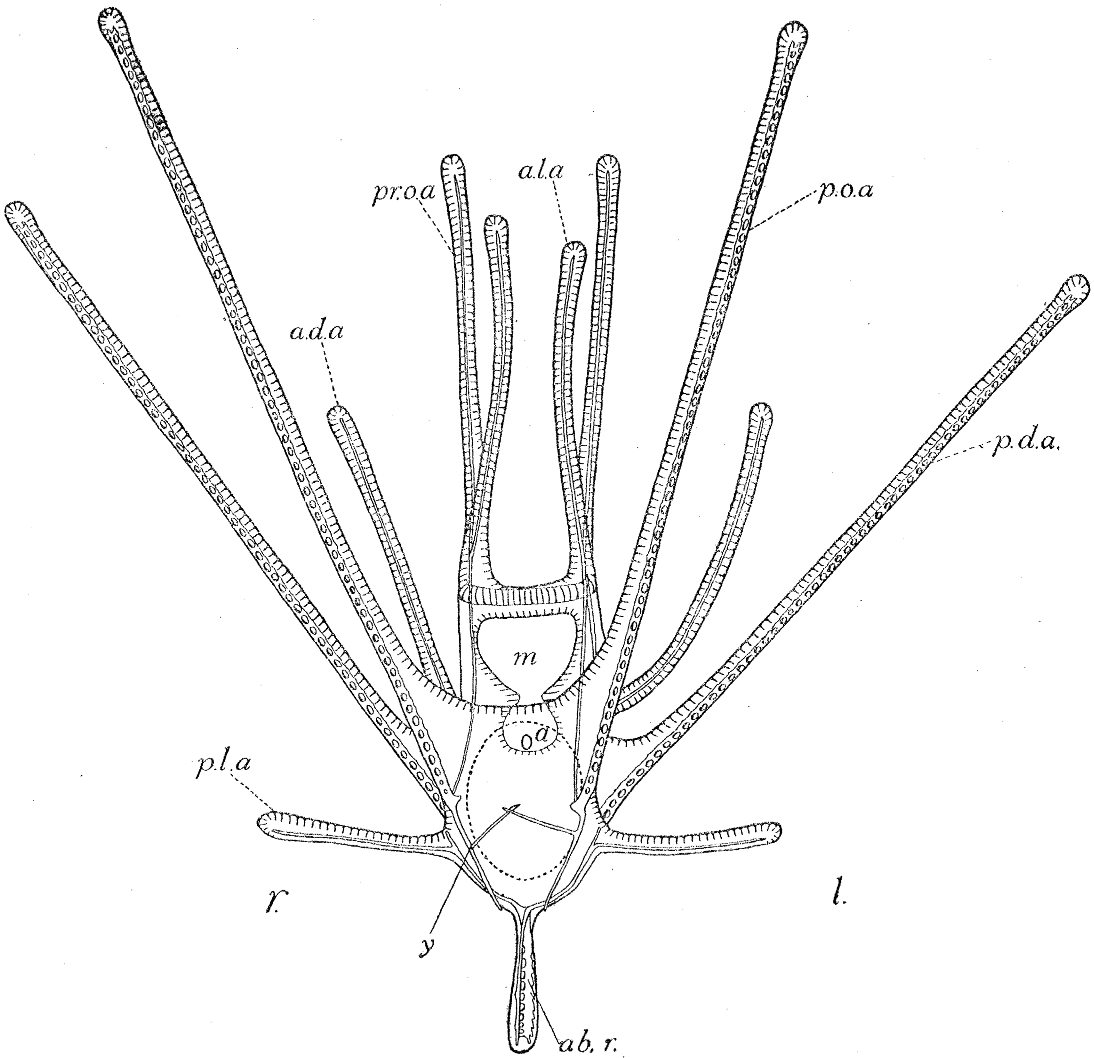


FIG. 4.—Ventral aspect of the same Echinopluteus. *a.*, anus; *y.*, the posterior extension of the right post-oral rod, part of which later gives rise to the plate *y* (genital **5**). Other lettering as in fig. 3. 1 × 135.

"echinus-rudiment." Inter-ambulacrum **5**, the largest of all, grows over the ventral surface towards the right side of the larva. Each post-oral arm of the Echinopluteus is supported by a latticed rod similar to that of the postero-dorsal arm (figs. 4 and **3**, *p. o. a.*). A slender continuation of this rod is directed backwards towards the posterior end of the arva, and from this a branch is sent out (at the point marked *y*) towards the middle line along the dorsal surface (fig. 4, *y*). Plate *4a* of the posterior inter-ambulacrum is laid down over this branch (*y*) of the *right* post-oral spicule. The remaining inter-ambulacrum (area **1**) is, of course, situated mid-way between areas **2** and **5**, and extends over on to the most anterior part of the ventral surface.

The Post-Larval Development of the Test.

Fig. 5 is a diagram of the disarticulated test of an adult *Echinocardium*, and brings out clearly the bilateral symmetry of the animal. Viewed from the ventral surface the outline of the test is ovate. The peristome is reniform, and situated considerably nearer the anterior than the posterior end of the body, the flexible membrane possessing a number of relatively small calcareous plates (Lovén, 1874, Plate XXXIX, fig. 225). The slit-like mouth is situated at the posterior border of the buccal membrane, and is partially concealed by a projecting lip (labrum). The five ambulacra appear to meet round the mouth so as to exclude four of the inter-ambulacra. This is due to the fact that the first (unpaired or peristomial) plate in inter-ambulacra **1**, **2**, **3** and **4** is greatly reduced (fig. 5). That belonging to area **5** is also small, but forms the lip or labrum already referred to.

The inter-ambulacra bear numerous, rather delicate, spines, those on the ventral surface, notably those on the sternal plates (fig. 5, *st.*), being spatulate. When the spines are removed, the plates are seen to bear numerous closely set tubercles of almost equal size. These are somewhat larger in the neighbourhood of the peristome, and tend to decrease towards the apical region. There is no distinction into primary, secondary, and tertiary tubercles as in *Echinus* (Gordon, 1926, p. 295). In each inter-radius, plates *2a* and *2b* (those which succeed the unpaired one), are very large, those in the unpaired inter-ambulacrum (**5**) being greatly lengthened in a radial direction (fig. 5, *st.*). To this lengthening of the sternal plates (and of the posterior end of the test generally) the apparent forward shift of the mouth is due.

On the dorsal surface the apical system of plates is central, while the highest part of the test is somewhat nearer the posterior end. The apical system, which consists of four genital and five ocular plates, is very small and compact. Genital **5** has entirely disappeared, while genital **2** extends backward in such a way as to separate genitals **4** and **1** from each other. In a regular urchin, *e.g.*, *Echinus*, the periproct is surrounded by the ring of five genital plates; but in *Echinocardium* the periproct is quite separated from the apical system of plates and the madreporite may be said to have extended backwards to replace the periproct and the fifth genital. This posterior extension of the second genital plate bears the pore-canals which communicate internally with the stone-canal (fig. 5). Each of the four genitals is pierced by a relatively large genital pore.

The apical parts of ambulacra **I**, **II**, **IV** and **V** are modified into slightly grooved petals, the pores being for the most part double (fig. 5). In area **III**, however, the pores are all simple, and the arrangement of the plates is quite different from that found in the other ambulacra (fig. 5). An internal fasciole (*i. fasc.*) is developed round the apical, deeply grooved portion of ambulacrum **III**, extending posteriorly on to the other petals, so that the apical system is enclosed within it.

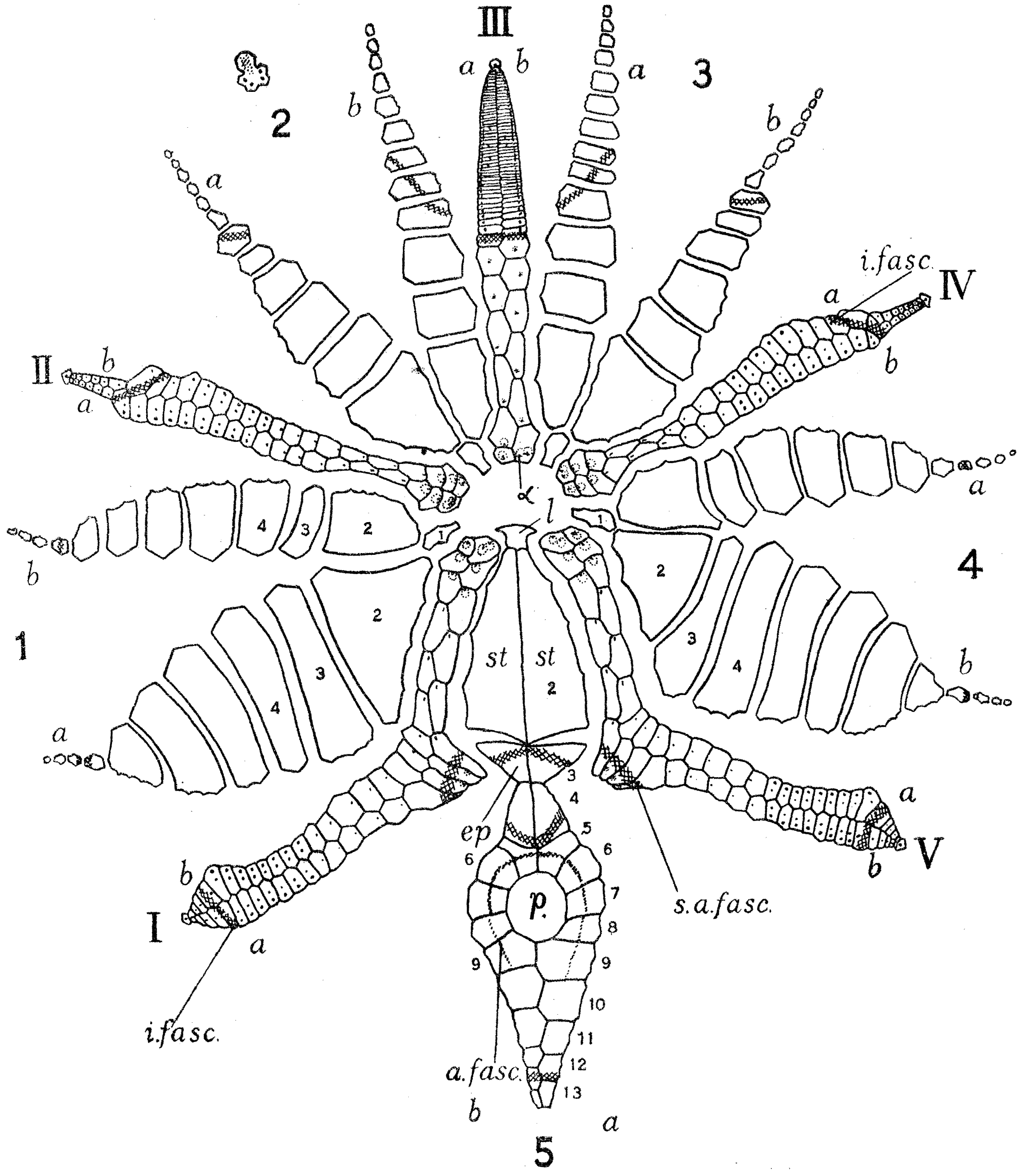


FIG. 5.—Diagram of the disarticulated test of an adult *Echinocardium* (after LOVÉN, 1874, Plate XXXIX, fig. 222) for comparison with fig. 2. *a. fasc.*, anal fasciole; *s. a. fasc.*, sub-anal fasciole; *i. fasc.*, internal fasciole; *p.*, periproct; α, pore of a "buccal" tube-foot; *l.*, labrum; *ep.*, episternal plate; *st.*, sternal plate. Other lettering as in text-fig. 2. [LOVÉN regards plate 2*a* of area **1** as being formed by the fusion of plate 2*a* with plate 3*a* (see p. 307).]

The posterior inter-ambulacrum extends backwards from the apical system for a considerable distance, and then dips almost vertically downwards, forming a wedge at the narrow posterior end of the test. Here, completely enclosed by a number of the inter-ambulacral plates (fig. 5, *p.*), lies the periproct. The periproct membrane bears a number of calcareous plates, those on the lower part (*i.e.*, towards the ventral surface) being much larger than the others, so that the anus is excentric (fig. 15).

No less than four kinds of tube-feet occur. These are—

(1) "*Buccal*" *tube-feet*, which occur on all the ambulacra in the neighbourhood of the mouth. The pores through which they emerge are simple and surrounded by peripodia (fig. 5, *α*). Five plates—those in the series **I***a*, **II***a*, **III***b*, **IV***a*, **V***b*—possess two "buccal" tube-feet and are termed "biporous." The development of these tube-feet will be described in detail later on (pp. 294 and 295).

(2) *Respiratory tube-feet.* These possess no suckers (nor discs), and are confined to the petals.

(3) *Prehensile tube-feet.* These are capable of much extension and are found only in the modified "petal" of ambulacrum **III**, and in one or two plates of areas **I** and **V**, which are enclosed within the sub-anal fasciole (*s. a. fasc.*). The development of these is also described on pp. 295 and 296.

(4) *Degenerate tube-feet* emerge from the minute, simple pores in the region between the petal and the plates which surround the "buccal" tube-feet (fig. 5).

Description of Imago.

The young urchin at metamorphosis differs so markedly from the adult that some term must be applied to it. To avoid using such awkward phrases as "the young urchin at metamorphosis" or "the just-metamorphosed urchin," the term imago, adopted by MacBride (1914), is used.

(*a*) *Ventral Aspect.*—An imago which was measured immediately the process of metamorphosis had been completed reached a length of 0·59 mm., including the spines, the diameter of the test alone being only 0·34 mm. In shape it is almost spherical (see fig. 6). The peristome is not situated exactly in the centre of the ventral surface, but slightly nearer the future anterior end of the body. This is due to the large size of the posterior inter-ambulacrum (fig. 2). The outline of the peristome is still irregular (see fig. 2, *p.*), but this condition is transient, and soon the peristomial margin of the corona becomes almost circular.

It will be seen from fig. 2 that the imago bears quite a large number of spines. That on each unpaired inter-ambulacral plate is still very small, while the primary* spines on the succeeding plates are quite well developed, and measure 0·125–0·14 mm. in length. Even these primary spines, however, increase considerably in length soon after meta-

* The distinction between primary and secondary spines gradually disappears as the urchin increases in size.

morphosis. The secondary spines, including those which belong to the sub-anal fasciole, are very short, and, in the case of the latter, no trace of the expanded clavate tip is, as yet, apparent. Thus, although the plates which bear them are large, the posterior end is at this stage scarcely more prominent than the rest of the test. The ambulacral plates have by this time come into contact with each other, and the sutures are almost invisible. In the sphæridia (which are borne on the first plate in the series **I***b*, **II***b*, **III***a*, **IV***b*, **V***a*) the six vertical prongs can still be made out, but each has commenced to broaden out at the tip. Soon the enlarged ends of the prongs meet and fuse to form a spherical body (fig. 16, *sph*). The tube-feet, which are surrounded by the first plates in the other series (**I***a*, **II***a*, **III***b*, **IV***a*, **V***b*), are short, and possess suckers, but no trace of calcareous discs.

The imago dredged from the North Sea is larger than any obtained in the laboratory, and measures 0·48 mm. in diameter, exclusive of the spines, the longest spines measuring 0·17 mm. Although all the distinctly larval tissue (remnants of pre-oral lobe, larval arms, etc.) has gone, large pieces of larval skeletal rods are still attached (see fig. 6). From its appearance it is plain that it is an imago, yet it is more advanced than the imagines obtained from artificial cultures. The five unpaired inter-ambulacral plates bear *two* spines apiece, a very small one near the peristome and a larger one farther back. The latter is not so far advanced as the primaries on the next two plates. Moreover, a tube-foot pore is present in the plates which bear the sphæridia—the first plate in the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series. Thus a pair of tube-feet must have been present in each ambulacrum; but one tube-foot was, in all probability, small.

It was at first thought that either (1) larvæ reared in the laboratory metamorphosed prematurely, the imagines being, though quite healthy, smaller and less advanced than those which passed the early stages of their development in the open sea; or (2) the imago in question might belong to a different species. On examining all the imagines which had been preserved, one was found which was somewhat larger than the others. It still showed traces of larval tissue, yet it also possessed a pair of tube-feet in each ambulacrum. Five of these (those in the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series) already possessed developing calcareous discs, some of which had reached the stage shown in fig. 24, C, while others are somewhat more advanced. The second set of tube-feet were very small. There were also two spines on the unpaired inter-ambulacral plate. It seems as if the imagines varied somewhat, but as the number of specimens examined is small, no idea of the variation can be obtained. It is probable that the more advanced forms are in the minority, as MacBride (1914) does not appear to have found any with more than five tube-feet in his cultures. In some of the advanced Echinoplutei two spines are formed on at least two of the peristomial plates of the inter-ambulacra, generally those belonging to areas **2** and **3**.

(*b*) *Dorsal Aspect.*—Fig. 6 shows the dorsal aspect of the imago that had passed its larval, free-swimming stage in the open sea (all spines have been omitted). The dorsal surface of the imago corresponds roughly to the right side of the larva. Many of the larval skeletal rods still adhere to the young urchin, and of these the following can readily be recognised: (*a*) the latticed rod which afforded support to the right post-oral larval arm (*p. o. r.*, fig. 6); (*b*) a similar rod which supported the right postero-dorsal arm (*p. d. r.*, fig. 6); (*c*) a small remnant of the aboral rod which supported the aboral spike.

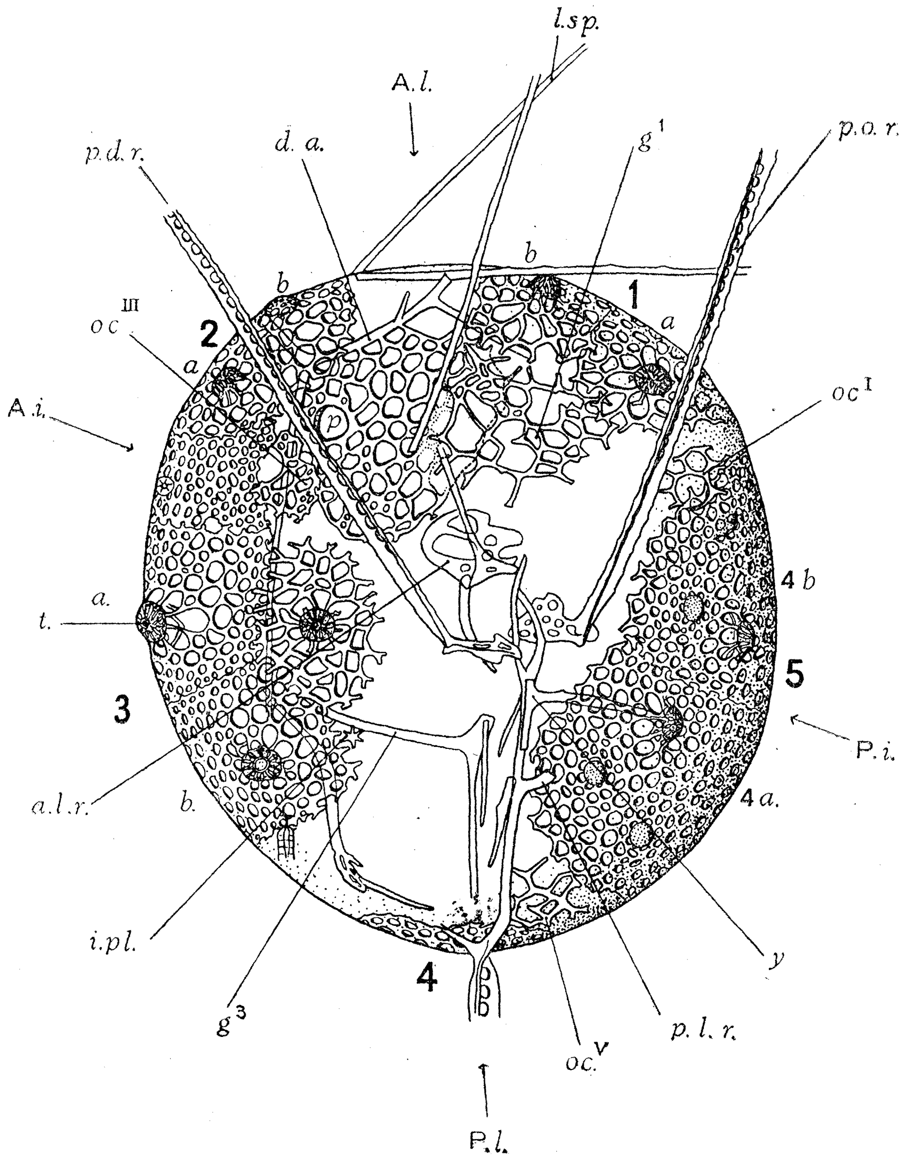


FIG. 6.—Dorsal aspect of an imago dredged from the North Sea. *A. l.*, anterior end of larval body; *P. l.*, posterior end of larval body (indicated by a remnant of the aboral rod (see figs. 3 and 4)); *A. i.*–*P. i.*, antero-posterior axis of the imago; oc^{I}, oc^{III}, oc^{V}, three of the ocular plates; g^1, genital **1**; *d. a.*, part of the dorsal arch around which genital **2** is formed; *p.*, madreporic pore; g^3, the dorsal branch given off from the right postero-dorsal rod, which later gives rise to genital **3**; *y.*, part of the posterior extension of the post-oral rod, which later gives rise to plate *y*; *l. sp.*, larval spicule; *p. l. r.*, postero-lateral rod; *t.*, tubercle of a primary spine; *p. d. r.*, right postero-dorsal rod; *p. o. r.*, right post-oral rod; *i. pl.*, a developing inter-ambulacral plate; *a. l. r.*, antero-lateral rod.

Camera lucida drawing. 1 × 200.

The posterior end of the larva (*P. l.*) is thus clearly marked in the imago. The aboral rod is continued forwards along the right side of the Echinopluteus as a larval spicule from which the rod (*p. l. r.*) which supported the right postero-lateral arm is given off (see figs. 3 and 4). This rod has been broken off near its point of origin (fig. 6, *p. l. r.*). Just in front of this is a small broken remnant (*y*), one arm of which is partly overlaid by plate *4a* of inter-ambulacrum **5**. This is undoubtedly part of the slender posterior continuation of the right post-oral rod (fig. 4, *y*). The posterior end of the right antero-lateral rod (*a. l. r.*) and of the postero-dorsal rod (g^3) are also quite evident. Soon after metamorphosis the long projecting larval spicules are broken off, and the remaining portions are resorbed, with the exception of those parts which, as will be shown later, form the foundations of certain plates belonging to the permanent skeleton.

The inter-ambulacra are longer than the ambulacra (see fig. 2), and consequently the aboral plates are visible on the dorsal surface of the imago. Only one of the ambulacra (area **III**) extends on to the dorsal surface, and near to it lies ocular **III** (oc^{III}). Only two other ocular plates are visible, namely, oculars **I** and **V**, situated on either side of the posterior inter-ambulacrum (No. **5**). To the right of ocular **III**, and under the right postero-dorsal rod, lies the madreporite (genital **2**). This plate, it may be recalled, is formed from the posterior end of the dorsal arch (fig. 2), and the posterior portion of this larval spicule is still to be seen (*d. a.*). The long median arm is directed backwards under ocular **III** and the aboral plates of inter-ambulacrum **3**.

Genital **2** is still very openly reticulate, and the madreporic pore (*p.*) is a single large opening situated in front of and slightly to the right of ocular **III**. Genital **1** lies to the right of, and is partly concealed by, the madreporite. It is larger than in the less advanced imagines, but is still very openly reticulate. Genitals **3** and **4** have not yet appeared. MacBride (1918) has found that the adult anus is already open in the imago and is situated in the centre of the dorsal surface. The mouth, which is still covered by the epineural veil, is in the centre of the peristome.

In many respects the imago resembles a regular urchin rather than a Spatangoid. In shape it is almost spherical: the ambulacra are all similar (see fig. 2), apetaloid, and already possess a number of plates in each column. The primary (terminal) tube-foot is already a mere nodule, and can only be made out in sections. The inter-ambulacra, too, are primitive and resemble those of a regular urchin in the arrangement of the plates, and in the fact that each bears a well-developed spine (which has been termed a primary spine, and probably corresponds to the primary spine in a regular urchin). The position of the mouth in the circular peristome, and of the anus in the dorsal surface, add to the resemblance.

But this resemblance is superficial, for already the bilateral symmetry of the adult is apparent (compare figs. 2 and 5). The peristome, though circular, is situated somewhat nearer the anterior than the posterior end of the body. Inter-ambulacra **1**, **5** and **4** are more developed than the two anterior ones, while the three anterior ambulacra (**II**, **III** and **IV**) are smaller (*i.e.*, possess fewer plates) than the two posterior ones. The most marked departure from the regular urchin, however, lies in the possession of a sub-anal fasciole. Although the posterior inter-ambulacrum differs from all the others (a characteristic of the adult as well as of the imago), it is the *four plates which bear the fasciolar spines* that are most prominent. In the adult, on the other hand, plates *2a* and *2b* are by far the largest, and are known as the sternal plates (fig. 5, *st.*). The imago shows, as yet, no differentiation of the labrum (fig. 5, *l.*) or of the sternum.

The Further Development of the Young Urchin.

A.—The Dorsal Surface.

The young urchin does not long retain the primitive spherical form of the imago. As development proceeds it commences to elongate antero-posteriorly, and soon becomes ellipsoidal. Fig. 7 represents the dorsal view of a small urchin a short time after metamorphosis. The total length (including the spines) is 1 mm., the test alone measuring 0·473 mm. in length, and 0·41 mm. in breadth. The majority of the larval spicules have either been broken off or have undergone resorption. The primary spines have elongated considerably, and now measure, on an average, 0·179–0·21 mm. in length. Those in the sub-anal fasciole have become clavate, and measure approximately 0·1 mm. The four primary spines enclosed within the fasciole (see fig. 2) are considerably larger than the others (0·315–0·352 mm.), and thus enhance the bilateral symmetry. At this stage the young Spatangoid bears a slight resemblance to the young form of the Clypeastroid *Echinocyamus pusillus* (Théel, 1892, Plate IX, fig. 107).

As the plates have increased in size they have extended over on to the dorsal surface, so that only a relatively small area is left free. Additional plates are being laid down in both ambulacra and inter-ambulacra. All the ocular plates (oc^{I}–oc^{V}) are now visible, but, with the exception of ocular **III**, they are partially concealed by the adjacent inter-ambulacral plates. Genital **2** is very conspicuous, and the larval spicule around which it was formed (part of the dorsal arch) is still quite evident. Genital **1** is small, but is not partially overlaid by the madreporite, as was the case in the imago represented in fig. 6.

Round three separate remnants of larval spicules a calcareous meshwork is being built up, the larval spicules forming, as it were, the foundations of new plates.* Two of these, as is clear from later stages, become genitals **3** and **4** (fig. 7, g^3 and g^4). The remaining one (*y*) is situated near to the posterior inter-ambulacrum, exactly in the position that genital **5** might be expected to occupy were it present. In the adult, it may be recalled, the fifth genital is absent. In all probability this plate is genital **5**. Its fate will be dealt with in describing subsequent stages. The developing plate lying near to genital **3** is an inter-ambulacral plate belonging to area **3**.

* In *Echinocyamus* (Théel, 1892, Plate IX, fig. 107) one or two remnants of larval spicules appear to be forming plates of the permanent skeleton just posterior to the large central plate which surrounds the water-pore.

Although the greater part of the larval skeleton has gone, very minute traces of the latticed postero-dorsal and post-oral rods are still to be seen. From the position* of these it is clear that genital **3** arises from the posterior downgrowth of the right postero-dorsal rod (fig. 3, g^3), while plate y is formed from the posterior extension of the right post-oral spicule (fig. 4, y).

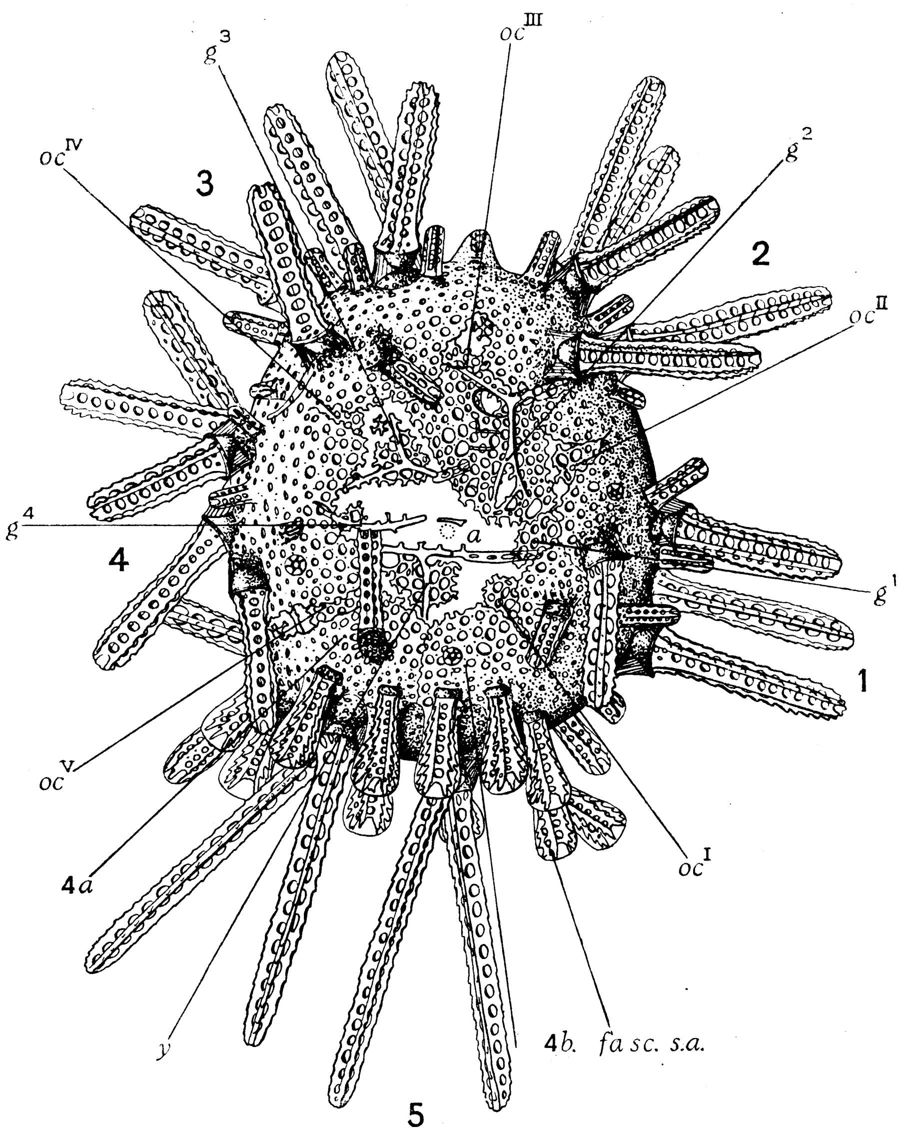


FIG. 7.—Dorsal view of a young urchin soon after metamorphosis. oc^{I}–oc^{V}, ocular plates; g^1–g^4, genital plates; *y*., the plate formed from part of the right post-oral rod (this plate is, in all probability, genital **5**); *a*., anus; *fasc. s. a.*, "sub-anal" fasciole; **1–5**, inter-ambulacra.

Camera lucida drawing. 1 × 140.

* Although the remnants of the latticed rods are faint, they appear to be actually continuous with the spicules from which the two plates arise, and in other specimens this is clearly the case.

In *Echinus miliaris* the writer (1926, p. 267) showed that genital **3** arose as a proliferation of the right postero-dorsal spicule, and that genital **5** was similarly formed from the right post-oral spicule. The fact that plate *y* in *Echinocardium cordatum* is formed from the same larval spicule as is genital **5** in *Echinus miliaris* seems to prove that plate *y* is indeed genital **5**.

The small spicule lying anterior to the anus (*a.*) is undergoing resorption and will soon disappear entirely. If it is assumed that plate *y* is genital **5**, the arrangement of the ocular and genital plates around the central anus recalls that found in a regular urchin such as *Echinus*. The membrane in the neighbourhood of the anus must represent the periproct of the adult.

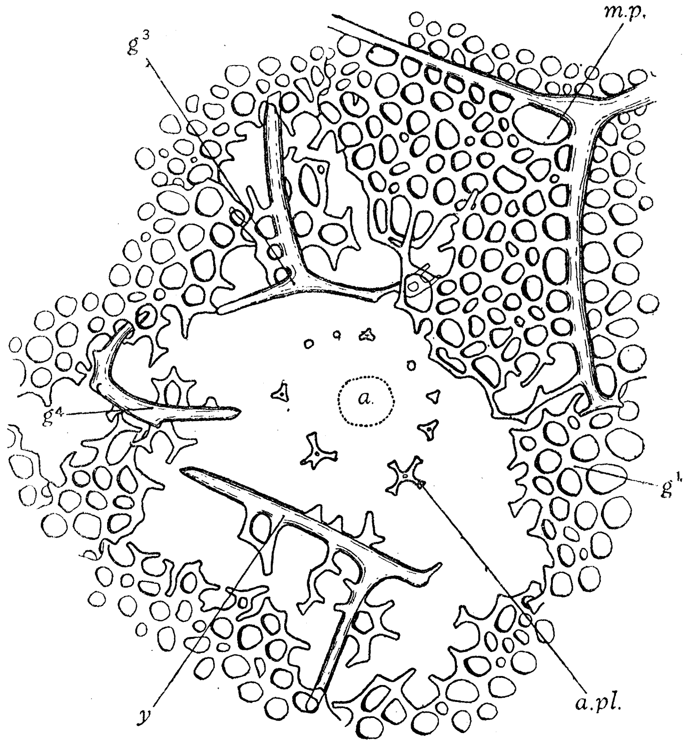


FIG. 8.—Part of the dorsal surface of a young urchin to show the original ring of anal plates. *m. p.*, madreporic pore in genital **2**; *a. pl.*, anal plate; *a.*, anus; *y.*, plate *y* (genital **5**); g^1, g^3, g^4, genital plates. Camera lucida drawing. 1 × 350.

Soon afterwards (or, in some cases, slightly before this) numerous small plates make their appearance in the periproct. Fig. 8 shows nine of them in a ring round the anus. Although these anal plates have appeared, genitals **3**, **4** and plate *y* are not so far advanced as in the previous figure, and the test of the young urchin measures only 0·4 mm. in length. Such slight individual variations are frequently met with. From this figure it is evident that the spicule which gives rise to genital **3** is a continuation of the right postero-dorsal rod.

As the urchin increases in size, more and more plates are added to both ambulacra and inter-ambulacra, and gradually the shape of the test alters to that shown in fig. 9 (length 0·9 mm., breadth 0·78 mm.). The anterior is now considerably broader than the posterior end, while the anus is somewhat nearer the latter. Within the original ring of

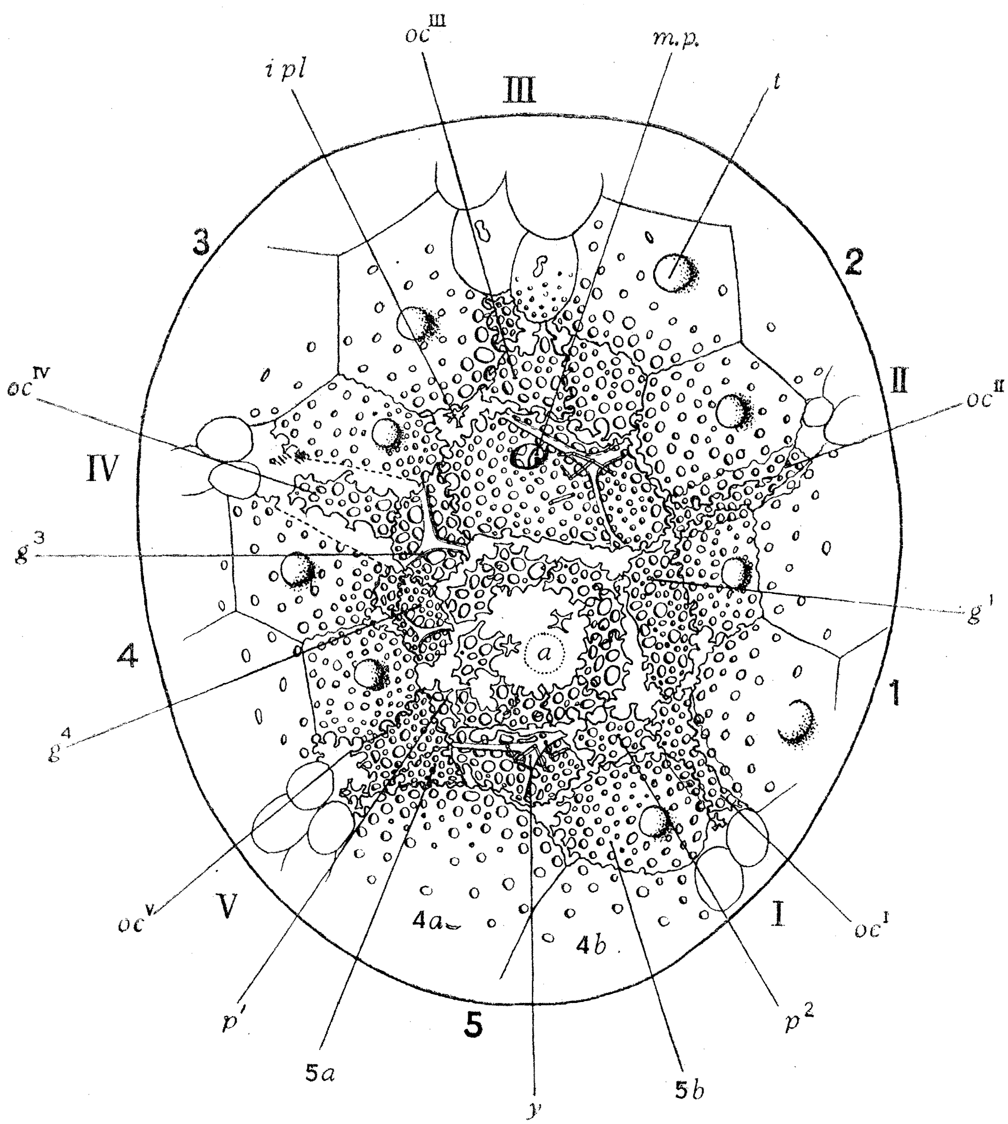


FIG. 9.—Dorsal surface of a young urchin measuring 0·9 × 0·78 mm. (exclusive of the spines) **I–V**, ambulacra; **1–5**, inter-ambulacra; oc^{I}–oc^{V}, ocular plates; g^1–g^4, genital plates; *m. p.*, madreporic pore; *i. pl.*, a developing inter-ambulacral plate; *t.*, tubercle of a "primary" spine; *a*, anus. Additional plates are indicated thus: 5*a*, 5*b*, p^1, p^2.

Camera lucida drawing. 1 × 130.

anal plates two additional ones have appeared. Just in front of the periproct lies the madreporite, and, passing round from the latter counter-clockwise, are genital **3**, genital **4**, a small developing plate, p^1, plate y (genital **5**), another plate, p^2, and, finally, genital **1**. There can be no doubt as to the correct identification of genitals **2**, **3**, **4** and *y*, as the larval spicules from which they were derived are still prominent. Oculars **I**, **II** and **IV** are still partly concealed by the inter-ambulacra, but not, of course, by the same plates as in the previous figure (fig. 7), since new plates have been laid down. The actual size of the oculars in question can only be determined by examination under crossed nicols. [Part of the plates overlying ocular **IV** have been omitted in fig. 9.] Genital **3**, which is internal to ocular **IV**, is contiguous with two of the plates of inter-ambulacrum **4**, but with only one in inter-ambulacrum **3**. Opposite the remaining portion of area **3** its place is taken by the madreporite. In the posterior inter-ambulacrum two additional plates have appeared. One of these, which has already acquired a primary tubercle, lies to the right of *y*, and is in reality plate *5b* of the adult (fig. 5, *5*). The other plate (*5a*) is much smaller, and is situated to the left of *y*. These two plates have succeeded in separating oculars **I** and **V**, respectively, from plates *4b* and *4a* of area **5**—those which bear part of the sub-anal fasciole (*cf.* fig. 7).

A number of the adapical ambulacral plates are now visible on the dorsal surface, and these—with the exception of the last formed ones—are oval in outline. Only those in the anterior ambulacrum (**III**), however, possess pores. At this stage many of the plates show, above the primary meshwork, a much more open meshwork, similar to that described by FEWKES (1887) on the plates of *Amphiura squamata*. This has been indicated merely by a few rods on the madreporite and on plate *y*, but is to be found on all save the smallest and most recently formed plates.

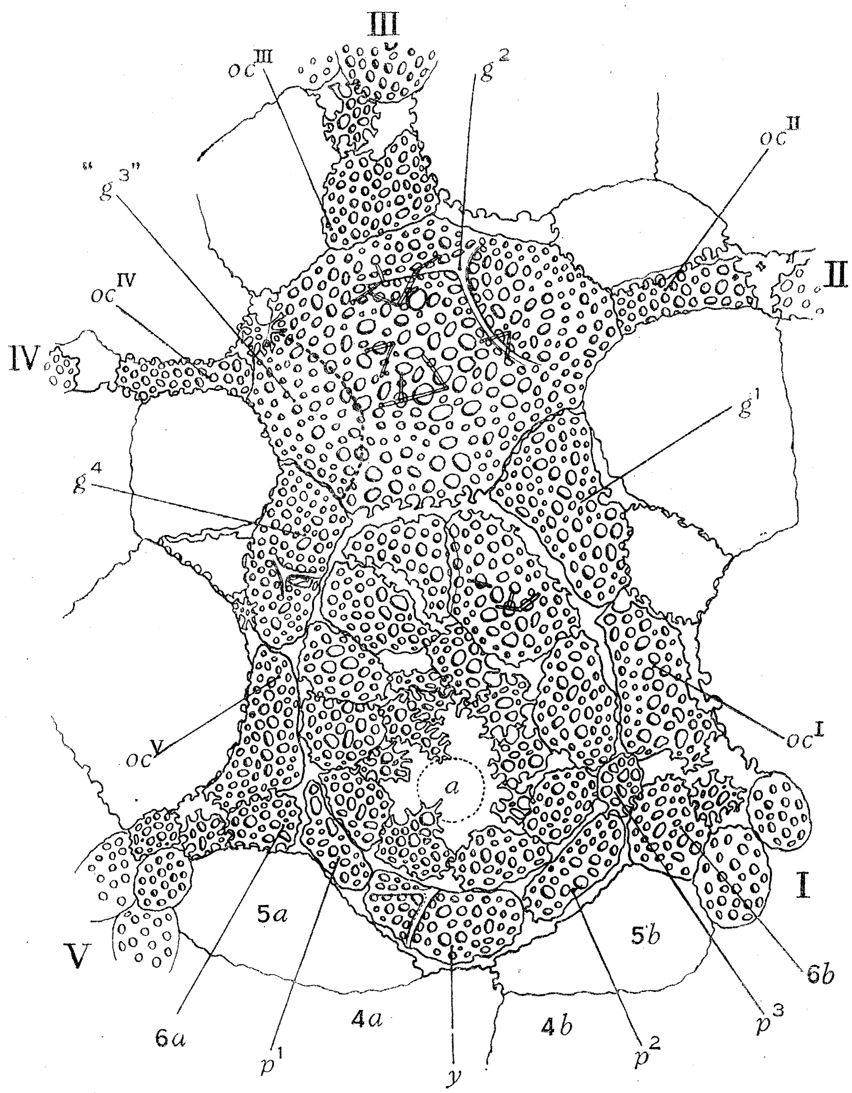
Although the specimen, of which part is represented in fig. 10, has increased in length to 1·43 mm., it really represents the next stage in the development of the dorsal surface. The periproct is now more prominent, having become almost ellipsoidal. The anus is no longer in the centre of the periproct, however, but much nearer the posterior end. The anal plates have increased in size, especially those in the neighbourhood of the madreporite, and additional plates have been laid down between these and the anus. To this is due the apparent backward shift of the latter. The plate *y* is still just anterior to plate *4a* of the posterior inter-ambulacrum. Oculars **V** and **I**, instead of being for the most part posterior to p^1 and p^2, as in fig. 9, are now *anterior* to these, and another plate (p^3) has appeared between ocular **I** and p^2. Plates *5b* and *5a* of inter-ambulacrum **5** have increased in size, while two additional plates (*6b* and *6a*) have been laid down external to p^2 and p^1. Plates *5b* and *5a* (fig. 9) were laid down one on either side of the plate *y* just as additional inter-ambulacral plates are formed on either side of a genital plate in *Echinus*; but from this point onwards all resemblance of *y* to a genital plate may be said to cease, for plates *6a* and *6b* have no relationship with it whatsoever.

At this stage no less than three sets of plates are laid down in the vicinity of oculars **I** and **V**, viz., (1) ambulacral plates, (2) inter-ambulacral plates, and (3) the plates which have been denominated by the letter *p*.

Since oculars **I** and **V** have progressed forwards,* genitals **1** and **4** have also, of necessity,

* To facilitate description the axis passing perpendicularly through the madreporite is regarded as "fixed" (see p. 302).

moved forwards. Genital **4** is now in contact with the madreporite, while part of the latter must have undergone resorption to accommodate genital **1**. The posterior border of the madreporite is thus relatively smaller than in the previous figure. The madreporic



TEXT-FIG. 10.—The periproct and the neighbouring plates from a specimen measuring 1·43 mm. in length. Genital **3** ("g^3") is missing: its position is indicated by a dotted line on g^2. Lettering as in the previous figure. Three new plates—6*b*, p^3 and 6*a*—are marked. The plates in which the meshes have been omitted are all inter-ambulacral plates. Camera lucida drawing. 1 × 130.

pore is still simple, but is now relatively small and rather difficult to distinguish. In the specimen from which this drawing was made genital **3** ("g^3") is not distinguishable, its presumed boundary being indicated by a dotted line. Examination under high power and also under crossed nicols failed to reveal any suture, separating it from the madreporite, since this plate is in contact with one plate of inter-ambulacrum **4** as well as with areas **3**, **2** and **1**. In the previous stage the madreporite was only contiguous with inter-ambulacra **2** and **3**.

In fig. 11 (length 1·37 mm., breadth 1·075 mm.) oculars **I** and **V** have advanced somewhat nearer to the madreporite, which latter is now in contact with genitals **3**, **4** and **1** (*cf.* fig. 9). Oculars **I**, **II**, **IV** and **V** are still relatively large plates, somewhat oblong in shape, but with no traces of the future ocular pores. Ocular **III**, which is also large, possesses a distinct notch in the anterior border. This represents an early stage in the formation of the pore. The periproct is very similar to that shown in the previous figure, but additional plates have been laid down, within the original circle, on all sides of the anus. External to the ring of anal plates an additional plate (p^4) has appeared

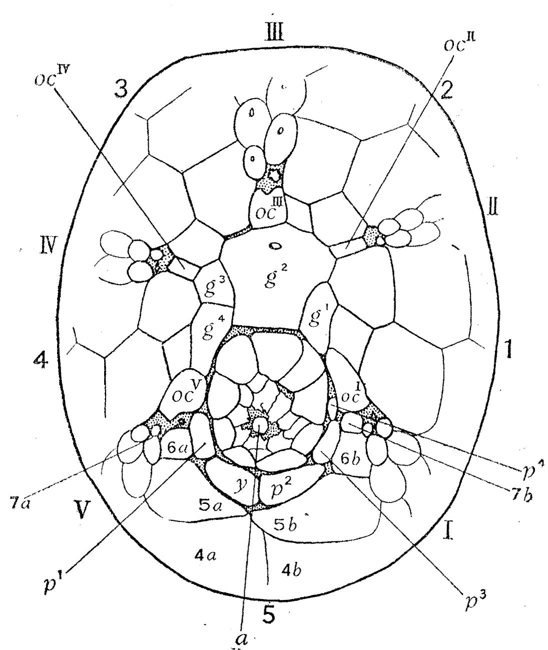


FIG. 11.—Dorsal aspect of an urchin measuring 1·37 mm. in length. New plates indicated are *7b*, *7a* and p^4. Other lettering as in previous figures. Camera lucida drawing. 1 × 53.

in the neighbourhood of ocular **I**. Just posterior to the same ocular another inter-ambulacral plate (*7b*) has been formed in the posterior inter-radius: the corresponding plate (*7a*) on the left side is a small six-rayed star situated posterior to ocular **V** and external to p^1.

When the test has reached 1·5 mm. in length, the first hint of the internal fasciole can be made out. At this stage it consists of a few short spines arranged in a single series on inter-ambulacra **2** and **3**, together with two or three spines on the anterior dorsal plates of ambulacrum **III**, and one or two on the anterior portion of the madreporite (see LOVÉN, 1883, Plate XV, fig. 173).

Hitherto the young urchin has given little indication of the oval shape characteristic of the adult, but in the next figure (length* 2·05 mm.) this is now apparent. The dorsal surface is already slightly humped, the highest point being at the anterior end of the periproct. The position of the latter is still practically horizontal. In the posterior (anal) inter-ambulacrum more plates have been added on either side of the periproct. The two columns (*a* and *b*) are just about to meet anteriorly completely to enclose the anal plates. The periproct has become somewhat flask-shaped, and although the original outer circle of anal plates can be distinguished, the four anterior ones are much larger than the others. Round the posterior two-thirds of this ring the plates y, p^1, p^2, . . . , form a crescentic band.

Numerous plates have also been added to ambulacra **I** and **V**, the last-formed plates being, in both cases, on a level with the anterior apex of the periproct (*cf.* previous figure).

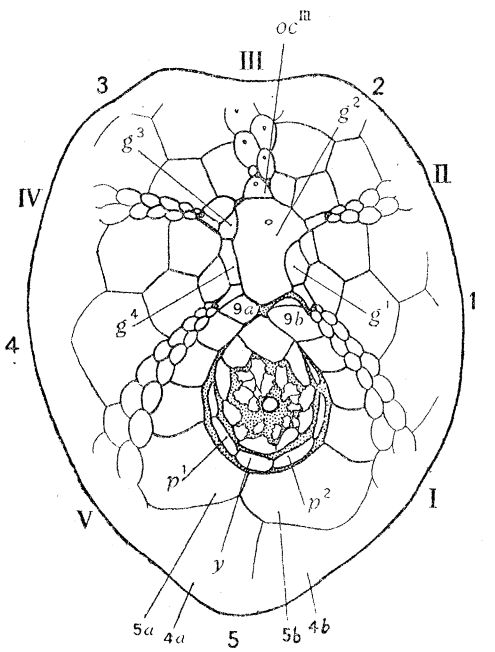


FIG. 12.—Dorsal surface of a specimen 2·05 mm. in length. The ovate shape characteristic of the adult is now evident. Plates 9*b* and 9*a* of inter-ambulacrum **5** have almost met to completely enclose the periproct. The apical system, with the exception of genital **5** (plate *y*) is now in front of the periproct. Lettering as in previous figures.

Camera lucida drawing. 1 × 35.

The madreporic plate has also undergone considerable alteration in shape, especially along the posterior border, which has become pointed. Plates *9b* and *9a* of area **5** have almost completely separated it from the periproct. Moreover, genitals **1** and **4** are now bounded by genital **2** along the entire inner border, while oculars **I** and **V** are also in contact with the madreporite. Ocular **III** has completely surrounded the " eye " (oculus), thus forming a definite ocular pore. The other ocular plates are still relatively long and narrow, and show no signs of the future pores. Although quite a number of ambulacral plates are visible on the dorsal surface, only those in area **III** possess pores and, therefore, tube-feet.

Traces of the larval spicules are still visible in the meshwork of the madreporite and of plate *y*. From the inner anterior portion of the madreporic plate a number of calcareous processes grow downwards and backwards. This is the first trace of the *madreporic apophysis* (" oberer Stützapparat "), so characteristic of the adult Spatangoid (see fig. 27, C).

Although the length of the specimen represented in fig. 13 is almost twice that of the urchin represented in fig. 12, the number of plates in both column *a* and column *b* of inter-ambulacrum **5** has only increased to twelve. The individual plates, however, have greatly increased in size.

* From this point onwards the length given is always that of the denuded test measured from the floor of the anterior groove to the posterior apex.

In the periproct, plates p^1, y, p^2 are quite prominent, while the original ring of anal plates does not stand out so clearly as in previous stages. The four anterior plates in the original ring, together with plates y, p^1, p^2 . . . , now form a continuous circle.

The madreporite is a considerable distance in front of the periproct. Genital **3** is now in contact with ocular **III**, having at last assumed its proper position relative to inter-ambulacrum **3**. Genital **4** is also in contact with ocular **IV**, while genital **1** is in contact with ocular **II**, so that the madreporite is now only contiguous with two inter-ambulacra (areas **2** and **5**). The madreporic pore is still simple. Oculars **I**, **II**, **IV** and **V** are relatively small, but now arch round the oculi ("eyes") in order to form the ocular pores. [In this particular specimen ocular **V** is not yet in contact with genital **2**, *cf*. previous figure (fig. 12), being separated from it by plate *11a* of area **5**.]

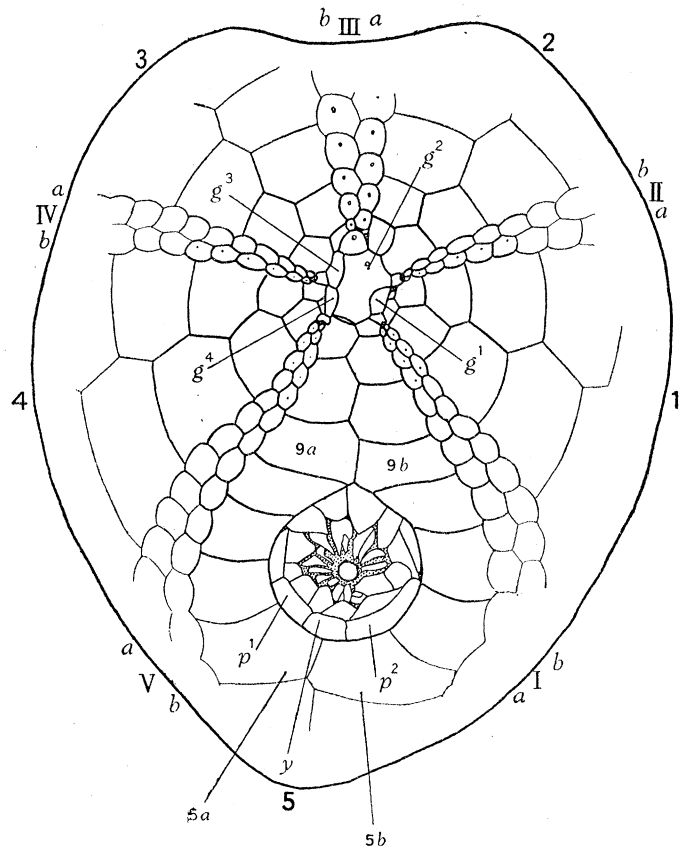


FIG. 13.—Dorsal aspect of a young urchin (l = 3·9 mm.). A number of simple pores are present in the incipient petal of area **I** and of area **V**. In each of ambulacra **II** and **IV** only one column (**II***a* and **IV***b*) is petaloid at this stage. The posterior inter-ambulacrum has surrounded the periproct and the latter is now much nearer the posterior end of the test. Plates p^1, y, p^2 are commencing to grow more rapidly than the anal plates. Camera lucida drawing. 1 × 25.

The internal fasciole is somewhat more advanced, the spines being, for the most part, in two rows on inter-ambulacra **2** and **3**. It traverses genital **3**, the median portion of the madreporite, and genital **1**, but appears to miss ocular **II**, as no trace of a minute tubercle can be detected on that plate. On the madreporite also there are, in front of the four fasciolar spines, one or two small spines similar to those which now occur on ambulacrum **III**. These spines, though also short, are not "tufted" at their extremities as are those in the fasciole (see fig. 26, *f.*). Behind the periproct, on plates *5b* and *5a*, a few clavate spines, similar to those in the internal fasciole, have appeared. These are the first indications of the anal fasciole (fig. 5, *a. fasc.*).

In ambulacra **I** and **V**, and in columns **IV***b* and **II***a*, a few of the adapical plates now exhibit small simple pores. In the majority of the ambulacral plates, however (including the last-formed one in the areas specified), no pores have as yet appeared. The apical system of plates is relatively smaller and more compact than in the previous specimen (fig. 12). The highest point is still just in front of the periproct, but the latter dips more posteriorly.

In fig. 14 (length 5·5 mm.) a considerable advance towards the condition found in the adult has been made. The periproct is situated much nearer the posterior end of the test, and slopes still more obliquely towards the ventral surface. The plates p^1, y, p^2 have become considerably enlarged, while the smaller plates surrounding the anus form an almost continuous meshwork (compare with previous figures). The number of plates in both column *a* and column *b* of inter-ambulacrum **5** is now thirteen (*i.e.*, only one additional plate has been formed in each column). The ocular pores have been completed in plates **I**, **II**, **IV** and **V**, which may now be said to have reached the adult condition. Many of the pores in ambulacra **I** and **IV** are double, or are undergoing division, and the plates which possess these pores are no longer oval, but have almost assumed the adult form (fig. 5). In ambulacra **II** and **IV** double pores are only present in the posterior column (**II***a* and **IV***b*), but simple pores have now been formed in several of the plates in columns **II***b* and **IV***a*. As the plates which possess double pores have altered in shape they have, to a certain extent, influenced the plates in the other two columns, so that the latter are no longer quite oval.

Ambulacrum **III** differs from the others, almost from the beginning, in the larger size of the plates as well as in the early appearance of the pores (figs. 9–13). Now the difference is more marked. The plates, though no longer oval, are relatively broad, and the more anteriorly placed pores are very large, though simple. These pores never divide. The internal fasciole, which is quite well marked, has now passed on to the adapical plates of ambulacra **II**, **I**, **V** and **IV**, and of inter-ambulacra **1**, **5** and **4**—*i.e.*, it has completely enclosed the apical system of plates.

The young urchin can now readily be recognised as a small Spatangoid. The petals are quite distinct, although columns **II***b* and **IV***a* are not yet petaloid. The internal fasciole (which surrounds the anterior modified "petal"), the anal and sub-anal fascioles are all present. The apical system of plates is small, compact, enclosed within the internal fasciole, and situated in the centre of the dorsal surface. However, it still shows one or two immature features, notably the possession of a single primary madreporic pore and the absence of the genital pores.

The change to the adult condition takes place gradually, and will be described briefly. Increase in size is due, not so much to the addition of new plates, as to the growth of those which have already been formed. In fig. 5* LOVÉN (1874) shows only thirteen plates in column *5a* and fourteen in column *5b*, while the specimen represented in fig. 14 has already thirteen plates in each column. LOVÉN does not mention the size of the specimen from which fig. 5 was built up, but in all probability it was quite adult.

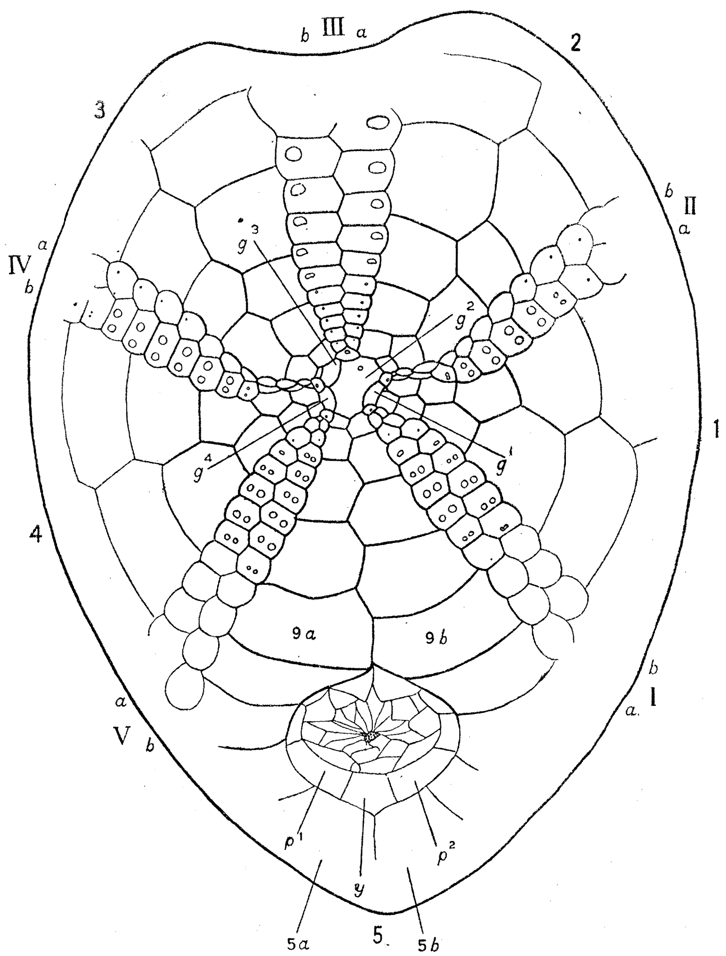


FIG. 14.—Dorsal aspect of a young urchin ($l = 5 \cdot 5$ mm.). The anterior ambulacrum **III** resembles that of an adult *Spatangus purpureus* at this stage, while columns **II***b* and **IV***a* are still apetaloid. The madreporic pore is still simple.

Camera lucida drawing. 1 × 21.

A few additional plates are laid down in ambulacra **II**, **I**, **V** and **IV**, but in area **III**, curiously enough, new plates are added in rapid succession, with the result that the intra-fasciolar part becomes very complex. This has been indicated very roughly in fig. 5, but the plating has been studied in detail by HAWKINS, and represented in two excellent figures (HAWKINS, 1920, Plate 69, figs. 4 and 5). In fig. 14 the plating in the

* Fig. 5 of the present paper copied from LOVÉN's figure.

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intra-fasciolar part of the anterior ambulacrum is simple, and very similar to that found in ambulacrum **III** of an a d u l t *Spatangus purpureus* (HAWKINS, 1920, Plate 69, fig. 1), except that the pores are simple instead of double. As development proceeds, plate-formation goes on apace, until, by the time the urchin has reached 10 mm. in length, the plates in the neighbourhood of ocular **III** are numerous, but very low. Already a few of the reduced plates* so characteristic of the adult modified "petal" can be made out in etched specimens. While this is taking place the anterior ambulacrum becomes more and more deeply grooved, while the petals tend to become more pronounced, and a number of the pores in columns **II***b* and **IV***a* become double (see fig. 5).

The madreporic pore remains simple until the urchin measures 9 mm. in length; then it divides, and already a few pores are to be found in specimens measuring 11·5 mm. in length. Meanwhile the *madreporic apophysis*† has been increasing in size. Fig. 27, E, represents this downgrowth in a specimen measuring 5·5 mm. in length (the specimen shown in fig. 14). A very shallow pit on the inner surface of each of the four genital plates in a specimen measuring 13 mm. in length indicates that the genital pores are in process of formation. These pores are fully formed in specimens measuring 15 mm. in length.

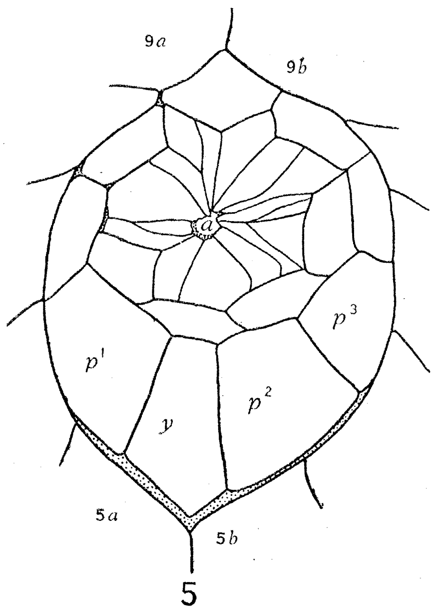

FIG. 15.—Periproct of a specimen 1·5 mm. in length. Plates p^1, y, p^2 are now very large. *a.*, anus. Camera lucida drawing. 1 × 190.

While these changes have been taking place the wedge at the posterior end of the body has become almost vertical, and the adult condition has practically been reached. At this stage the periproct (fig. 15) can scarcely be seen from the dorsal surface. The plates p^1, y, p^2 are now by far the most prominent, and the posterior plates of the original circle (see figs. 9–12) can scarcely be distinguished from the anal plates within the outer ring (which now includes y, p^1, p^2 . . .). The plates p^1, y and p^2 are the first to acquire spines, and in specimens of 5·5 mm. in length they each bear a number of short secondary spines.

In *Echinus miliaris* the writer showed that genitals **3** and **5** differ from the others in texture (GORDON, 1926, figs. 17 and 19*d*). In *Echinocardium* also the same curious difference exists, genital **3** and

* "Demi-plates," "occluded" plates and "included" plates are all present in the modified "petal" (see HAWKINS, 1920, Plate 69, figs. 4 and 5).

† The function of this downgrowth (the "oberer Stützapparat") has been described by HOFFMANN (1871, p. 27). To the free hinder border of the apophysis a double fold of mesentery is attached; this runs along to the anus, and attaches the rectum to the inner shell wall.

plate *y* (genital **5**) being, in young specimens, paler than the other plates. One of the oculars (generally ocular **IV**) is also similar to these two genitals in texture. This difference tends to disappear as the plates become more compact, and is very transient in the case of the ocular plate. In one specimen measuring 6 mm. in length genital **3** is still (when examined under the microscope) distinctly paler than the surrounding plates. The periproct represented in fig. 15, taken from a specimen measuring 15 mm. in length, was mounted in canada balsam. If the preparation be held up to the light or examined under the microscope, plate *y* is seen to differ markedly from the other plates—even from the thin, rather delicate plates around the anus.

B.—Ventral Surface.

Fig. 16 represents the oral aspect of a young urchin a short time after metamorphosis. Although the test is smaller than that of the urchin represented in fig. 7, it is comparatively farther advanced as the relatively enormous length of the four posterior spines indicates. Moreover, on the dorsal surface, the first (original) ring of anal plates has appeared in the periproct. The total length, including the spines, is 1·23 mm., that of the test alone being 0·436 mm., while the long posterior spines measure 0·536 mm. The bilateral symmetry is now quite pronounced.

From observations made on living urchins at this stage, it is evident that *Echinocardium* uses the enormous posterior spines as stilts with which to lever itself along. The peristomial margin of the test is almost circular (*cf.* fig. 2, *p.*). In the five tube-feet the primordia of the calcareous discs have appeared, while the sphæridia are well-developed globular bodies. The sutures have been omitted in the figure as they did not stand out very clearly in the specimen (a whole mount) from which the drawing was made. The peristomial (first or unpaired) plate in each inter-ambulacrum bears a well-developed spine (*sp.*[1]) which, it may be recalled, appeared in the late pluteus about the same time as the sphæridia. These spines (*sp.*[1]) bend over the mouth, which latter is situated in the centre of the peristome.

The urchin does not appear to feed just yet, for no trace of food can be seen in the digestive tract. This is true for those specimens dredged from the ocean, where proper food was available, as well as for those reared in the laboratory. By the time the test has increased to 0·65–0·7 mm. in length, however, the animal has commenced to feed.

In the next figure (fig. 17, length 0·71 mm., breadth 0·668 mm.) numerous minute buccal plates (*b. pl.*) have appeared in the peristomial membrane. Those in the outer ring are slightly larger than those in the inner. The fifteen peristomial plates of the corona have been drawn in more detail than the others which occupy the curved outer edge of the ventral surface. The second series of ambulacral plates* (the **I***b*, **II***b*, **III***a*,

* It has been deemed advisable to retain LOVÉN's terms "first and second series" here also, although the second series of plates are laid down slightly in advance of the first series. A full explanation of LOVÉN's system of naming the areas, and the plates in each area, has already been given (GORDON, 1926), and need not be repeated.

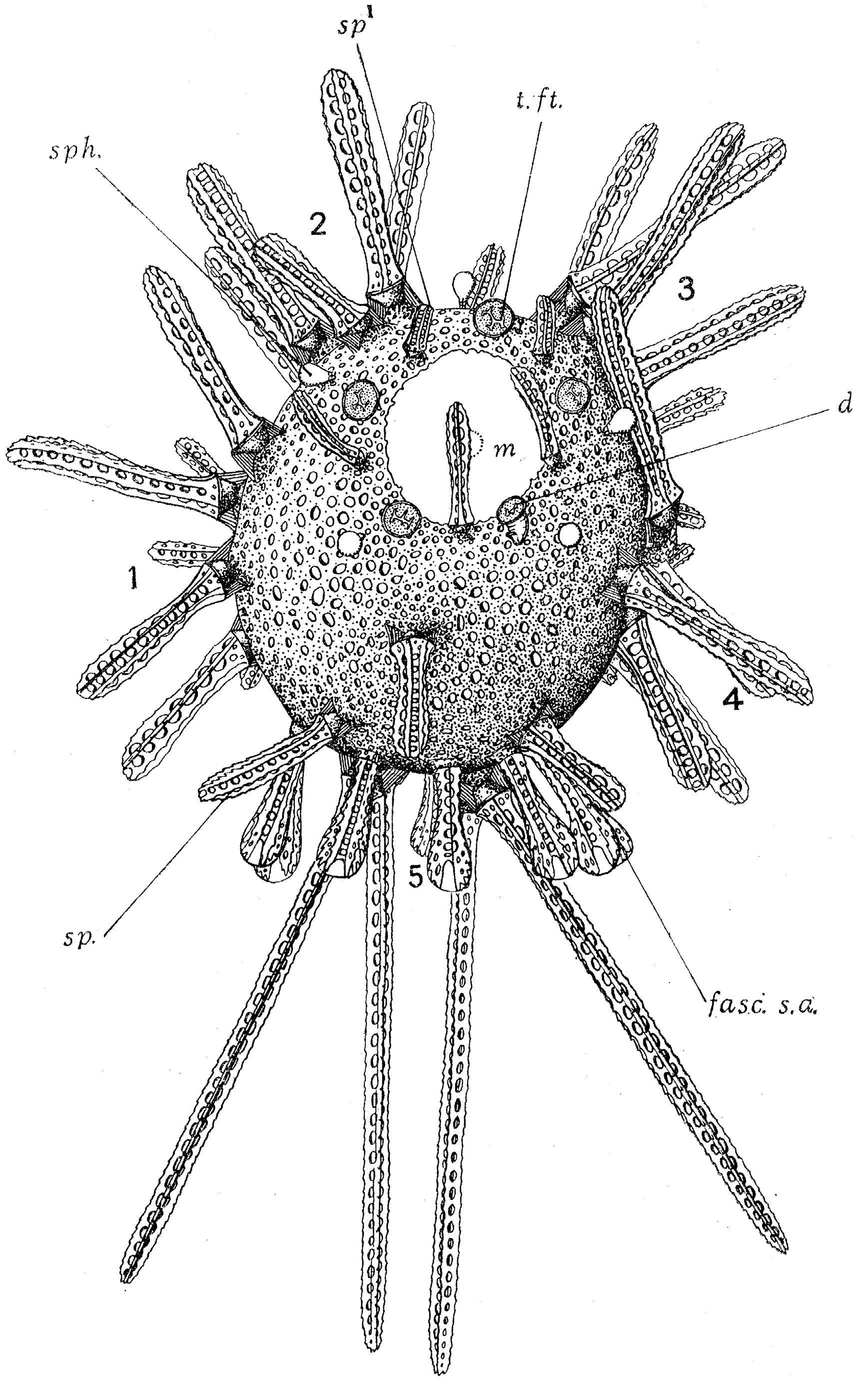

FIG. 16.—Ventral aspect of a young urchin ($l = 1 \cdot 23$ mm. inclusive of the spines). *t. ft.*, one of the five tube-feet which occur in the first plate of the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series; *d.*, developing disc of a tube-foot; *fasc. s. a.*, "sub-anal" fasciole; *sp.*, spine; *sp.*[1], secondary spine on the unpaired inter-ambulacral plate; *sph.*, sphæridium; *m.*, mouth; **1**–**5**, the inter-ambulacra.

Camera lucida drawing. 1 × 140.

IV*b*, **V***a* series) are now smaller than the other series (*cf.* figs. 2 and 1, c), and possess pores indicating that the tube-feet in this series have now appeared. Three of the plates in the first series (plates **II***a*, **IV***a* and **V***a*) have acquired a second pore—*i.e.*, they are now biporous. Each of the ten peristomial ambulacral plates is partly overlaid by the adjacent unpaired inter-ambulacral plate, this portion (lamina), which shows up well under crossed nicols, ending in an acute point beneath the small tubercle ($t.^1$).

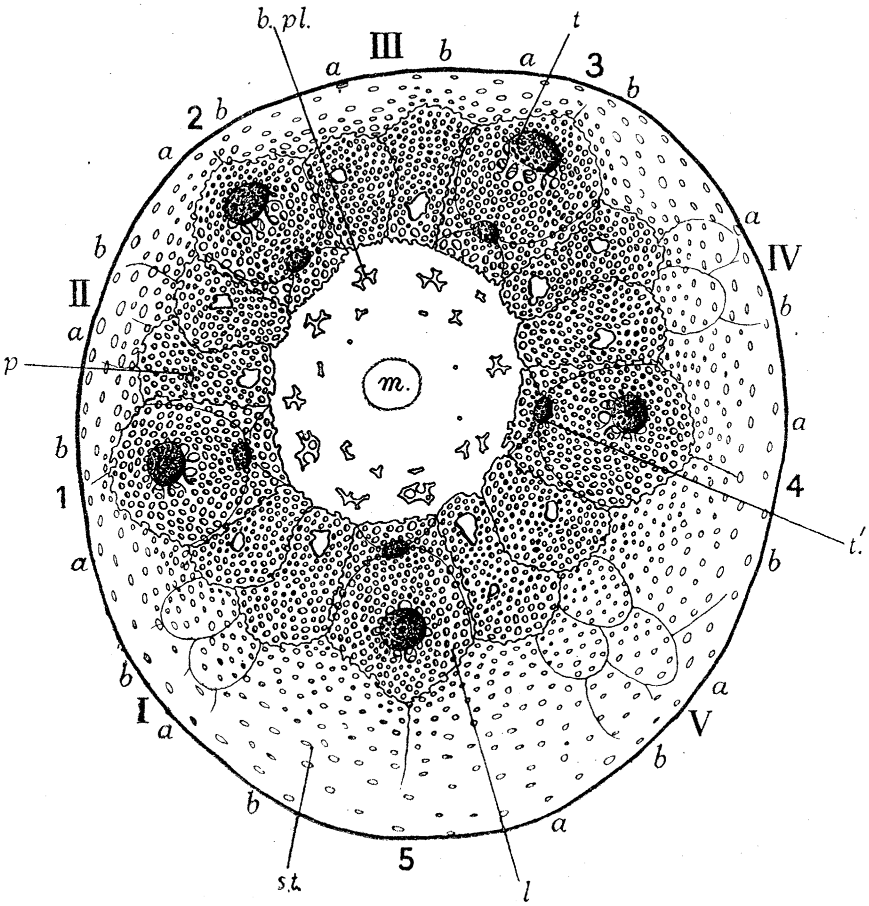

FIG. 17.—Ventral surface of a young urchin measuring 0·71 × 0·668 mm. (excluding the spines). **I–V.**, ambulacra ; **1–5**, inter-ambulacra ; *a* and *b*, the two columns of ambulacral and of inter-ambulacral plates ; *m.*, mouth ; *b. pl.*, buccal plate ; *t.*, primary tubercle on the unpaired inter-ambulacral plate ; $t.^1$, the secondary tubercle on the same plate (the spine $sp.^1$ (fig. 6) is attached to $t.^1$) ; *l.*, labrum ; *st.*, sternal plate ; *p.*, second pore of a biporous plate.

Camera lucida drawing. 1 × 140.

For a more detailed drawing of the projecting laminæ, see LOVÉN, 1883, Plate XV. fig. 183. The laminæ seem to disappear in course of time, but traces of them can still be made out in a specimen measuring 3·1 mm. in length. The succeeding ambulacral plates have now become oval, but do not as yet possess pores.

Each unpaired inter-ambulacral plate now bears two spine bosses (tubercles), a small one ($t.^1$) next the peristome and a much larger one ($t.$) immediately behind this. The

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order in which these tubercles (and their associated spines) appear is variable. As has already been stated (p. 269), some imagines have only one spine on each of these plates at metamorphosis. This is the spine which is attached to the tubercle *t.*[1], and is formed at the same time as the sphæridia. In an occasional imago there are already two spines on each plate, the smaller one being nearest the peristome and only as long as, or slightly longer than, the sphæridia. In a number of advanced Echinoplutei the unpaired plates in areas **2** and **3** have each, in addition to the small spine found on *all* the inter-radii, a larger spine situated farther from the peristome. The second tubercle *t.*, therefore, in spite of its large size, is sometimes formed *after* metamorphosis (in all the areas or only in areas **1**, **5** and **4**), and sometimes it is formed in the pluteus.

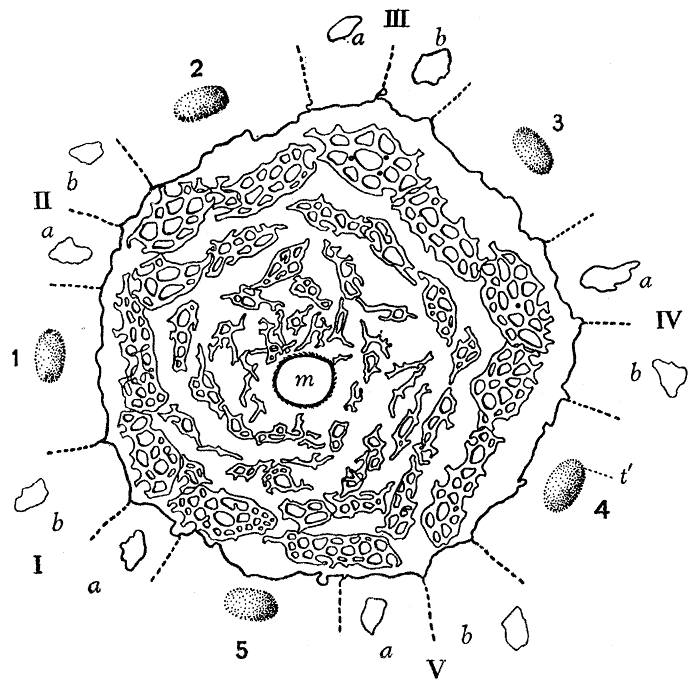

FIG. 18.—The peristome of an urchin measuring 0·95 mm. in length. Lettering as in fig. 17. Camera lucida drawing. 1 × 180.

This larger tubercle, *t.*, corresponds to the primary tubercle found in all the other inter-ambulacral plates (fig. 2).

All the unpaired inter-ambulacral plates are, at this early stage, similar in shape and almost equal in size (*cf.* fig. 5). Plates *2a* and *2b* in each area are now considerably larger than in the imago, but those in the unpaired inter-ambulacrum (**5**) are slightly in advance of the others. The peristome, although certainly nearer the anterior than the posterior end of the body, is not so excentric as fig. 16 appears to indicate. This is owing to the fact that, in whole mounts, the fasciolar spines and the long posterior primary ones tend to raise the posterior end of the test.

When the test has increased to 0·95 mm. in length, all the peristomial plates in the ambulacral series **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* are biporous, while in some areas a small pore

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is also present in the second plate of the series **I***b*, **II***b*, **III***a*, **IV***b*, **V***a*. But the most marked changes have taken place in the peristomial or buccal membrane (fig. 18). The margin of the corona is no longer circular, but sub-pentagonal. Many more buccal plates have been laid down, but the arrangement of these is irregular. Those next the corona are considerably larger than the others. The oldest specimen reared in the laboratory had reached this stage (length of test, 1 mm.). The buccal plates next the margin (ten in number) are much larger than those represented in fig. 18, but the smaller plates within this ring are comparatively few.

In the specimen represented in fig. 19 (length 1·45 mm.), the test has elongated markedly in an antero-posterior direction, and the peristome, which is now definitely pentagonal, is more anterior. The buccal membrane is, of course, very flexible, and when the mouth is open, as in this case, the smaller buccal plates become crowded together. The plates in the outer ring, thirteen in number, are now of relatively large size.

The unpaired inter-ambulacral plates still bear only two spines. Plates *2a* and *2b* have enlarged in all the areas, although not to such an extent as the two sternal plates (*st.*). On these plates (*i.e.*, plates *2a* and *2b* of all the inter-ambulacra) the primary tubercles can still be distinguished, for although a few others have been formed, the latter are relatively small.

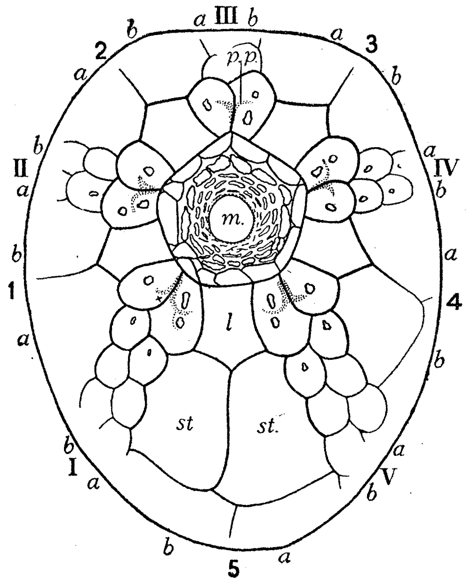

FIG. 19. — Ventral surface of a young urchin 1·45 mm. in length. *m.*, mouth ; *l.*, labrum ; *st.*, sternal plate ; *p. p.*, developing peripodium ; + indicates the position of the sphæridium on plate **I***b* of area **I**. Other lettering as in previous figures.

Camera lucida drawing. 1 × 47.

The ambulacra occupy the five angles of the pentagon, the peristomial margins of plates *1a* and *1b* being together smaller than that of the unpaired inter-ambulacral plates (compare with fig. 5). On plates 1*a* and 1*b* also, calcareous processes are growing upwards in the neighbourhood of the pores to raise the peripodia (*p.p.*, fig. 19), while in one or two of the succeeding plates additional pores have appeared. The sternal plates although large, only extend posteriorly as far as plate *4b* and plate *4a* of ambulacra **V** and **I**, respectively (*cf.* fig. 5).

Even when the test measures 3·1 mm. in length and 2·53 mm. in breadth (fig. 20), the peristome is still pentagonal and the mouth is still near the centre of the buccal membrane. An enlarged view of the latter is given in fig. 21. There are now fifteen buccal plates in the outer ring, but those in the vicinity of areas **II**, **2**, **III**, **3** and **IV** are considerably larger than the others. This specimen shows the large proportion of the peristomial border (of the corona) formed by the five inter-ambulacral plates.

A certain amount of "movement" of the ambulacral plates towards the peristome appears to have taken place in areas **I** and **V**. Plates *5a* of ambulacrum **I** and *5b* of area **V** are now in contact with the sternal plates, while plate *2b* of area **V** has reached the labrum. A similar "movement" has, of course, occurred in the other areas, but to a lesser extent. Although the peripodia are quite well marked, there are still only five

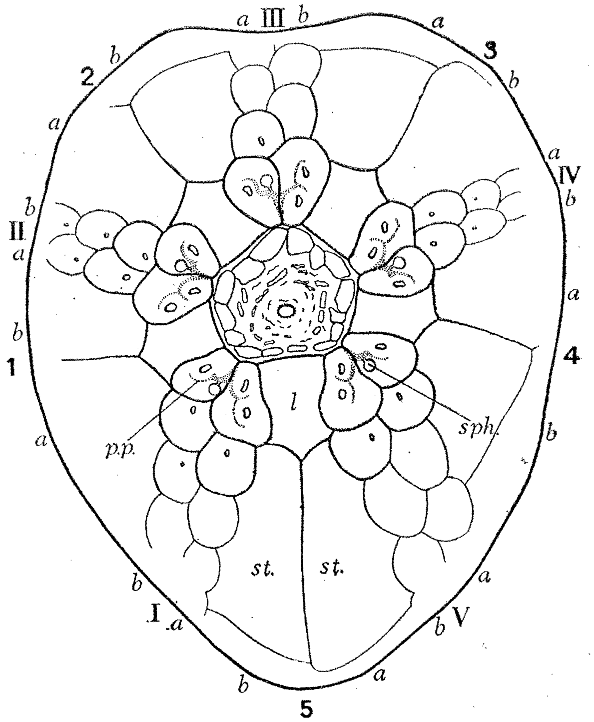

Fig. 20. — Ventral surface of a young urchin ($l = 3 \cdot 1$ mm.). *p. p.*, developing peripodium; *sph.*, sphæridium. Other lettering as in previous figures.
Camera lucida drawing. 1 × 28.

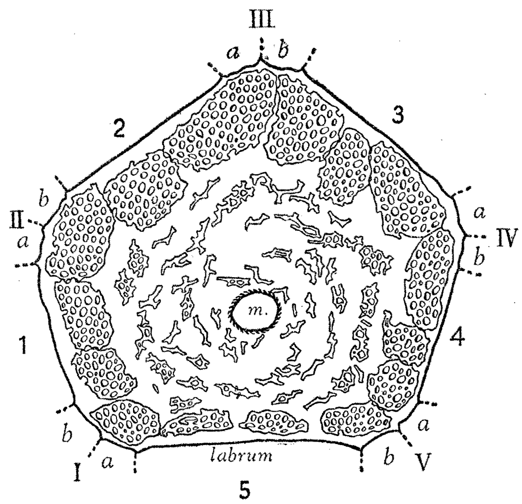

Fig. 21.—An enlarged drawing of the peristome of the specimen represented in fig. 20.
Camera lucida drawing. 1 × 80.

sphæridia. These are the sphæridia which were laid down in the Echinopluteus, and occur on the first plates in the series **I***b*, **II***b*, **III***a*, **IV***b*, **V***a*.

The unpaired plate in each inter-ambulacrum is becoming slightly constricted towards the aboral end. That in area **5** (the labrum, *l.*) is already somewhat larger than the others. The number of tubercles on all these plates (except that in area **1**) has increased, but the primary tubercle is still quite evident. On plates *2a* and *2b*, however, the tubercles have become so numerous that those belonging to the primary spines (fig. 2) can no longer be distinguished. The spines on the sternal plates, moreover, now resemble those found in the adult in that they possess somewhat flattened, recurved tips.

As development proceeds the peristome gradually becomes reniform, and the margin of the corona alters in accordance with this, especially along the posterior border (fig. 22). The labrum has extended laterally, and is now much broader than the corresponding plate in the other areas, although it does not as yet project anteriorly to form a lip. The buccal plates in the outer ring are, as in previous stages (figs. 18 and 21), large, while many more plates have been laid down internal to areas **II**, **III** and **IV**. If the number and size of the plates in the vicinity of the labrum be compared in figs. 21 and 22, it is obvious that a certain amount of resorption has occurred. The two plates α and β are in process of being resorbed, but this cannot be shown clearly in a drawing. The number of plates in the outer ring, exclusive of α and β, is thirteen, but this is subject to slight variation. Some of the plates within this outer ring are now quite large, but these are, for the most part, anterior to the mouth.

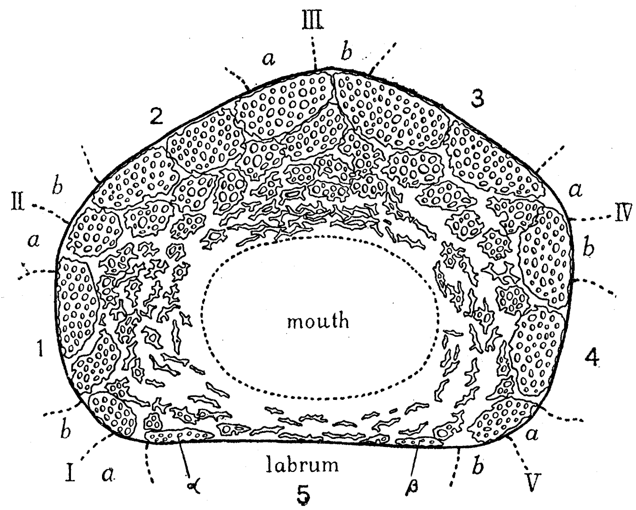

FIG. 22.—The peristome of a specimen measuring almost 4 mm. in length. Camera lucida drawing. 1 × 60.

In fig. 23 the mouth is completely closed, with the result that the buccal plates have become separated from each other, including those in the outer ring. Fig. 23, A, represents the peristome of another urchin of about the same size, with the mouth slightly open. The mouth is much nearer the unpaired inter-ambulacrum (**5**) than is the case in figs. 18 and 21. This apparent backward shift is due to (1) the great increase in the number and size of the buccal plates on the anterior part of the membrane, (2) the decrease in the number of plates in the neighbourhood of the labrum owing to resorption, together with (3) the outgrowth of the anterior border of the labrum.

The coronal plates in the region of the peristome have altered greatly in shape as well as in size, and this has been accompanied by a rearrangement of the plates relative to each other. Of the unpaired inter-ambulacral plates, the labrum is now larger than, and of quite a different shape from, the others, but all have now attained their adult shape (*cf.* fig. 5).

Plate *1b* of ambulacrum **III** is much higher than the corresponding plate in the other ambulacra. Moreover, it is still in contact with plate *2a* of inter-ambulacrum **3** (*cf.* figs. 19 and 20), and remains so even in the adult condition (fig. 5). Plate *1a* of area **III**, however, is now no longer in contact with plate *2b* of area **2**, being separated from it by ambulacral plate *2a*. Plate 1 of inter-ambulacrum **2** is now also bounded by part of plate *2b* as well as by plate *1b* of ambulacrum **II** (*cf.* figs. 19 and 20). Similarly, the unpaired plate of area **1** is now in contact with plates *2b* and *2a* of areas **I** and **II**,

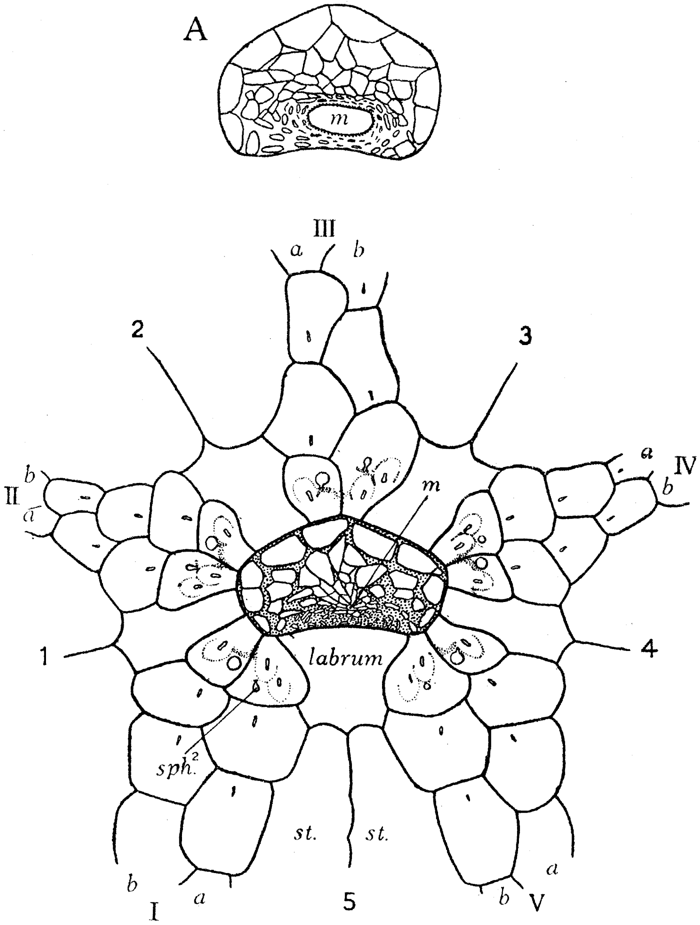

FIG. 23.—The peristome and surrounding plates of an urchin measuring 7 mm. in length; *sph.*², a developing sphæridium; the mouth (*m.*) is completely closed. A., the peristome of an urchin of approximately the same length, with the mouth open.
Camera lucida drawings. 1 × 15.

respectively, as is also the case in the adult (fig. 5). The labrum now extends backwards to meet plate *2a* of area **I** as well as plate *2b* of area **V**. The corresponding plate in inter-ambulacrum **4** has also extended in a radial direction to meet plate *2a* of ambulacrum **V** and plate *2b* of ambulacrum **IV**. The peristomial plate of inter-ambulacrum **3** also extends aborally to meet plate *2a* of area **IV**, as is the case in the adult (fig. 5).

This alteration in relative position* may be due to a " movement of the ambulacral

* This rearrangement of the plates in the ten meridia relative to each other during development is probably of constant occurrence throughout the Echinoidea.

plates towards the peristome," but this is not the only cause, for, since new plates are being added to the inter-ambulacra as well as to the ambulacra, there would be a corresponding "movement" of the inter-ambulacral plates. The chief cause is that while ambulacral plates are laid down more rapidly than inter-ambulacral plates, the latter increase in size more rapidly. That the rate of growth varies in different parts of the corona is obvious. The unpaired inter-ambulacral plates are of equal size in young urchins (fig. 17), the maximum breadth of each being equal to that of the first pair of ambulacral plates. In course of time the unpaired plates become relatively longer and narrower (figs. 19 and 20), and this is particularly true of the plate in areas **1** and **4** (fig. 23). The labrum also elongates at first (fig. 20), but later on it broadens out enormously, especially along the anterior border (fig. 23). The first pair of ambulacral plates, with the exception of that in column *b* of area **III**, tends to broaden out also (figs. 19, 20 and 23). In young forms, too, the succeeding ambulacral plates (plates *2a*, *3a* . . . , *2b*, *3b* . . .) are smaller than the first pair (figs. 17 and 19). Later on (figs. 20 and 23) they grow much more rapidly than the first pair, and soon exceed them in size, especially in areas **III**, **I** and **V** (fig. 5). The second pair of inter-ambulacral plates (*2a* and *2b*) increases enormously in size, especially those of area **5** (the sternal plates, *st*., fig. 5). As a result of this the next two pairs (**5**, *3a*, *3b*, *4a*, *4b*) become relatively smaller (*cf*. figs. 2 and 5). This lengthening of the posterior (anal) inter-ambulacrum undoubtedly exerts an influence over the adjacent ambulacra (**I** and **V**), and also over column *a* of area **1** and column *b* of area **4**. Thus there are considerably more plates in the apetalous portion of the bivious ambulacra than in those of areas **II** and **IV**, and the plates in column *a* and column *b* of areas **1** and **4**, respectively, are broader than those in the remaining two columns (fig. 5).

Although measuring only 7 mm. in length, the specimen represented in fig. 23 does not differ markedly from the adult. As development continues the labrum grows forward along its anterior border to form a projecting lip (fig. 5). The small buccal plates, which lie just in front of the labrum (fig. 23, A), undergo resorption while this is taking place, so that the mouth is ultimately bounded posteriorly by the lip. The buccal plates become more compact and increase in size; in course of time the membranous spaces between them become greatly reduced.

The plates around the peristome increase in size, but with one exception retain almost the same positions relative to each other as in fig. 23. Plate *1* of inter-ambulacrum **4** articulates with plate *3b* of ambulacrum **IV**. There is no resorption of tubercles near the peristome in *Echinocardium* such as occurs in *Echinus miliaris* (GORDON, 1926), but the five short spines (*sp*.[1]), which bend over the mouth in the young urchin (fig. 16), become indistinguishable from the other small spines formed later on the unpaired inter-ambulacral plates.

C.—The Tube-Feet.

(α) *The "Buccal"* Tube-Feet.*—The five tube-feet which are present at metamorphosis possess circular suckers in which there is, as a rule, no trace of any calcareous disc at this stage. Soon afterwards (fig. 16, *d*) a single spicule is laid down in each sucker, and this is elaborated into a disc of the type represented in fig. 24, *d* and *e*. These differ markedly from the compound disc found in the ambulatory tube-feet of *Echinus miliaris* (Gordon, 1926, fig. 13), but resemble those of the primary (terminal) tube-feet in arising from a single primordium. They are formed in a different manner from, and are much less regular than, those in the terminal tube-feet of *Echinus* (Gordon, 1926, fig. 12). They are, moreover, markedly convex, for the openly reticulate central portion is raised above the level of the more compact outer rim. Round the margin a number of short processes (shaded in fig. 24, *d* and *e*) arise. Later these grow into short blunt processes

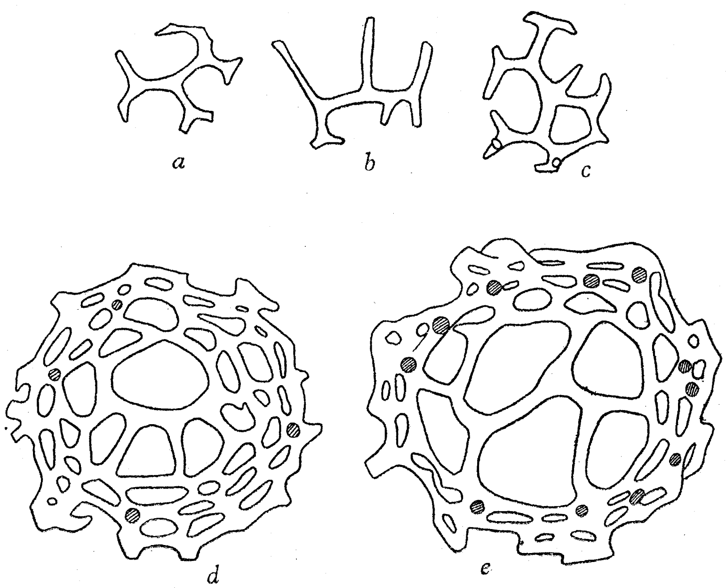

Fig. 24.—*a–e*, stages illustrating the development of the disc of a "buccal" tube-foot. Camera lucida drawings. 1 × 725.

which project obliquely over the irregular edge, while a small vertical process arises from the centre of the disc. When the urchin has reached a length of about 2–2·5 mm., a considerable number of "buccal" tube-feet (*i.e.*, those in the neighbourhood of the peristome, see p. 269) possess calcareous discs similar to, or somewhat more advanced than, those shown in fig. 24, *d* and *e*. The number varies, as there are three in ambulacrum **III**, five in each of ambulacra **II** and **IV**, and four in each of areas **I** and **V**.

At this stage also the "buccal" tube-feet belonging to the peristomial plate of the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series each possess one or two incipient papillæ (*p.*, fig. 25, *a*) and, as the

* It might seem preferable to restrict the use of the term *buccal tube-foot* to denote podia occurring on the peristomial or buccal membrane as distinct from those of the corona, but, as is explained later (p. 303), the buccal membranes of Regular Urchins and of Spatangoidea are not homologous, and in the latter group the "buccal" tube-feet arise outside the buccal membrane.

urchin increases in size, more and more of these are formed (fig. 25, *b–d*). Each finger-like process or papilla is supported by an axial rod (*a. r.*), and each calcareous rod arises from a single primordium. The base of the axial rod is formed in the same manner as the disc, but a vertical rod is soon formed. So far as can be made out, this rod arises from a single central upgrowth, but a number of other processes grows up from the surrounding parts to fuse with this a short distance from the base.

The disc, in all probability, develops later into an axial rod. Fig. 25, *d*, certainly suggests this, and the disc is, when fully formed, about the same size as the base of a well-developed rod. In course of time more and more papillæ are formed, and in the adult the end of the tube-foot is crowded with them. They are longest round the periphery,

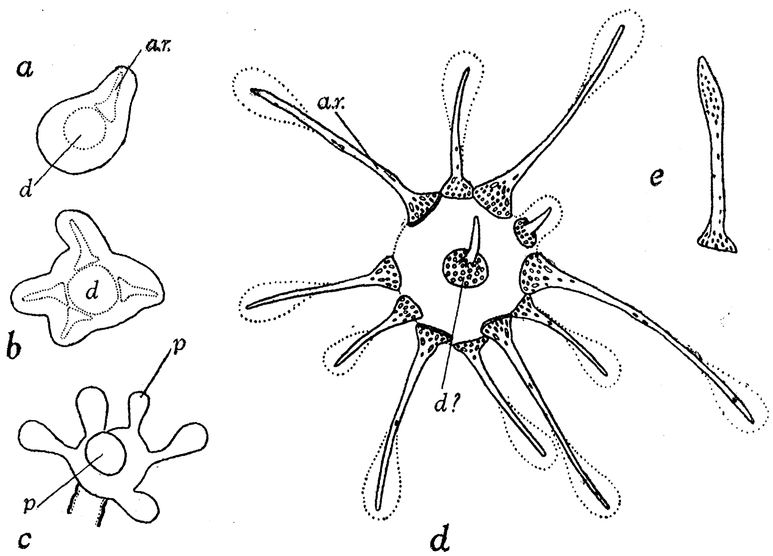

FIG. 25.—*a–c*, three stages in the development of a "buccal" tube-foot (from specimens stained in eosin—the stain masks the calcareous elements); *d*., a more advanced tube-foot (from a specimen macerated in a 4 per cent. solution of NaOH) showing the axial-rods in detail; *e*., an axial rod from a prehensile tube-foot; *p*., a developing papilla; *a. r.*, axial rod; *d*., ? possibly the original disc. Camera lucida drawings. 1 × 180.

becoming smaller and smaller towards the centre, where only a very small area, if any, is left bare.

No trace of the annulus or "*psellion*" has been detected in the early stages. LOVÉN (1883, Plate XV, figs. 179, 180 and 181) figures quite large spicules belonging to the annulus in the developing "buccal" tube-feet of *Echinocardium flavescens*. The fully formed podium in this latter species, however, possesses a well-developed annulus (LOVÉN, 1883, Plate XI, fig. 128).

(β) *The Prehensile Tube-Feet.*—In the modified "petal" or intra-fasciolar portion of the anterior ambulacrum, another type of tube-foot is developed. These tube-feet bear a slight resemblance to the "buccal" tube-feet, and are capable of much extension. Their function has been described by MACBRIDE, 'Cambridge Natural History,' vol. 1, "Echinodermata," p. 552. The papillæ or finger-like processes are comparatively few in number, and are confined to the margin of the "sucker." Each is supported by a calcareous axial rod of the type represented in fig. 25, *e*, and fig. 26, *c* and *d*. On one side of the tube-foot stalk, just beneath this circle of papillæ, lies a rather large bow-shaped spicule (see Lovén, 1883, Plate XI, fig. 128). The latter, which is clothed with ectoderm, is placed quite superficially. It is attached to the ectoderm of the tube-foot stalk at the centre only, while the ends are quite free. Down the same side of the stalk are scattered a few small spicules similar to that represented in fig. 26, *e*. Some of these are smooth, some have a few, others many, minute spinulations.

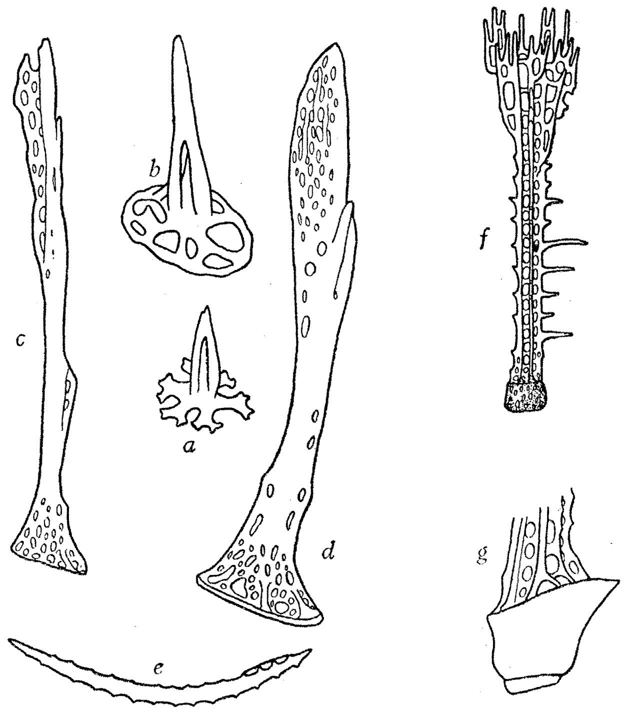

Fig. 26.—*a* and *b*, two early stages in the development of an axial-rod from a prehensile tube-foot (1 × 840). *c.*, a later stage showing the expansion at the tip of the rod; *d.*, a fully formed rod (*c.* and *d.*, 1 × 420); *e.*, a small spicule from the stalk of a prehensile tube-foot; *f.*, a fasciolar spine (1 × 180); *g.*, the asymmetrical base of a typical spine. Camera lucida drawings.

During development the first traces of the papillæ appear when the length of the test has reached, approximately, 2·25 mm. No disc corresponding to the disc of the "buccal" tube-feet is formed. The axial rod is smaller than that formed in the papilla of a "buccal" tube-foot (*cf.* fig. 25, *d* and *e*). Moreover, it is formed in a somewhat different manner. The base of the rod arises as an irregular six-rayed star, but sometimes only five or even four rays may develop (fig. 26, *a*). The base is thus reminiscent of the base of a typical Echinoid spine (Gordon, 1926, figs. 5 and 6). From the centre of this star two or three vertical processes arise and fuse with each other a short distance above the base (fig. 26, *a*). As the vertical rod increases in size the basal rays elaborate to form a circular base (fig. 26, *b*). Later the vertical rod broadens out at the tip. Fig. 26, *c*, represents one in which the expansion at the tip has commenced, while fig. 26, *d*, represents a fully formed rod. In course of time the small bow-shaped spicules are laid down in the stalk of the tube-foot.

γ. *The Formation of the Pores.*—In *Echinus miliaris* the tube-feet are budded off one by one (alternately) from the radial canal. As each is budded off a calcareous plate is laid down above (aborally) to it. This ambulacral plate increases in size and grows round the developing tube-foot to form the greater part of the pore. The lower border is formed by the preceding plate (GORDON, 1926, fig. 20, p. 288).

In *Echinocardium,* on the other hand, a relatively large number of ambulacral plates are laid down in the pluteus quite independently of tube-feet (figs. 2 and 16). Thus, in the imago, only five ambulacral plates out of a total of fifty-five (see numbers given for imago C (Table 1) on p. 263) possess pores. After metamorphosis, ambulacral plates are added rapidly, while tube-feet make their appearance very, very slowly (figs. 17, 19, 20, 9, 11, 12 and 13). Since the plates precede the tube-feet the pores must be formed in a different way from those of *Echinus.* They are, in fact—with the exception of those belonging to the first five tube-feet—formed by resorption of part of the test from within to accommodate the developing tube-feet. The ambulacral plates are, in young specimens, considerably thinner in the parts where the pores will later be formed than elsewhere. The pores of the petaloid portions and of the modified " petal " also appear to be formed in the same way, although the tube-feet appear soon after the ambulacral plates have been laid down and while the plates are still small. The ocular pores are formed in a different way. The plate is at first dorsal to the oculus, and later grows right round it.

D.—The Fasciolar Spines.

In the early stages all the spines are formed in exactly the same way as the typical spines in *Echinus miliaris* (GORDON, 1926, pp. 268–272, figs. 5–7). Later they become variously modified at their extremities, those on the sternal plates, for example, becoming spatulate. The majority of the spines in *Echinocardium* are directed backwards owing to the fact that the expanded base is much more developed on one side than on the other (fig. 26, *g*). In the imago there is a slight indication of this asymmetry (figs. 7 and 16). The fasciolar spines, however, project at right angles to the test, and possess a symmetrical, but poorly developed, base (fig. 26, *f*). They remain short, and each of the six prongs is elaborated at the tip, so that the distal end of the spine becomes " tufted " (fig 26, *f*). Examination of a number of fasciolar spines from the same test reveals the fact that the " tufted " extremity is subject to considerable variation. Many of these spines also bear rather long thorny processes along one side, while in others the thorns are about equally developed on both sides. When the latter is the case, the thorns are never so prominent as those shown in fig. 26, *f*.

E.—The Perignathic Apophysis.

On the inner surface of the peristomial (unpaired) plate of inter-ambulacrum **4** the calcite sends out a number of branches which, in course of time, form a delicate, openly meshed sheet. When the urchin measures 3·1 mm. in length (exclusive of the spines), this thin sheet of calcareous tissue is quite prominent. As development proceeds, the anterior border bends over towards the single pore in plate *1b* of area **IV**, and in course of

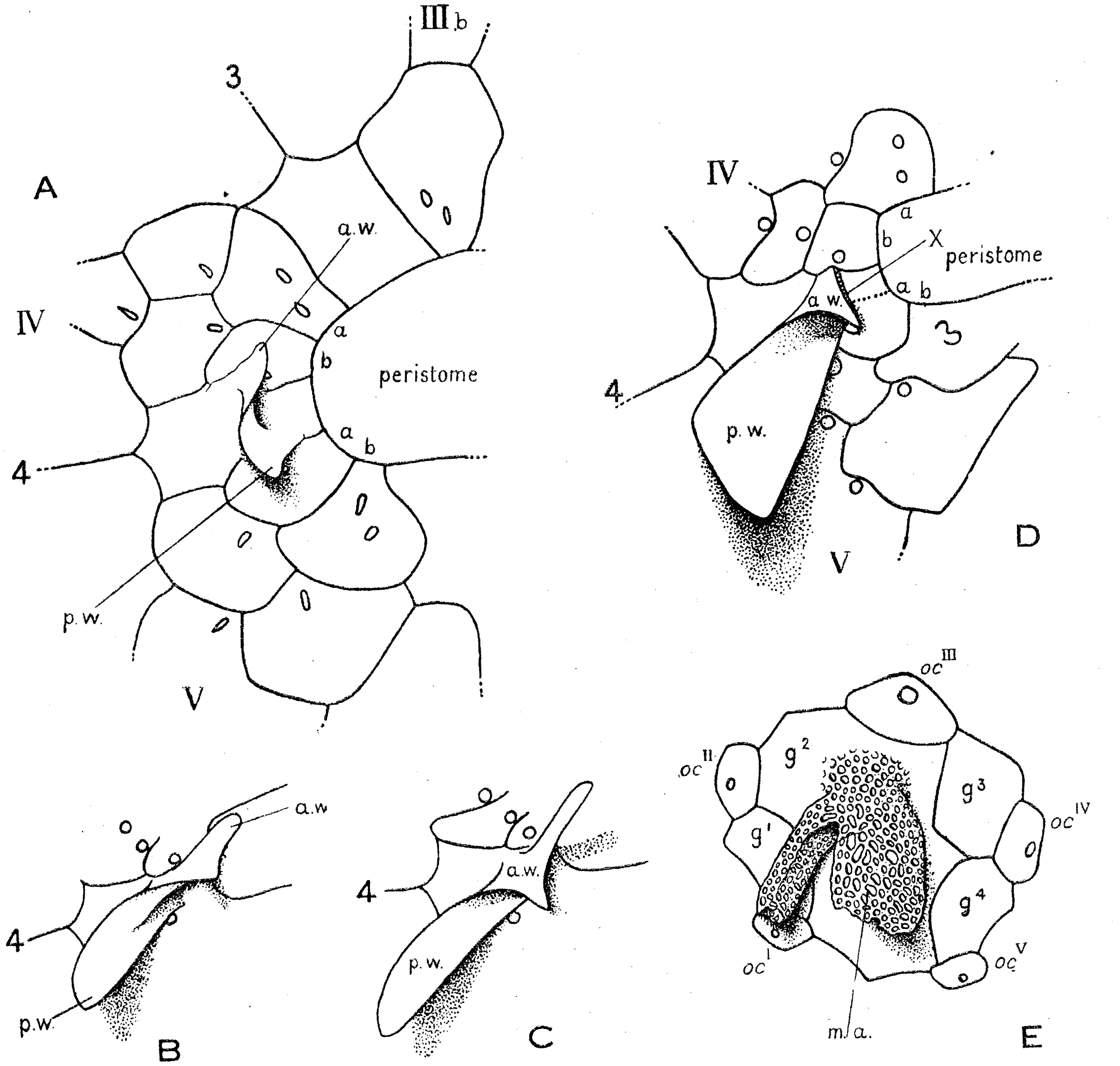

Fig. 27.—A., an early stage in the development of the perignathic apophysis (length of urchin 7 mm.). 1 × 25. B., the perignathic apophysis of a specimen 45 mm. long showing the incipient bifurcation of the anterior "wing." 1 × 3. C., the same structure from a slightly larger specimen, showing the bifurcate anterior "wing." 1 × 3. D., part of the perignathic apophysis from an adult specimen showing the fully developed posterior "wing"; the anterior "wing" has been broken off at *x*. *a. w.*, anterior "wing"; *p. w.*, posterior "wing." 1 × 3. E., inner aspect of the apical system of the specimen represented in fig. 14. *m. a.*, madreporic apophysis; oc^{I}–oc^{V}, oculars; g^1–g^4, genitals, 1 × 100. A and E camera lucida drawings.

time the structure represented in fig. 27, A, results. This structure, named by HOFFMANN (1871) the "Stützapparat am Munde," may be termed the *perignathic apophysis*. In older specimens the anterior "wing" tends to become bifurcate (fig. 27, B and C), while the posterior "wing" elongates rapidly, and ultimately forms a broad blade (fig. 27, D). In fig. 27, D, the largest specimen available, the anterior "wing," had been broken off as a hole was pierced through the peristome to ensure proper fixation of the internal organs.

HOFFMANN (1871, pp. 40–41) found that the "Stützapparat am Munde" in *Spatangus purpureus* serves as a point of attachment for four large mesenteries—two dorsal and two ventral. The mesenteries, which have been studied in detail by HOFFMANN, attach the alimentary canal to the inner wall of the test. His figures (HOFFMANN, 1871, Plate VI, figs. 41, 43, 44*a*, 44*b*, and Plate VIII, fig. 68) show that in this species there is a large left sheet, which does not appear to be represented in the perignathic apophysis of *Echinocardium cordatum*.

This perignathic apophysis is, in all probability, the last remnant of the perignathic girdle transformed to fulfil a new function (see p. 310.)

DISCUSSION.

The Spatangoids are generally regarded as having descended from some early Diademoid (regular) ancestor. In ontogeny one might expect to find some evidence for this. MACBRIDE (1903) regards the imago of the regular urchin as exhibiting a number of Asteroid features, and in the same way the imago of *Echinocardium* is, in many respects, a regular urchin. These features have been enumerated on p. 272. Of these, the most important is the position of the central anus within the apical system of plates; but already several features of the Atelostomata are apparent. In addition to those mentioned on p. 272, all traces of the elements of the lantern of Aristotle have gone, unless the five spines ($sp.^1$, fig. 16) developed on the unpaired inter-ambulacral plates be, as MACBRIDE (1914) suggests, homologous with the teeth. There are some difficulties in the way of accepting this suggestion. In the first place the teeth develop *within* the test, not external to it, as these spines undoubtedly do. Then, again, the tooth is essentially a compound structure, and each calcareous element differs from all the other calcareous elements of the test (GORDON, 1926, fig. 14). Even supposing the spine to represent only the first (unpaired) cone of the tooth, it is difficult to imagine how such a structure could possibly be transformed into a spine. These five spines do not appear until quite late, probably about the same time, relatively speaking, as do the teeth in *Echinus*, but they have no connection whatever with the dental sacs.*

The lozenge of four inter-ambulacral plates so characteristic of the imago of *Echinus* (GORDON, 1926, fig. 16) is repeated at a very early stage in the development of *Echinocardium* (fig. 1, A), and soon after this the first pair of ambulacral plates is laid down

* These spines are formed in the late Echinopluteus directly above the reduced homologues of the dental sacs in Echinus.—E.W.M.

The posterior inter-ambulacrum, however, is precociously developed. That the labrum and the sternal plates should not be distinguishable, at metamorphosis, from the corresponding three plates in the other inter-radii is understandable, since the early ancestor of the Spatangoids must have possessed similar inter-ambulacra. But why the next two plates (*3a*, *4a*, *3b*, *4b* of area **5**, see fig. 2) should be so exaggerated in the imago is not clear. Perhaps the sub-anal fasciole is of great functional importance to the young Spatangoid, and the plates which bear it have consequently become important also. The precocious development of the sub-anal fasciole is in itself interesting, since that fasciole is a recent acquisition, and is present only in that section of the family SPATANGIDÆ known as the PRYMNODESMINÆ.

The way in which the inter-ambulacral plates are laid down is very suggestive to those who seek evidence of the evolution of a double series of plates from the single column found in *Bothriocidaris*. The relatively large number of plates laid down in the Echinopluteus enables their mode of formation to be studied in more detail than is possible in *Echinus* or *Strongylocentrotus*. In fig. 1, A, plate *4* is apparently median, as also is plate *6* in fig. 1, B. As more plates are added, the first one of a pair is situated very near to the median line, but seems to recede from it as the next plate is being formed. It might be imagined that a double series of plates arose from a "linear series, the component parts of which have, owing to crowding, become somewhat displaced and arranged themselves in pairs, the first remaining single" (GORDON, 1926, p. 305, written of the component parts of a tooth in *Echinus*, also inter-ambulacral in position).

In *Echinocardium* the post-larval development is much more complicated than that in a regular urchin. In addition to increase in size and in the number of plates, the whole contour of the test gradually changes, while a backward migration of the periproct and a forward movement of the peristome take place. In a young form such as that represented in fig. 7 the apical system of plates (assuming that the plate *y* is genital **5**) resembles that of, say, *Echinus*. Genital **3**, however, is mostly posterior to, instead of anterior to ocular, **IV**. This is due to the relatively large size of the madreporite, which may be said to have displaced genital **3**, since it separates it from ocular **III**. Genital **2** has also insinuated itself between genital **1** and ocular **II**. In its large size the madreporite in the imago of a Spatangoid resembles that of the adult *Echinus*.

The backward migration of the periproct requires some consideration, and the following points will be dealt with one by one: (*a*) the development of the anal system of plates in the periproct, (*b*) the development of the posterior inter-ambulacrum, and (*c*) the rearranging and compacting of the apical system of plates.

(*a*) *The Development of the Plates in the Periproct.*—Soon after metamorphosis a ring of plates (on an average 9–11 in number) is laid down around the anus and within the circle of five genital plates (fig. 8). In *Echinus*, on the other hand, only one plate (the suranal) is laid down at first, and this plate occupies the whole of the periproct. Later it undergoes resorption along part of the margin, recedes from the genital ring at one side, and, in the resulting gap, smaller anal plates are laid down. Even in the adult the suranal, though much less conspicuous, can still be distinguished from the other anal plates. From figs. 8 and 9 it is clear that in *Echinocardium* no one plate corresponds to the suranal, for in the early stages all are of equal importance, and they appear practically simultaneously.

As development proceeds, the anal plates in front of the anus increase in size much more rapidly than the others (figs. 10–12). Of the additional plates laid down within this original circle, those in front of the anus are larger and somewhat more numerous than those posterior to it. Meanwhile plate *y* (the fifth genital) retains its position relative to the outer circle of anal plates, and additional plates, p^1, p^2 . . . , appear on either side of it (figs. 10–12). This crescentic band of plates encircling the posterior two-thirds of the anal group partly compensates for the rapid growth of the anterior anal plates. In course of time the plates in this crescent, notably p^1, *y* and p^2, grow rapidly, and in the adult condition they are by far the most conspicuous (fig. 15).

The anus, situated at first in the centre of the original ring of anal plates, soon becomes more posterior in position (fig. 10), owing to the enlargement of the anterior anal plates. Even if plates p^1, *y*, p^2 be included, its position is slightly posterior. Later, owing to the enormous growth of plates p^1, *y* and p^2, it is anterior in position—*i.e.*, nearer the dorsal than the ventral apex of the periproct (fig. 15). The apparent migration of the anus within the periproct is thus due to a difference in the rate of growth of the various plates.

(*b*) *The Development of the Posterior Inter-Ambulacrum.*—At metamorphosis this inter-ambulacrum (**5**, fig. 7) has seven plates, of which the last two (*4b* and *4a*) are situated near to plate *y* (genital **5**). In course of time plates *5b* and *5a* make their appearance one on either side of *y* (fig. 9), and these soon insinuate themselves between plate *y* and plates *4b* and *4a*. Up to this point the pairs of inter-ambulacral plates (*2b* and *2a* up to *5b* and *5a* of area **5**) touch each other posterior to *y*. The next pair of plates—*i.e.*, *6b* and *6a*—diverge one on either side of *y* (fig. 10). Additional plates are then added on anterior to *6b* and *6a*, and as a result of this the periproct becomes encircled. This goes on until plates *9b* and *9a* have appeared : these now touch each other in front of the periproct (fig. 12). Up to this point the whole periproct has moved backward to a certain extent, but the anterior border is still practically in the centre of the dorsal surface.

Once plates *9b* and *9a* of area **5** have come into contact with each other, and additional plates are added to each column, the periproct recedes much more rapidly from the madreporite. As the sternal plates are still enlarging, two backward movements are taking place simultaneously, and this is apparently the reason for the humping of the dorsal surface just in front of the periproct. Owing to the backward growth of the sternal plates, the posterior plates (including the periproct) are prevented from passing on to the ventral surface, and are gradually tilted more and more until eventually they form an almost vertical wedge at the posterior end of the test.

(*c*) *The Re-arranging and Compacting of the Apical System of Plates.*—While the unpaired inter-ambulacrum is growing forward on either side of the periproct, ambulacra **I** and **V** also grow forward to keep pace with it (figs. 9–12). As a result of this, oculars **I** and **V** are carried forward towards the madreporite, as also are genitals **1**, **3** and **4**. Thus the plates in the apical system all move forward with the exception of genital **5** (plate *y*). The madreporite, of necessity, undergoes alteration in shape as these plates come into contact with it one by one. Thus genital **2** is at first very broad (fig. 9), and becomes gradually longer and narrower (figs. 12–14), while the posterior border becomes pointed as plates *9b* and *9a* separate it from the periproct. As in the case of *Echinus miliaris*, the apical system of plates occupies a relatively large part of the dorsal surface in the early stages (figs. 7 and 9), and a relatively small part in the adult (figs. 5 and 14). But in the regular urchin no rearrangement of the plates takes place (apart from the growth of genital **4** towards the periproct) (GORDON, 1926, fig. 19*d*, and p. 287).

In an animal which is steadily increasing in size, no one point can, strictly speaking, be regarded as " fixed " or stationary. It is, however, necessary to choose some arbitrary " fixed point " with reference to which the movement or rearrangement of the plates in *Echinocardium* may be discussed. Hitherto, to facilitate description, the madreporic plate (or, rather, the axis passing perpendicularly through the madreporite) has been regarded as a " fixed point," and the " movement " of the plates relative to this has been discussed. If, however, the pentagon formed by the most aboral plates in the ambulacra be regarded as a " fixed point," an entirely different view of the re-grouping of the apical system is obtained. Comparing figs. 11 and 13, the rearrangement, with respect to this pentagon, is due to the backward growth of the madreporite.

To sum up, inter-ambulacrum **5** diverges on either side of genital **5** (plate *y*) to surround the periproct. Genital **5** thus remains in the neighbourhood of the anal plates, and additional plates, p^1, p^2 . . . , are laid down on either side of it. These plates ultimately become incorporated into the periproct system. Up to the time when the periproct is encircled by the anal inter-radius, the backward movement of the former has been slight. Once it is enclosed, however, the " growth-pressure " exerted by the additional inter-ambulacral plates results in a more rapid displacement of the periproct and of the posterior end of the test generally. This is partially impeded by the lengthening of the sternal plates, and eventually the posterior plates are forced to assume a vertical position. Meanwhile the adjacent ambulacra (**I** and **V**) grow rapidly forward (keeping pace with the posterior inter-ambulacrum), and displace the ocular and genital plates immediately anterior to them until the whole apical system (apart from genital **5**) comes to lie in front of the periproct.

A study of a large number of specimens shows that the number of anal plates in the original circle is subject to slight variation. The number of plates in the crescent (p^1, p^2 . . .) also varies slightly. But in spite of these slight differences the pattern is very constant. WESTERGREN (1911) also found that the anal plates in *Echinoneus cyclostomus* were more regular than was generally supposed. In specimens from the Pacific Ocean he found several large plates towards the posterior end of the periproct (in this species the periproct is infra-marginal, and the " posterior " end of the periproct would be that nearest the mouth). These probably correspond to plates p^1, y, p^2 . . . , but in forms from the West Indies they were invariably replaced by a number of relatively small plates.

The alteration of the peristome from a circular to a pentagonal form, and later to the " reniform " condition found in the adult, has already been dealt with and need not be discussed further. The outer ring of buccal plates, which is so prominent in young forms (figs. 19–21), may correspond to the ten large buccal plates in a regular urchin. Although they appear slightly in advance of the other buccal plates, the number varies somewhat. As a rule there are 10–15. That there happens to be ten in one or two specimens may be a mere coincidence. In *Echinus miliaris* (GORDON, 1926, fig. 3) the ten large buccal plates are laid down in the larva and are at first arranged in five inter-ambulacral pairs. Later they become rearranged into five ambulacral pairs, and each surrounds a buccal tube-foot. In *Echinocardium* these plates in the outer ring are laid down opposite ambulacra and inter-ambulacra indiscriminately, vary somewhat in number (but generally exceed ten), and never at any time possess pores. It is clear that the entire peristome in Spatangoids, is situated within the water-vascular ring, while in *Echinus* it extends beyond the water-vascular ring. Since there are no tube-feet in the peristome of a Spatangoid, the large buccal plates which surrounded them have probably disappeared entirely. The buccal plates which are present probably correspond to the small buccal plates which, in *Echinus*, are situated internal to the ring of large buccal plates. Although the number of buccal plates varies somewhat, the pattern is again regular.

While resorption is constantly going on to a slight extent in the case of the individual plates as they increase in size and alter in shape (*e.g.*, the madreporite must undergo partial resorption along the posterior border and also laterally to allow of the forward movement of the other genital plates), resorption at the peristomial margin of the corona is negligible. The fifteen peristomial plates (ten ambulacral and five inter-ambulacral) formed in the Echinopluteus (fig. 2) persist right up to the adult condition (fig. 5). There is, however, a marked difference in the rate of growth of the different coronal plates (p. 293), resulting in a re-arrangement of the various elements of the corona.

In *Echinocardium* the number of plates in each of the ten meridia is relatively small, and growth, after a certain stage, is chiefly due to increase in size of the plates already present. In *Echinus*, on the other hand, many plates are laid down in each inter-ambulacral column, while the number of triads in an adult ambulacrum is large (HAWKINS, 1920, Plate 63, fig. 2). This rapid increase in the number of plates is accompanied by a movement of the plates towards the peristome, where a certain amount of resorption occurs. Once the perignathic girdle becomes continuous, this movement is arrested to a great extent. Resorption at the peristomial margin practically ceases, but the individual plates are subject to great stress (" plate-crushing "), and become greatly reduced.

If there were anything like a corresponding "streaming of plates" towards the peristome in a Spatangoid, a much greater amount of resorption would, in all probability, take place, for the perignathic girdle has practically gone and would not, therefore, impede the movement. It seems, however, that movement of the plates towards the peristome is very slight. Indeed, it is practically non-existent, for no tube-feet pores ever reach the margin, and no sphæridia pass on to the buccal membrane (*cf.* GORDON, 1926, figs. 21–27). This is undoubtedly correlated with the relatively small number of coronal plates. Instead of being reduced, many of the plates in the neighbourhood of the peristome remain relatively high (figs. 23 and 5). "Growth-pressure" is, of course, exerted to a certain extent. Its influence is particularly apparent at the posterior end of the test in the region of the sub-anal fasciole, and also (to a lesser extent) in the alteration in shape of the individual coronal plates during development.

The ambulacra are very primitive indeed, for the plates are primaries throughout, with the exception of those in the modified "petal." HAWKINS (1920, Plate 69, fig. 4) found that there are also one or two reduced plates in the intra-fasciolar portion of ambulacra **I** and **V**. The oral plates which surround the "buccal" tube-feet have become slightly specialised, while the subsequent plates (up to the commencement of the petals) are of the primitive "Bothriocidaroid" type. In the petals the plates also remain relatively simple, but the pores are double and well developed. This is, of course, correlated with the functional importance of the respiratory tube-feet.

The rapid production of plates in the modified anterior "petal" forms a striking contrast to the relative paucity of coronal plates. There can be no doubt that this is a secondary complexity associated with the prehensile function of the tube-feet in this region (MACBRIDE, 'Cambridge Natural History,' vol. 1, "Echinodermata," p. 552). In many Spatangoids (*e.g.*, *Spatangus*) the anterior "petal" is "morphologically and functionally degenerate" (HAWKINS, 1920, p. 417), owing to the fact that the tube-feet in this region have lost their respiratory function. In a young *Echinocardium cordatum* (fig. 14) the anterior "petal" is relatively simple, and recalls that of *Spatangus purpureus*. Later on the plating becomes complex, but there is no hint of combination into, *e.g.*, triads. It is interesting to note that the plating is almost an exact copy of that found in such Palæozoic Echinoids as *Lovenechinus* (see HAWKINS, 1920, Plate 63, figs. 10 and 11, Plate 69, fig. 5). Regarding this point HAWKINS (1920, p. 384) says that it "seems to imply that reversionary tendency in racial old age (*Echinocardium* being one of the most recent of the Spatangoids) that has been aptly termed 'second-childhood.'"

To quote again from the same author: "The character of ambulacral plating is intimately connected with, and indeed determined by, the growth of the water-vascular system. To the activity of budding from the radial canal all other features are secondary and subsequent" (p. 417). In *Echinus* this is evidently the case, for the tube-feet *precede* the ambulacral plates, and only the ten large buccal plates are laid down independently of the formation of tube-feet. In *Echinocardium,* however (see p. 282), the tube-feet often appear long after the ambulacral plates have been laid down. In the modified "petal" (where the tube-feet appear soon after the corresponding ambulacral plates are laid down) it is possible that the tube-feet may be budded off from the radial canal *before* the plates are laid down, but that they remain as small *internal* buds for a short time. It is also possible, but *improbable,* that all the tube-feet may be budded off prior to the formation of the corresponding ambulacral plates, and that the development of the former is, in many cases, retarded for a considerable period. Only a careful examination of serial sections would settle this point, and properly fixed material would be essential.

That the majority of the pores remain simple throughout life in *Echinocardium* is another primitive (reversionary) feature, for in the very young *Echinus miliaris* (Gordon, 1926, fig. 22) the pores are simple and arranged in a single series in each ambulacral column. The difference which exists between columns *a* and *b* of ambulacra **II** and **IV** (figs. 13 and 14) is reminiscent of the condition found, *e.g.*, in the adult *Heteraster oblongus* (Hawkins, 1920, Plate 69, fig. 2), and in *Agassizia,* where the apicad plates are petaloid in one column but non-petaloid in the other.

Echinoneus cyclostomus (Westergren, 1911) appears to be, in many respects, intermediate between *Echinus* and *Echinocardium.* It is unfortunate that so little is known of the early development of the test. The ambulacra are simple, narrow and apetaloid, the peristome is central, the periproct is infra-marginal (*i.e.*, is situated on the ventral surface just posterior to the mouth. This species passes through a toothed stage, but later the teeth disappear. Resorption at the peristomial margin has almost ceased, but there appears to be still a little in inter-ambulacra **2** and **4** (Lovén, 1874, Plate IX, figs. 82 and 83). In adult specimens the first plate of the ambulacral series **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* appears to be biporous. Hawkins (1920, p. 444) suggests that the lower simple pore (the other one is, in this species, double) is not a tube-foot pore, but a relic of the surviving "branchial incision" which has become encircled by the ambulacral plate Lovén (1874, Plate IX, fig. 80) figures what appears to be part of a peripodium round this single pore, and (1874, Plate IX, fig. 81) what appears to be a suture on the inner surface of plate *1b* of ambulacrum **V**. This single pore may be derived from the peristomial notch, in which case it would not be a true tube-foot pore. For, as far as the available evidence goes, there is a notch on the peristomial border in young forms. But *two* such notches are present—one in the first plate in each column—in early stages, and one of these (that on the first plate of the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series) disappears quite early. It seems strange that one notch should vanish and the other be enclosed by the ambulacral plate. Moreover, in the Regularia Ectobranchiata the "branchial incisions" are inter-ambulacral, not ambulacral, in position (Lovén, 1874, Plate XVII, figs. 142 and 145). At first sight the notches on the margin of the corona in *Echinoneus* seem to indicate that some of the pores are being destroyed owing to resorption of part of the calcite (as in the case of *Echinus*). But this is very unlikely, seeing that there are no buccal tube-feet on the buccal membrane. Should any pores be obliterated, the tube-feet also would be destroyed.

In *Micropetalon purpureum* (WESTERGREN, 1911), one of the first pair of ambulacral plates in each area possesses two pore-pairs, and is doubtless "biporous."

As to the origin of the two pores in the biporous plates, the writer can only put forward a mere tentative suggestion. In *Echinus* it has been shown that the tube-feet, which are originally surrounded by the first plate in the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series, are expelled from the corona and, later, form the secondary series of buccal tube-feet (GORDON, 1926, pp. 296–301). The tube-feet are, moreover, laid down in the same order as are the plates, the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series preceding the other series. In *Echinocardium* the reverse is the case. The plates in the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* are laid down in advance of those in the first series,* while the tube-feet appear in the reverse order. This seems rather strange unless it is assumed that the first five tube-feet, which are the only ones to appear in the Echinopluteus, are budded off precociously, and that the rest of the tube-feet are budded off, after metamorphosis, in the same order as the plates were laid down. The first five tube-feet may correspond to the secondary buccal tube-feet of *Echinus*. As there is no resorption (or, at any rate, very little) at the peristomial margin, the first five tube-feet remain in the corona. On the other hand, these five tube-feet may have no connection with the secondary buccal tube-feet in *Echinus*. ÜBISCH (1913, Plate VII, fig. 16) found that the primary buccal tube-feet in *Arbacia pustulosa* belong to the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series. From this it would appear that the first five ambulatory tube-feet in the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series later become the secondary buccal tube-feet. This implies that the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series of tube-feet (and of plates) appears slightly in advance of the other series. It may be that at some stage in the evolution of the Spatangoids the formation of the tube-feet was delayed, and that (secondarily) five tube-feet were developed precociously in the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series. These are the only tube-feet present in the imago as a rule, and they may be functionally important at this stage. Later on the tube-feet appear, one by one, in the same order as the plates have previously been laid down, and one is formed in the first plate of the first series as well as in all the other plates.

In the sucker of each ambulatory tube-foot in *Echinus* a compound disc is formed. A similar disc also occurs in the tube-feet of *Echinoneus* (WESTERGREN, 1911). In *Echinocardium* the disc has disappeared entirely in the majority of the tube-feet, including the prehensile ones. But a simple disc is formed in the young "buccal" tube-feet. This is probably primitive, and is in keeping with such primitive features as the "Bothriocidarid" type of ambulacral plating. In *Echinoneus* there are small calcareous spicules in the stalk, just as is the case in the prehensile tube-feet of *Echinocardium*. The development of papillæ and the formation of axial rods has accompanied functional specialisation.

* See footnote, p. 285.

LOVÉN (1874, p. 47) found that in young regular urchins (*e.g.*, *Strongylocentrotus* and *Salenia*) corresponding inter-ambulacral plates occur in the series **1***a*, **2***a*, **3***b*, **4***a*, **5***a* and **1***b*, **2***b*, **3***a*, **4***b*, **5***b*. In other words, the plating is identical in areas **1**, **2**, **4** and **5**, but reversed in area **3**. (This may be partially obscured in older forms owing to certain areas undergoing more rapid resorption than the others.) In the irregular urchins which possess sterna (Atelostomata Sternata) he almost invariably regards plates *2a* and *3a* of area **1** as fused together (*i.e.*, plate *2* in column **1***a*, fig. 5, is always marked *2* + *3* in LOVÉN's figures). In the Echinopluteus, however, area **1** is similar to the other inter-ambulacra in that plates *2a* and *3a* are quite distinct (fig. 2). From fig. 2 it will be seen that plate *2b* precedes plate *2a* in inter-ambulacra **1**, **2**, **4** and **5**, while in area **3** the reverse is true. This, as far as has been made out, is quite a constant feature. The two series of corresponding plates are therefore identical with those in a regular urchin. Since areas **1** and **4** are similar (fig. 2), plate *2a* is in both cases somewhat larger than plate *2b*, but owing to the position of these two areas in the test, the larger plate is in the posterior column in area **1** and in the anterior column in area **4**. This produces a slight asymmetry in the otherwise bilateral corona (fig. 2).

During development it appears that no fusion of the plates in area **1** can take place since plate *2a* is, from the first, larger than plate *2b*. LOVÉN must have assumed that areas **1** and **4** are not identical in the very young urchin, and that the smaller plate of the pair in question was situated in the posterior column in both cases (*i.e.*, he assumed that plate *2a* of area **1** is smaller than plate *2b*). This would make the bilateral symmetry, as far as the inter-ambulacra are concerned, complete.

The plating in all LOVÉN's figures (from Plate XXII, fig. 179 onwards) has been studied, and the result is tabulated as follows [assuming that the second plate in column **1***a* is simple, not compound as marked in the figures] :—

TABLE 2A.

The corresponding plates fall into two series, thus :—	(1) **1***b*, **2***b*, **3***a*, **4***b*, **5***b*. (2) **1***a*, **2***a*, **3***b*, **4***a*, **5***a*.	(1) **1***a*,* **2***b*, **3***a*, **4***b*, **5***b*. (2) **1***b*,* **2***a*, **3***b*, **4***a*, **5***a*.
Number of genera represented ...	19	6
Classification of the genera. (Order and Sub-order.)	Atelostomata Sternata } 19	Atelostomata Asternata } 1 (*Cassidulus*) Gnathostomata Clypeastrina } 5

An asterisk * represents departures from the normal, namely, the arrangement found in regular urchins; (1) is the series which is the first to be laid down. It may be recalled that in regular urchins there is also an unpaired plate in each inter-ambulacrum.

TABLE 2B.

The corresponding plates fall into two series, thus :—	(1) **1***b*, **2***b*, **3***a*, **4***a*,* **5***b*. (2) **1***a*, **2***a*, **3***b*, **4***b*,* **5***a*.	(1) **1***b*, **2***a*,* **3***b*,* **4***b*, **5***b*. (2) **1***a*, **2***b*,* **3***a*,* **4***a*, **5***a*.
Number of genera represented ...	3	1
Classification of the genera. (Order and Sub-order.)	Gnathostomata, Clypeastrina } 2 Atelostomata, Sternata } 1 (*Collyrites*)	Atelostomata, Sternata } 1 (*Holaster*)

An asterisk * represents departures from the normal, namely, the arrangement found in regular urchins; (1) is the series which is the first to be laid down. It may be recalled that in regular urchins there is also an unpaired plate in each inter-ambulacrum.

The two series are identical with those found in regular urchins in nineteen out of twenty-one genera belonging to the Atelostomata Sternata (Table 2A). Of the two exceptions (Table 2B) *Collyrites* has a reversal of the plating in area **4** as well as in area **3**. This results in a symmetrical arrangement of the inter-ambulacra about the antero-posterior axis (LOVÉN has not indicated any fusion of the plates in this instance). In *Holaster* area **2** is reversed instead of area **3**. This does not in any way alter the symmetry. LOVÉN here indicates that plates *2a* and *2b* of area **1** have united.

The apparently normal plating in the Clypeastrina (Table 2A), occurring in five genera out of a total of seven, differs from that found both in the regular urchins and in the majority of the Atelostomata Sternata. Here area **1**, as well as area **3**, is reversed, and this results in a perfectly bilateral symmetry. Thus perfect bilateral symmetry of the inter-ambulacra may result from the reversion of the plating in either area **1** or area **4**.

LOVÉN sometimes indicates the presence of more than one compound plate—*e.g.*, in *Palæotropus josephinæ* (LOVÉN, 1874, Plate XXXII, fig. 197) there is a single plate next the unpaired (peristomial) plate in area **1** which he regards as plates *2b*, *2a* and *3a* united. In areas **2** and **3**, as well as in area **4**, there is a similar single plate next the peristomial one. This he regards as plates *2a* and *2b* united together. It may be doubted whether so much complete fusion of plates would have occurred during development. This form is primitive in spite of the fact that it possesses a sub-anal fasciole (LOVÉN, 1874, Plate XIII, figs. 108, 110, 111). It may be that no fusion of the plates takes place, but that plate *2b* displaces plate *2a* (*i.e.*, separates it entirely from the peristomial plate) in areas **1**, **2** and **4**, while plate *2a* displaces plate *2b* in area **3**. In *Ananchytes sulcata*, for example, plate *2b* has separated plate *2a* from the unpaired plate in area **4**, and the same is true for area **1** if no fusion of plates *2a* and *2b* (as indicated by LOVÉN, 1874, Plate XXIV, fig. 181) has occurred. In *Desoria australia* (LOVÉN, 1874, Plate XXVIII, fig. 187) plate *2b* of area **4** has been separated from the unpaired plate by *2a*. Still, plate *2a* is larger than plate *2b*, and must have appeared *after* *2b*, for in the case of the succeeding plates, those in column *b* precede the corresponding ones in column *a*. Assuming that the large plate in area **1** is plate *2b* only (not plate *2a* + plate *2b* as indicated by LOVÉN), it also displaces plate *2a*.

The suggestion that no fusion of plates takes place is only tentative, and may not be true. The difference existing between areas **1** and **4** (see fig. 5) cannot be due entirely to the fact that area **4** is bounded on either side by two ambulacral columns belonging to the second series—namely, **IV***b* and **V***a*—while area **1** is bounded by one column (**I***b*) of the second series and one (**II***a*) of the first series. The difference between the two series of ambulacral columns is slight, and would not alter the inter-ambulacral plates to a very marked extent. This is clearly seen in the case of areas **2** and **3** (fig. 5). Here **2**a is bounded by two columns (**II***b* and **III***a*) belonging to the second series, while area **3** is bounded by two columns (**III***b* and **IV***a*) of the first series. The asymmetry must be largely due to the arrangement of the inter-ambulacral plates themselves. The reversion of either area **3** or area **2** (*Holaster*) results in corresponding columns being next the anterior ambulacrum, and these areas are therefore symmetrical about the antero-posterior axis (fig. 5). Where either area **1** or area **4** is also reversed, the plates are symmetrical about the same axis, and the slight difference between the two areas is confined to the plates nearest the peristome (see LOVÉN, 1874, Plates XXII and XXIII). This slight difference is possibly due to the fact already mentioned, namely, that one area is bounded by two similar ambulacral columns and the other by two dissimilar ones.

KLINGHARDT (1911) found that the plating of areas **1** and **4** in fossils of *Micraster glyphus* was not in agreement with LOVÉN's analysis. He also found that the arrangement varied somewhat from specimen to specimen. The arrangement represented in fig. 67 (KLINGHARDT, 1911, Plate X) is very similar to that found in *Micraster cor anguinum* (LOVÉN, 1874, Plate XXXIII, fig. 201). Assuming that plates *2a* and *2b* are separate in the latter species, they are almost identical (KLINGHARDT does not indicate any fusion of plates). In fig. 64 (KLINGHARDT, 1911) plate *2a* of area **4** has separated plate *2b* from the peristomial plate, and in both areas the plates in column *a* precede those in column *b*. In fig. 66, on the other hand, the plates in column **1***a* and **4***b*, respectively, are the first to be laid down.

In the same paper KLINGHARDT found that in certain fossils two small remnants of the perignathic girdle are present. For example, in *Ananchytes ovata* (KLINGHARDT, 1911, Plate IV, fig. 23) there is a small apophysis (Stützapparat) on the unpaired plate of inter-ambulacrum **4**, and on the right side of the mouth there is a still smaller one. The latter, it is interesting to note, is a m b u l a c r a l in position and projects from plate *1a* of area **II**. This right " Stützapparat " may be a rudiment of an auricula, for, in another specimen (KLINGHARDT, 1911, Plate VIII, fig. 54), traces of auriculæ are present in other ambulacra.

In *Hemipneustes radiatus* (KLINGHARDT, 1911, Plate II, fig. 11) two apophyses are present, but both of these are ambulacral in position: the larger one is apparently on plate *1a* of ambulacrum **V**, the smaller one on plate *1a* of ambulacrum **II**. These processes are much more insignificant in the fossil forms than is the single perignathic apophysis in *Spatangus* or in *Echinocardium*. From this it might be inferred that on the disappearance of the teeth the perignathic girdle degenerated until, in these fossil forms, it was represented by mere vestiges. Ere they finally disappeared, one of these became of secondary importance as it assumed a new function and enlarged until, in the most recent forms, it became quite prominent (fig. 27, A–D). That the perignathic apophysis is a recent acquisition is suggested by its relatively late appearance during development. The first traces of it are only apparent when the test measures approximately 2·5 mm. in length, while in *Echinus* the auriculæ appear very soon after metamorphosis. There is no hint of a right perignathic apophysis in *Echinocardium*.

Summary.

The Development of the Permanent Skeleton in the Echinopluteus.

(*a*) *Inter-Ambulacra.*—After the single peristomial plate is formed, the plates in column *b* appear slightly in advance of the corresponding plates in column *a* in each of the four areas **1**, **2**, **4** and **5**. In area **3** the reverse is the case. Area **5** is in advance of the others almost from the very beginning, and, at metamorphosis, the four last-formed plates (**5**, *3a*, *3b*, *4a*, *4b*)—those which bear the sub-anal fasciole—are the largest in the whole test. The three posterior areas (**1**, **5** and **4**) have each seven plates at metamorphosis, while areas **2** and **3** have each only six.

(*b*) *Ambulacra.*—The plates in the series **I**_b_, **II**_b_, **III**_a_, **IV**_b_, **V**_a_ are laid down slightly in advance of the corresponding plates in the other series (**I**_a_, **II**_a_, **III**_b_, **IV**_a_, **V**_b_). Each peristomial plate belonging to the **I**_a_, **II**_a_, **III**_b_, **IV**_a_, **V**_b_ surrounds a tube-foot. Each corresponding plate in the remaining series bears a sphæridium. More plates are laid down in each of areas **I** and **V** than in each of the three anterior areas.

(*c*) *Apical system of plates.*—The oculars only make their appearance after a number of ambulacral plates have been formed in each area. Only two genital plates are present at metamorphosis, namely, genitals **2** and **1**. The primordia of the other genital plates are present in the form of broken remnants of larval spicules.

The Imago.

The imago is spherical, the anus is central, and the periproct is situated within the apical system of plates. The mouth is in the centre of the circular peristome. The labrum and the sternal plates are similar to the corresponding plates in inter-ambulacra **1**, **2**, **3** and **4**. The ambulacra are similar and apetaloid. The symmetry is bilateral, since the posterior areas are more advanced than the anterior ones.

The Further Development of the Test.

(*a*) *The Dorsal Surface.*—Genital **3** is formed from part of the right postero-dorsal rod, genital **4** from part of the right anterior extension of the aboral rod; genital **5** (plate *y*) from the right post-oral rod (*genital* **5** *arises from the same larval spicule in Echinus*). Genital **5** moves backward with the periproct, and becomes the most posterior plate of the adult anal system. The posterior inter-ambulacrum divides. The plates in column *a* are laid down on one side of the periproct, those in column *b* on the other. Later the two columns again meet in front of the periproct; plates *9a* and *9b* separate the latter from the madreporite. Ambulacra **I** and **V** also grow forward, keeping pace with the two columns of area **5**, so that oculars **I** and **V** also meet genital **2**. As more plates are added to area **5** the whole periproct is carried backward. This backward movement is partially impeded by the elongation (backwards) of the sternal plates. As a result of this, the dorsal surface humps just in front of the periproct, and the latter gradually assumes an almost vertical position.

Tube-feet are formed in area **III** long before they make their appearance in the other areas. The pores in area **III** never divide. Those in the petaloid portions of the remaining areas (**I**, **II**, **IV** and **V**) soon undergo division. In each of areas **II** and **IV** only the column (**II***a* and **IV***b*) is petaloid at first; later, columns **II***b* and **IV***a* also become petaloid. The internal fasciole appears quite early, but does not at first extend backwards beyond the madreporite. Later it encloses the apical system completely. Plating in the intra-fasciolar portion of ambulacrum **III** is at first very simple, and similar to that found in an adult *Spatangus*. After the urchin measures 9–10 mm. in length, however, plate-formation proceeds much more rapidly at ocular **III**, and the plating becomes complex. There is no attempt at combination, *e.g.*, into triads.

The madreporic pore remains simple until the test has reached a length of 9–10 mm., and the genital pores are formed ere it has increased to 15 mm. in length.

(*b*) *The Ventral Surface.*—Buccal plates are laid down soon after metamorphosis. The plates in the outer ring, 10–15 in number, become large, and the peristome gradually assumes a pentagonal outline. Later the peristome becomes reniform, and the mouth is situated at the posterior border. This apparent backward shift of the mouth is due to (*a*) the great increase in number and in size of the anterior buccal plates, (*b*) the resorption of many of the buccal plates at the posterior border to make way for the advancing labrum. The sternal plates (**5**, *2a* and *2b*) increase enormously in length, while plates **5**, 3*a*, 3*b*, 4*a*, 4*b* become greatly reduced. Resorption at the peristomial margin is slight, no tube-feet ever reach the margin, and no spine tubercles are resorbed.

(*c*) *The Tube-Feet.*—The tube-feet are formed very gradually, and those in the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* appear slightly in advance of the corresponding ones in the other series. The pores (with the exception of the ocular pores and of the first five pores in the series **I***a*, **II***a*, **III***b*, **IV***a*, **V***b*) are formed by resorption of part of the calcite from within.

The "buccal" tube-feet soon acquire a simple calcareous disc. Later, papillæ grow out from the sucker and each is supported by a slender rod. In the case of the prehensile tube-feet no central disc is formed. The papillæ are confined to the periphery, and the axial rod arises from a six-rayed star.

(*d*) *The Spines.*—All the spines are formed in the same way as the typical spines of *Echinus*, to begin with. Later on they become variously modified at their extremities.

(*e*) *The Perignathic Apophysis.*—A thin sheet of calcite grows up from the inner surface of the unpaired plate in area **4**, and becomes two-winged. It is probably a remnant of the perignathic girdle transformed to fulfil a new function, namely, that of serving as a point of attachment for the mesenteries which hold the digestive tract in place.

(*f*) *The Madreporic Apophysis.*—From the inner surface of the large madreporic plate a huge bifurcate apophysis is also formed. To this apophysis the mesenteries, which fix the rectum to the shell wall, are attached.

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