Skeletal Development in Arbacia, Echinarachnius and Leptasterias

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V. *Skeletal Development in* Arbacia, Echinarachnius *and* Leptasterias.

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(*Communicated by Prof.* E. W. MacBride, *F.R.S.*)

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Contents.

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A.—ARBACIA PUNCTULATA, Gray.

Introduction.

The echinopluteus of the genus *Arbacia* has been known since 1853. Echinoplutei of the species at present under investigation were first reared in 1880 by Fewkes, and two years later Garman and Colton (1882) succeeded in rearing them through the metamorphosis. The Mediterranean species *Arbacia lixula*, L. (syn. *A. pustulosa*, Gray) has also been reared through metamorphosis, and Übisch (1913) was the first to attempt an analysis of the test of the imago.

The composition of the corona in the imago of *A. pustulosa*, as described in the paper just referred to (Übisch, 1913), is very different from that in the imago of *e.g. Echinus* or *Strongylocentrotus*. The opportunity of working at the Marine Biological Laboratory, Woods Hole, presenting itself, it was thought that a study of the development of the test in *Arbacia punctulata*, Gray, might reveal some points of interest. Accordingly, cultures of this common sea-urchin were started on July 28, 1926, and the echinoplutei were fed on the diatom *Nitzschia closterium* W. Sm. forma *minutissima*. Forty days later (September 6th) the first imago was obtained and the echinoplutei continued to metamorphose throughout the rest of September. Early in August a shallow glass vessel containing filtered sea-water was infected with plankton obtained by towing, and, by the first week of September, the bottom and sides of the vessel were well coated with diatoms. Many of the imagines, which measure 0·5 mm. in diameter including the spines, were transferred to this vessel and a number increased considerably in size. The largest specimen obtained in this way was 1·63 mm. in diameter inclusive of the spines; the diameter of the test alone was 0·9 mm.

The writer had to leave Woods Hole at the end of September, so that it was not possible to rear the small urchins beyond this stage. Larger specimens were found by making a careful examination of stones and empty bivalve shells dredged from the *Arbacia* grounds during late September. In this way a complete series of postlarval stages was obtained.

The Development of the Permanent Skeleton in the Echinopluteus.

Figures of the echinopluteus of *Arbacia punctulata* have been given by Garman and Colton (1882, Plate 17, figs. 1–4), and Fewkes* has given a number of illustrations (see Garman and Colton, 1882, footnote on p. 247). Still it is necessary to give here one outline drawing (fig. 1) to illustrate a point that seems to have passed unobserved until now, namely, the presence of a pair of true antero-dorsal arms in the fully formed echinopluteus (fig. 1, *a.d.a*). Each antero-dorsal arm is supported by a simple calcareous

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* In 'Mem. Peabody Acad. Sci.,' vol. 1, No. vi, 1881. Three of the figures are reproduced by Agassiz (1883, Plate ix, figs. 38–40).

rod. Just as in the Spatangoid larva (Gordon, 1926, *b*, fig. 3) this antero-dorsal rod arises as a branch from the dorsal arch.

Übisch (1913, Plate vii, figs. 9–12) has given four excellent figures of the echinopluteus of *Arbacia pustulosa*. In his fig. 9 two incipient branches have already appeared

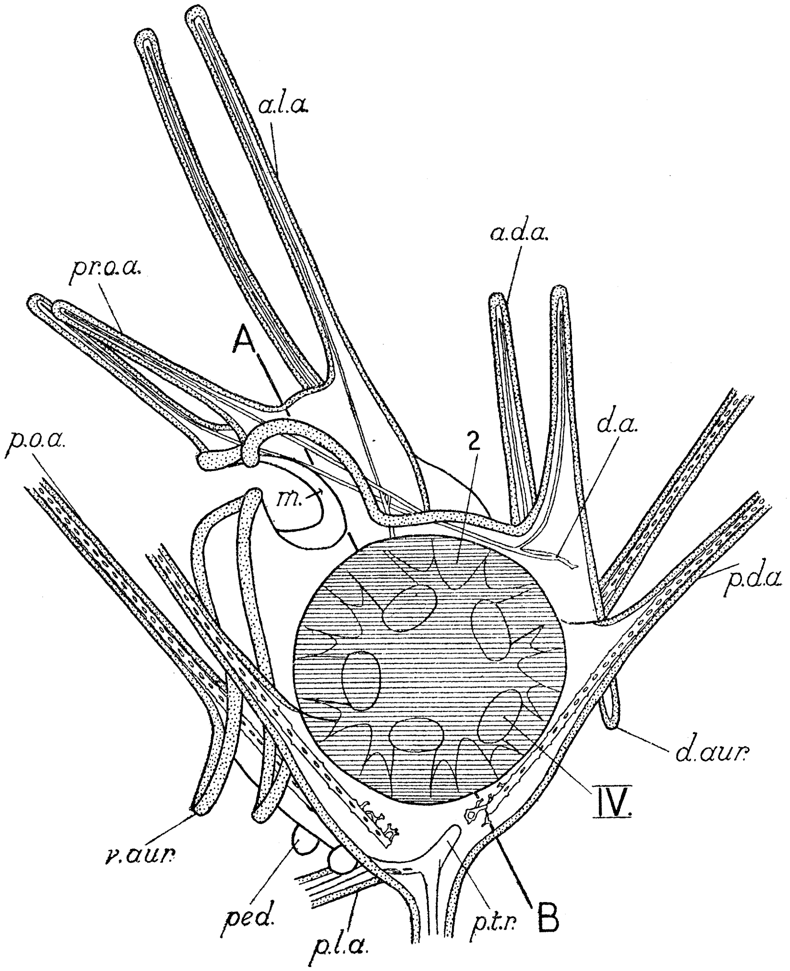

Fig. 1.—Fully formed echinopluteus of *Arbacia punctulata* seen from left side. The shaded portion is the echinus-rudiment in which the terminal tube-feet and the inter-ambulacral spines can just be discerned. AB, the primordial plane of symmetry; IV, terminal tube-foot in ambulacrum IV; **2**, median spine of inter-ambulacrum 2; *m.*, larval mouth; *p.o.a.*, post-oral arm; *pr.o.a.*, præ-oral arm; *a.l.a.*, antero-lateral arm; *a.d.a.*, antero-dorsal arm; *d.a.*, dorsal arch; *p.d.a.*, postero-dorsal arm; *d.aur.*, dorsal auricular lobe; *p.t.r.*, posterior transverse rod; *p.l.a.*, postero-lateral arm; *ped.*, pedicellaria; *v.aur.*, ventral auricular lobe. Camera-lucida outline, from preserved specimen, 1 × 150.

on the dorsal arch. It seems very probable, therefore, that these branches will later form antero-dorsal rods, and that the upper pair of dorsal auricular lobes (his figs. 9 and 10) are the developing antero-dorsal arms. In *A. punctulata* the pluteus has not nearly attained to its full development when the echinus-rudiment first makes its appearance (*cf.* Garman and Colton, 1882, Plate xviii, figs. 1 and 2, with fig. 1 of the present paper). Indeed, the antero-dorsal arms do not appear until after the echinus-rudiment has been formed.

The full grown echinopluteus of *Arbacia* resembles that of a Spatangoid (*e.g.*, *Echinocardium cordatum*, Pennant) in having six pairs of well-developed arms, but differs from it (*a*) in the absence of an aboral spike and aboral rod and (*b*) in the possession of two pairs of auricular lobes (fig. 1, *d.aur.*, *v.aur.*). These auricular lobes are homologous with the vibratile lobes possessed by many echinoplutei, *e.g.*, the larva of *Echinarachnius parma*, Lamk. (fig. 15, *d.v.l.*).

The echinopluteus represented in fig. 1 differs considerably from the more simple type represented in fig. 15 but intermediate forms occur. Mortensen (1921) has described and figured a number of such forms, *e.g.*, the echinoplutei of (1) *Echinometra lucunter*, Linn., and (2) *Lytechinus variegatus*, Lamk. (Mortensen, 1921, Plates I and III; p. 73, fig. 26). These echinoplutei are, as regards general shape, somewhat similar to the echinopluteus of *Echinarachnius parma* (fig. 15). They differ from the latter in having a well-developed posterior transverse rod, from which two short postero-lateral rods arise. The postero-lateral arms are situated at the posterior end of the larval body and are considerably more pronounced than the postero-lateral lobes (*p.l.l.*) in fig. 15. Still they are very short compared with the other larval arms. The dorsal ciliated band in the echinopluteus of both *Lytechinus* and *Echinometra* is very similar to that found in the echinopluteus of *Echinarachnius* (fig. 15), but from the dorsal arch a small calcareous branch is directed outward and downward* into each antero-dorsal lobe. No such antero-dorsal branch has been observed in the echinopluteus of *Echinarachnius parma* where the posterior transverse rod is absent.

It seems that the more highly developed are the posterior transverse rod and the postero-lateral rods, the more highly developed are the antero-dorsal arms (*e.g.*, in the echinopluteus of *Arbacia* or of Spatangoids). In forms that possess very short postero-lateral arms together with a well-formed posterior transverse rod the antero-dorsal arms and rods tend to be small. The echinoplutei figured by Mortensen (1921, Plates I and III, and p. 73, fig. 26) have very small echinus-rudiments, and it is possible that, in older larvæ, the antero-dorsal branches from the dorsal arch may be considerably longer. The echinopluteus, the skeleton of which is represented in fig. 20, p. 58 (Mortensen, 1921), is stated to be "in beginning metamorphosis, the absorption of the body rods has begun" (p. 57). The antero-dorsal and postero-lateral rods, therefore, would have attained their full size; the former are quite long although still directed outward and downward. When the posterior transverse rod is absent so also are the antero-dorsal rods, although small antero-dorsal lobes may be present (fig. 15 *a.d.l.*).

In the echinopluteus of *Arbacia punctulata* the postero-lateral arm bears longer cilia than do the other arms, and, in the distal half, there is a dense accumulation of bright

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* The antero-dorsal rod in *Arbacia punctulata* is at first directed outward and downward and later bends upward to support the antero-dorsal arm (figs. 1 and 3, *a.d.r.*).

red pigment. Spots of the same pigment are found scattered along the remaining arms, becoming more dense at the tips and on the auricular lobes. On the larval body the red pigment is abundant above the four plates formed from the posterior ends of the latticed rods and above genital **2**. Smaller patches occur on the præoral lobe, on the left side and above genital **1** on the right side. The echinus-rudiment is characterised by the presence of a greenish yellow pigment.

When the echinus-rudiment is still small and the antero-lateral arms are very short, genital **1** is formed on the right side as an openly meshed plate at the posterior end of the right antero-lateral rod. In mounted specimens the antero-lateral rod is often broken across just above genital **1**. At this time, also, the two post-oral and the two postero-dorsal latticed rods begin to elaborate at their posterior extremities. Those on the right side give rise to genitals **5** and **3** respectively, those on the left side to oculars **V** and **IV** (see figs. 3 and 5).* Genital **2**, the madreporic plate, is formed at the posterior end of the dorsal arch as in other Echinoidea.

The number of pedicellariæ (fig. 1, *ped.*) varies. One is invariably formed above each of genitals **3** and **5**; sometimes one is formed above genital **2** also; in other cases one is also formed on ocular **V** or even on each of oculars **IV** and **V**.

The order in which the calcareous elements appear in the echinus-rudiment is very similar to that which the writer has described for *Echinus miliaris*, Müller (Gordon, 1926 *a*). Oculars **I**, **II**, and **III** first appear, to be followed immediately by three plates in each inter-ambulacral area. Of the inter-ambulacral plates, the median one may be slightly in advance of the lateral ones but all three appear to be almost on a level with each other. Meanwhile the calcareous disc in each terminal tube-foot is being formed and two very slender triradiate spines are laid down above (external to) each ocular plate. These spines develop in the same way as do the tetraradiate spines in *Echinus* with one exception, namely, that each of the three vertical prongs remains single (*cf.* Gordon, 1926, *a*, p. 273, figs. 8 and 9B).

Above each inter-ambulacral plate a single clavate spine is formed. The development of these spines differs markedly from that of a typical echinoid spine (*cf.* Gordon, 1926, *a*, figs. 5–7 with fig. 2 of the present paper). The base assumes the form of a triradiate spicule, not of a six-rayed star, but the rays slope downward instead of lying in one plane. A single prong grows outward and upward from each of two basal rays (fig. 2, *a*). Each prong soon divides but the inner grows much more rapidly than the outer branch and again divides (fig. 2, *b*). The inner branch fuses with that from the other prong

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* This corroborates what Übisch (1913) has described for *A. pustulosa.* This opportunity is taken of correcting an error in Gordon, 1926, *a*, p. 268; in the sentence beginning "Neither Bury (1889) nor Übisch (1913) . . ." Übisch's name should have been omitted. Elsewhere in the paper it was stated correctly that "Übisch (1913, Plates 6 and 7) gives figures to show the position of the future genital plates and describes the order in which these make their appearance in the plutei . . ." In a recent paper (Übisch, 1927, 'Zeitschr. Wiss. Zool.,' vol. 129, No. 4), published after this part of the MS. was completed, this point is mentioned (p. 554).

to form a short cross-bar; the outer branch, in each case, repeats these two divisions (fig. 2, *c*). In this way a few median meshes are formed (fig. 2, *d*). Soon the external lateral branches increase in size and elaborate to build up a number of irregular lateral meshes (fig. 2, *d*). While this has been taking place, the basal rays have each forked and the branches so formed have fused with those from the adjacent rays (fig. 2, *d*).

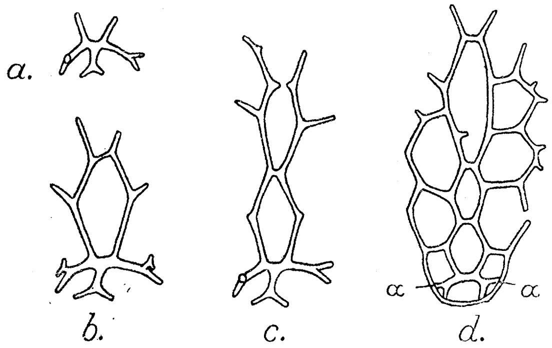

FIG. 2, *a–d*.—Four stages in the development of a spatulate spine. Camera-lucida drawing 1 × 400.

A branch α is sent down on either side to fuse with the base (fig. 2, *d*, α). Further elaboration results in a spine of the type represented in figs. 4 and 5. The median spine in each inter-ambulacrum is always in advance of the lateral ones; *e.g.*, fig. 2, *b*, represents the median and fig. 2, *a*, a lateral spine from the same area.

In course of time the first ten ambulacral plates make their appearance. The **I***a*, **II***a*, **III***b*, **IV***a*, **V***b*, series is only very slightly in advance of the other series. The primordium of each plate is situated adoral to a lateral inter-ambulacral plate and thus appears to belong to the inter-ambulacrum. The distance between two members of a pair is, however, slightly less than that between any two adjacent pairs. As each triradiate increases in size one ray elongates more rapidly than the remaining two. Since this longest ray is invariably directed towards the median inter-ambulacral plate, the apparent inter-ambulacral position of the spicule is thereby enhanced (fig. 3, *a*, *b*). Fig. 4 shows that, in the imago, the ten ambulacral plates together form by far the greater proportion of the peristomial margin of the corona. Of the inter-ambulacral plates, only the five median ones reach the peristome.

The primordia of the first tooth cone and of the alveoli appear soon after the ambulacral plates. The development of the lantern of Aristotle is similar to that already described for *Echinus miliaris* (GORDON, 1926, *a*).

The ten large buccal plates appear just prior to metamorphosis as minute triradiate spicules situated adoral to the ten ambulacral plates. The **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series is slightly in advance of the other series (fig. 4, *b.pl.*).

Fig. 3 is a diagram of the test from an advanced echinopluteus. Above are the five genital plates (g^1–g^5), below the corona. This diagram, unlike the others (GORDON, 1926, *a*, fig. 16; 1926, *b*, fig. 2, and fig. 16 of the present paper) has been built up about the **II 4** plane AB. named by ÜBISCH (1913) the primordial plane of symmetry, instead of about Lovén's antero-posterior plane. The bilateral symmetry of the apparently radial test is thus brought out very clearly. Of the genital plates, genitals **I** and **2** each arise in connection with a simple larval spicule (fig. 3, *a.l.r.* and *d.a.*); genitals **3** and **5** each from a latticed larval spicule (fig. 3, *p.d.r.* and *p.o.r.*). These two sets of genital plates are placed symmetrically about AB. The posterior transverse rod ["hinter Querstab" of Übisch (1913)], from which the two postero-lateral rods arise (fig. 3, *p.t.r.* and *p.l.r.*), will later give rise to genital **4**.

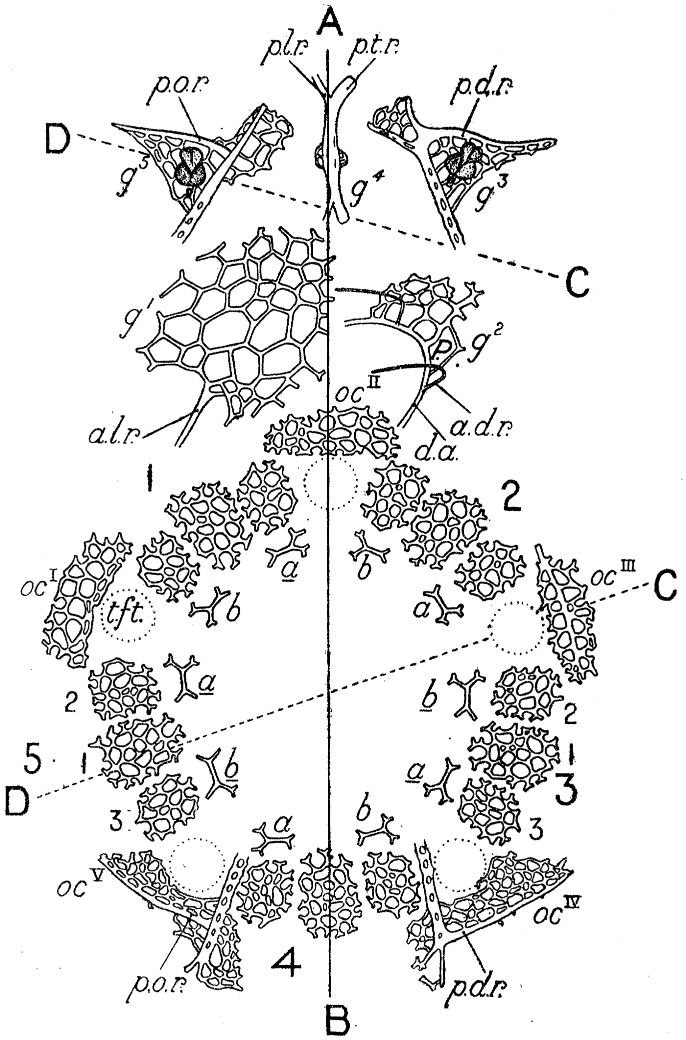

Fig. 3.—Diagram of the complete test from an advanced echinopluteus. g^1–g^5, genital plates; *a.l.r.*, antero-lateral rod; *p.o.r.*, post-oral rod; *p.l.r.*, postero-lateral rod; *p.t.r.*, posterior-transverse rod; *p.d.r.*, postero-dorsal rod; *a.d.r.*, antero-dorsal rod; *d.a.*, dorsal arch; P., water pore; oc^{I}–oc^{V}., ocular plates; 1–5 inter-ambulacra; *a.b.*, ambulacral plates; *t.-ft.*, terminal tube-foot; AB. primordial plane of symmetry (Übisch); CD. Lovén's antero-posterior plane of symmetry.

The ocular plates (fig. 3, oc^{I}–oc^{V}) have been retained in the corona to which, in the opinion of the writer, they really belong since they also are laid down on the left side of the larva. Oculars **IV** and **V**, which arise as proliferations of the left postero-dorsal and post-oral rods as is the case in *Echinus miliaris* (GORDON, 1926, *a*, p. 264, and fig. 2), are also symmetrically placed about the **II 4** plane.

In *Arbacia pustulosa* ÜBISCH (1913, figs. 12 and 13, Plate vii) also found that oculars **IV** and **V** were formed from the posterior ends of the left latticed spicules. In fig. 13 he has identified three small plates as the remaining three oculars. In area **I** two small plates are represented, either one of which might be regarded as the ocular; in area **III** he has selected the largest of three small plates as the ocular. He writes (p. 132), "Nach der Lage dieser fünf Platten kann kein Zweifel sein, dass wir es mit den fünf Ocellarplatten zu tun haben, obgleich sie noch nicht in Connex mit den Primärtentakeln sind. Ich erwähnte anlässlich der fig. 4 (imago of *Echinus microtuberculatus*, dorsal view),

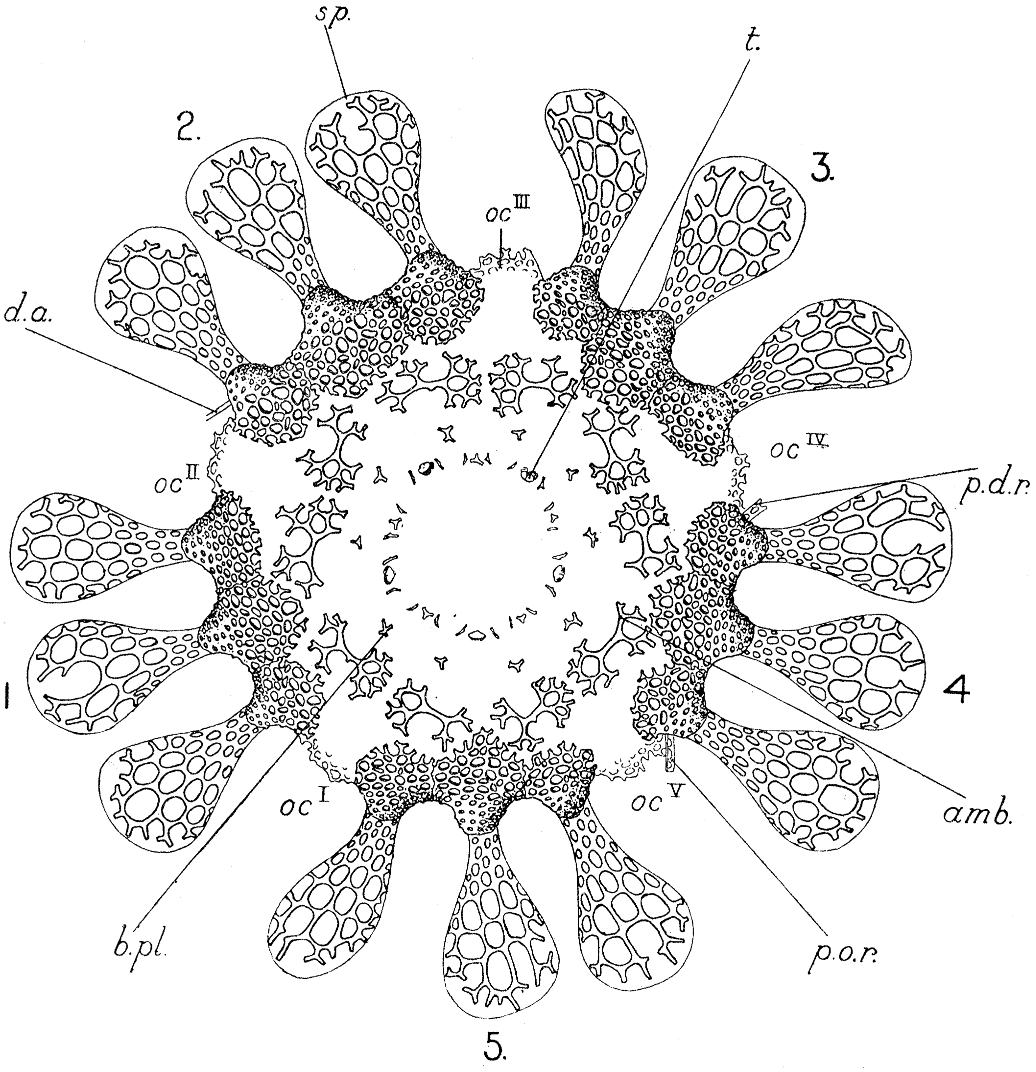

FIG. 4.—Ventral (oral) aspect of an imago in which all the tube-feet have been omitted. 1–5 inter-ambulacra; oc^{I}–oc^{V}., ocular plates; *d.a.*, dorsal arch; *sp.*, spine; *t.*, tooth; *p.d.r.*, postero-dorsal rod in ocular IV; *amb.*, ambulacral plate; *p.o.r.*, post-oral rod in ocular V; *b.pl.*, buccal plate. Camera-lucida drawing, 1 × 186.

dass es im Beginn der Bildung der Ocellarplatten fast so aussieht, als gehörten sie zur Corona, und dass sie erst später ihre mehr centrale Lage in den Winkeln der Basalia einnehmen, dass man sie aber trotzdem nicht als zur Corona gehörig beträchten dürfe. Fig. 13 (imago of *Arbacia pustulosa*, dorsal view) rechtfertigt diesen Satz. Denn bei *Arbacia* ist es augenscheinlich, dass die Ocellar-platten zum apicalen Plattensystem gehören. Auch werden, wie fig. 12 zeigt, zwei von ihnen (**IV** and **V**) genau wie die Basalia **2** und **3** gebildet."

In *A. punctulata* oculars **I**, **II** and **III** are the first plates to appear in the echinus-rudiment, and are, from the beginning, associated with the corresponding terminal tube-feet. As the echinus-rudiment enlarges, oculars **IV** and **V** are soon brought each into intimate association with a terminal tube-foot, as represented in fig. 3.

Each inter-ambulacrum consists of three well-formed plates (fig. 3, **1**, **2** and **3**); the median one extends beyond the lateral ones aborally as well as adorally. Of the ten ambulacral plates (fig. 3, *a* and *b*) those of the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series are somewhat larger than the remaining five although the difference is not so pronounced as in *Echinus miliaris* (Gordon, 1926, *a*, p. 266, fig. 3). The lantern of Aristotle has been omitted from the diagram, and the primordia of the ten large buccal plates have not yet appeared. Apart from the fact that ambulacral plate **II***a* is larger than **II***b* and that genital **1** is larger than genital **2**, the symmetry about the axis AB is complete. The test is very asymmetrical about Lovén's axis CD.

Fig. 3 taken in conjunction with figs. 4 and 5 is intended to elucidate the composition of the entire test at metamorphosis. The specimen represented in figs. 4 and 5 was macerated in an 8 per cent. solution of potassium hydroxide until the ten ambulacral plates separated from each other when the treated imago was transferred to distilled water. The five terminal tube-feet (indicated by dotted circles in fig. 3, *t.ft.*), with their simple calcareous discs, have been omitted in fig. 4. The first pair of ambulatory tube-feet had already been budded off from the radial water vessel, but no traces of the compound discs were as yet apparent. In fig. 5 the two slender triradiate spines on each ocular plate have been omitted.

Übisch (1913), from an examination of whole specimens with the aid of a Zeiss polarisation apparatus (p. 120), analysed the corona of the imago of *Arbacia pustulosa* as follows:—"Die Corona besteht im innersten Ring aus je einer Ambulacral- und einer kleinen Interambulacralplatte. Dann folgen die Fussplatten der spatelförmigen Stacheln und die oben erwähnten fünf radiären Plättchen" (p. 134). In the last sentence the word "radiären" is probably a misprint for "interradial" as he has already mentioned on p. 133 that the median inter-ambulacral plate is separated from the corresponding genital by a small plate.

Now, in whole mounts, the sutures are exceedingly difficult to detect in very young specimens, even with the aid of crossed nicols. In fig. 16 of Übisch's paper there are two "pairs"* of ambulatory tube-feet in each ambulacrum so there must be two well-

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* The tube-feet in echinoids arise alternately from the radial water vessel; those in the I*a*, II*a*, III*b*, IV*a*, V*b* series precede the corresponding ones in the second series just as is the case with the ambulacral plates.

formed ambulacral plates next the peristome and possibly another pair of developing plates aboral to the second pair of tube-feet. The small inter-ambulacral plate next the peristome (Übisch, 1913, fig. 16) and that next the genital plate (Übisch, 1913, fig. 15) are probably the thin ad- and aboral parts of the single, large, median inter-ambulacral plate. The central part of the plate is much thicker because of the presence of the tubercle to which the spine is attached.

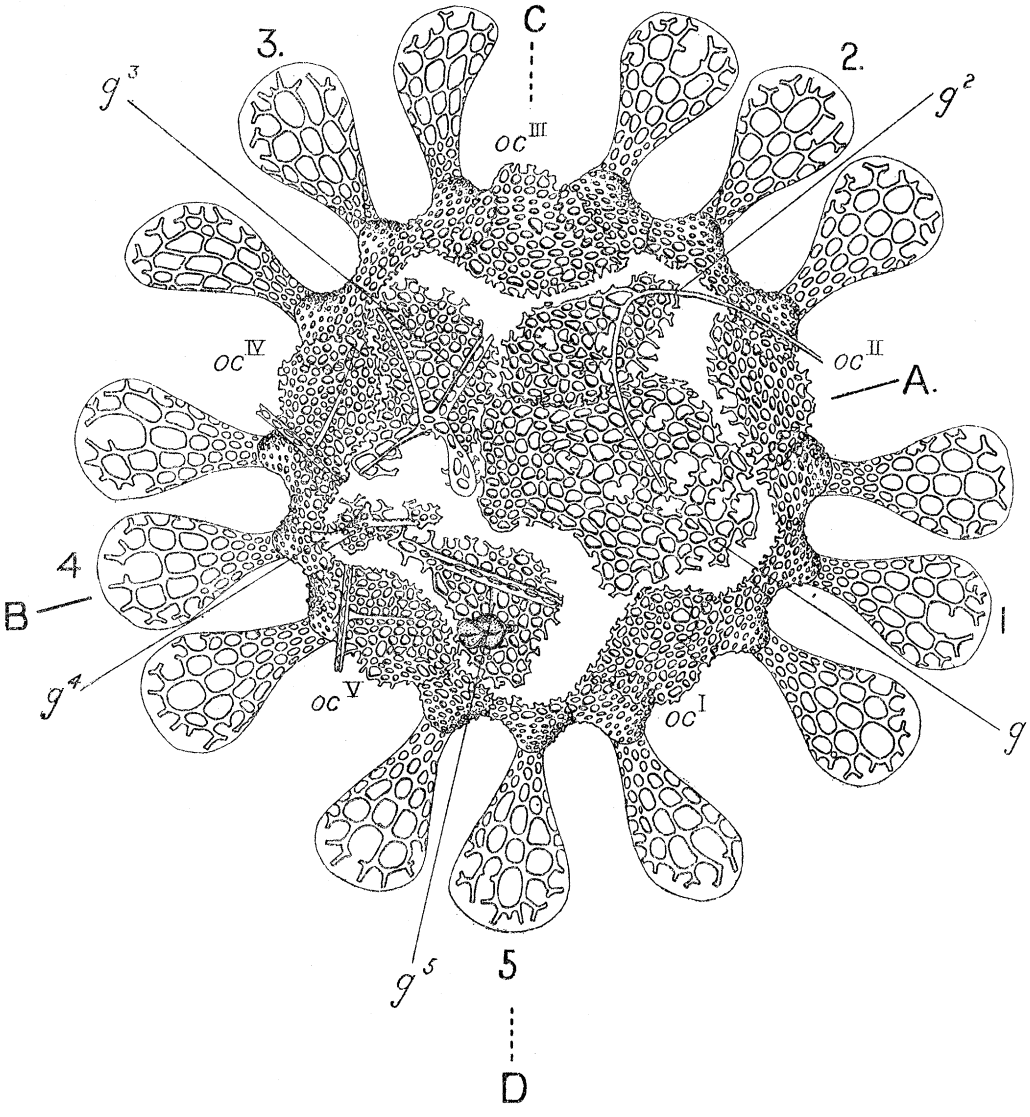

FIG. 5.—Dorsal (aboral) aspect of the imago represented in fig. 4. g^1–g^5., genital plates; AB., Ubisch's primordial plane of symmetry; CD., Lovén's antero-posterior plane; other lettering as in fig. 4. Camera lucida drawing, 1 × 186.

The Post-larval Development of the Test.

The post-larval development of the test of *Arbacia punctulata* is, in many ways, so similar to that of *Echinus miliaris* that a detailed account is uncalled for. Since the auriculæ are incomplete arches (MacBride, 1906, p. 538), the question arises as to whether or not more resorption of the peristomial border will occur. Special attention was also paid to the development of the arbacioid type of triad.

α. *The Apical System.*—Very soon after metamorphosis a projecting ledge of calcite begins to grow out from the median external border of each ocular plate (fig. 4, oc^{III}). In *Arbacia* this ledge is longer and more acute than is that in *Echinus* so that Übisch (1913, Plate vii, fig. 15, *st.*) thought that it was a special type of spine. Four (in rare cases three) anal plates are formed in the periproct and these persist throughout the life of the individual. No one of these corresponds to the sur-anal plate in *Echinus*.

β. *The Ambulacrum.*—As in *Echinus*, the plates in the I*a*, II*a*, III*b*, IV*a*, V*b* series precede the corresponding ones in the second series. Each of columns I*a*, II*a*, III*b*, IV*a*, V*b* commences with two primaries followed by triads. In fig. 6 ($d = 2 \cdot 5$ mm.) the first primary in column *b* no longer reaches the adradial suture (for terminology of

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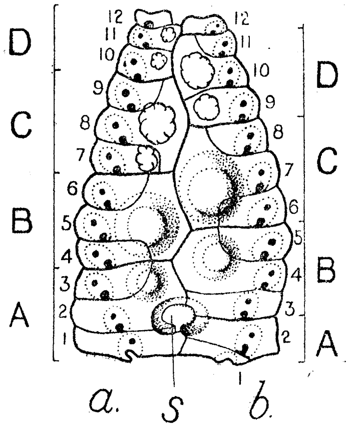

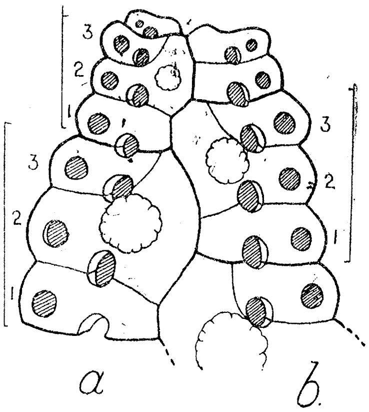

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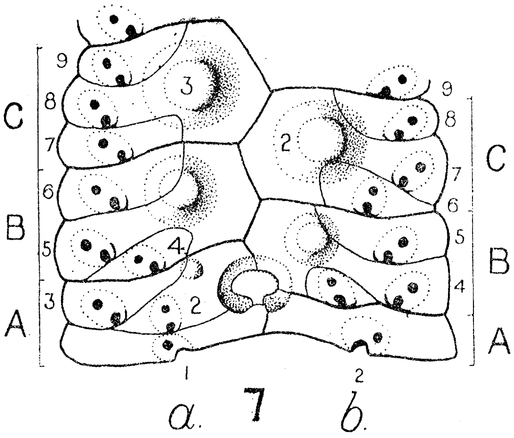

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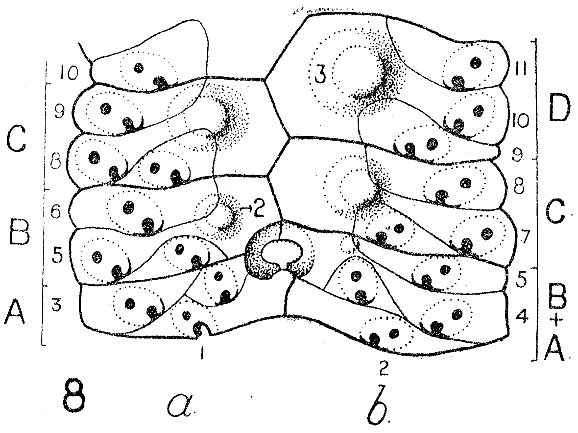


Figs. 6–8.—Stages in the early development of ambulacrum III or V. *s.* sphæridium. Fig. 9.—The apical plates of an ambulacrum from a specimen measuring 12 mm. in diameter to show young triads consisting of two primary plates and a demiplate. Camera-lucida drawings; figs. 6 and 7, 1 × 40; fig. 8, 1 × 27; fig. 9, 1 × 35.

the sutures see Gordon, 1926, *a*, fig. 15). Each of the remaining columns—I*b*, II*b*, III*a*, IV*b*, V*a*—commences with a triad consisting of two primary plates and a demiplate (see fig. 6, column *a*).

A typical arbacioid triad consists of a median primary plate with, ab- and adorally, a demiplate. In the early stages the first or orad plate is a *primary* (fig. 6, triad D of each column, and fig. 9), which later becomes reduced to a demiplate. The third, or apicad plate is, on the other hand, a demiplate from the beginning, since it never quite reaches the perradial suture (fig. 9).

Figs. 6–8 represent three stages in the early development of ambulacrum **III** or **V** Thus column *a* in this series corresponds to column *b* in the figures given in a previous paper for *Echinus* (Gordon, 1926, *a*, p. 291, figs. 21–27). The pore-pairs are still arranged uniserially in each column when the corona measures 2·5 mm. in diameter (fig. 6). Pore 1*b* is still simple and is, moreover, incomplete owing to the fact that the calcite on the peristomial margin has undergone resorption. The sphæridium (*s.*) on plate 1*a* is now situated in a depression or pit; when first formed it is placed superficially as in the imago of *Echinus miliaris*. Triads B and C in column *a* and C in column *b* are of the arbacioid type, the others each possess two primaries and a demiplate.

Ere the test has increased to 5 mm. in diameter (fig. 7) pore 1 of column *b* has disappeared completely and the second pore-pair is now incomplete. The grouping of the pore-pairs into rows of three has commenced. Owing to growth pressure many of the plates in the peristomial region have been reduced, *e.g.*, plates 2*a*, 4*a* and 3*b* no longer reach the adradial suture while the adradial border of plate 6*b* is very small. The first tubercle in column *a* has almost disappeared although situated at some little distance from the peristomial margin of the corona.

The crowding of the pore-pairs and reduction of the plates near the peristome continues. In the next figure (fig. 8, $d = 10$ mm.) plates 1*a*, 7*a*, 2*b* and 6*b* have been completely cut off from the adradial suture. Tubercle 1*a* has disappeared while that on triad B of column *b* is greatly reduced in size.

Fig. 10 represents the peristomial region of ambulacrum **V** of an adult measuring 45 mm. in diameter. The arrangement of the pore-pairs in rows of three is well-marked in column *b*, but this arrangement does not hold in the immediate neighbourhood of the peristome in column *a*. Pore-pairs 2*a* and 3*b* have been forced nearer to the perradial suture during development than have pore-pairs 1*a* and 2*b* (*cf. Echinus miliaris*, Gordon, 1926, *a*, p. 291, fig. 27). The peristomial border, in spite of its alteration in shape, has undergone very little resorption for, in column *a* only pore-pair 1 and in column *b* only pore-pair 2 is in contact with the buccal membrane (*cf.* figs. 7 and 8). In column *a* the upper tubercle represented in fig. 10 is opposite pore-pairs 16, 17 and 18, and therefore belongs to the sixth triad F. The fourth tubercle—that nearest the median pit—has almost disappeared. The same is true of the third tubercle in column *b*. From this it is certain that tubercles 1, 2 and 3 of column *a* and 1 and 2 of column *b* (shown in fig. 7) have entirely disappeared during development.

In *Arbacia* the amount of resorption of calcite at the actual peristomial margin is small in spite of the fact that the auriculæ are incomplete arches. This is in keeping with the fact that each area bears but a single sphæridium which remains in a pit near the peristome throughout the life of the urchin (*cf*. *Echinus miliaris* where each ambulacrum bears numerous sphæridia three of which pass, during development, from the ambulacrum on to the buccal membrane.—Gordon, 1926, *a*). The adoral triads, at first narrow and high, become relatively broader and lower ; much of the calcite together with the primary tubercle gradually disappears until, in the adult, only a small part of each plate—that around the pore-pair—remains.

γ. *The Inter-ambulacrum*.—At metamorphosis the inter-ambulacrum differs considerably from that found in the imago of *Echinus* (*cf*. fig. 3 with Gordon 1926, *a*, fig. 16, p. 282). Plates 2 and 3 are on a level with plate 1 instead of being aboral to it, and this unusual arrangement persists after metamorphosis. Fig. 11 represents a complete inter-ambulacrum from a specimen measuring 2·5 mm. in diameter exclusive of the spines. The lower, median, apparently simple plate is, in reality, the group of three plates laid down in the echinopluteus. This compound structure is very convex and in fig. 11 the peristomial margin cannot be seen. In fig. 11*a* the same group of plates is represented as viewed from the peristome. When examined carefully under a binocular microscope, traces of the two sutures can be detected ; the convexity of the structure renders examination under crossed nicols useless. Each of the three small tubercles (t^1) next the peristome bears one of the spatulate spines present in the imago (figs. 4 and 5). These spines are now very inconspicuous and the two lateral ones soon drop off. Each of the three plates also bears a large primary tubercle (t^2). Careful focussing under the microscope reveals what appears to be a transverse suture

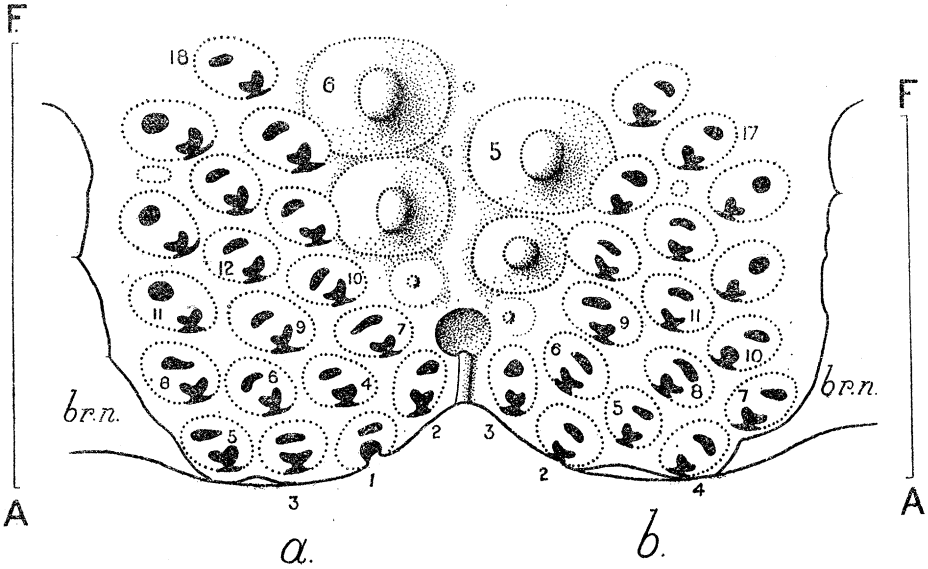
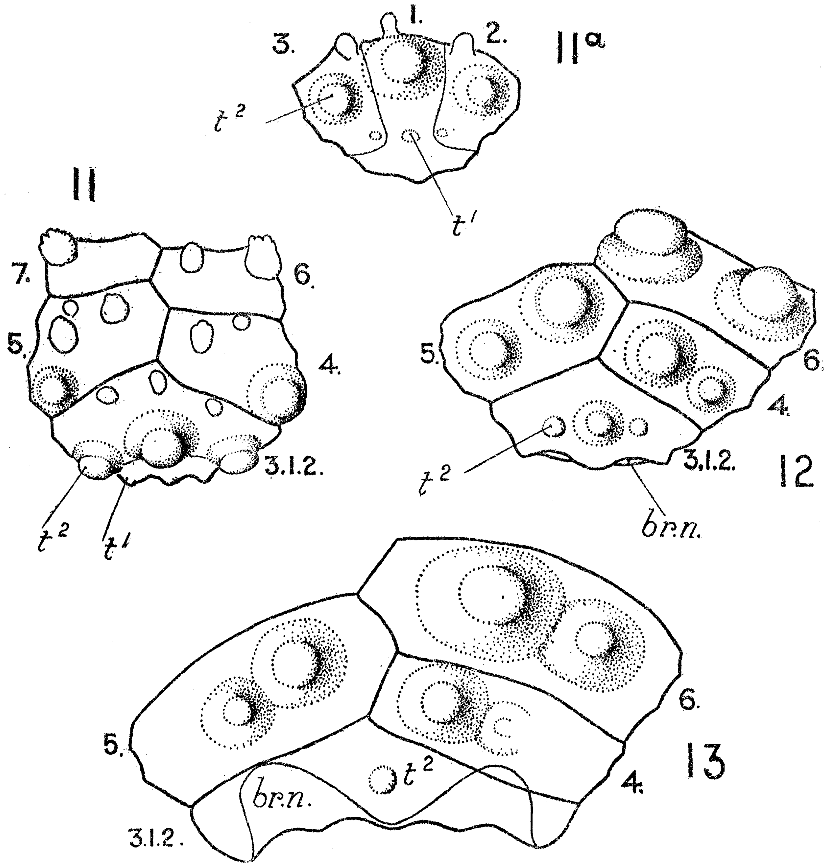


Fig. 10.—Peristomial region of ambulacrum III in an adult measuring 45 mm. in diameter ; *br.n.*, branchial notch. Camera-lucida drawing, 1 × 14.

in the median plate on a level with its tubercle t^1. It is known from the early development of the inter-ambulacrum that there can be no suture here. An examination of the inner surface of the median plate shows that the lower part is now much thicker than the rest of the plate, and that this thickened portion terminates on a level with the small tubercle t^1. Aborally two typical inter-ambulacral plates have been laid down in each column (plates 4–7, fig. 11). An examination of all the inter-ambulacra shows that in columns **1***b*, **2***b*, **3***a*, **4***b*, **5***b* the plates are slightly in advance of the corresponding ones in columns **1***a*, **2***a*, **3***b*, **4***a*, **5***a*. Thus, inter-ambulacra **1**, **2**, **4** and **5** are each similar to that represented in fig. 11 and inter-ambulacrum **3** is a mirror image of the others.



Figs. 11–13.—Stages in the early development of an inter-ambulacrum—areas 1, 2, 4 and 5 are similar to that represented in the figures; in area 3 the plating is reversed. Fig. 11, inter-ambulacrum from a specimen measuring 2·5 mm. in diameter; 11*a* the same viewed from the peristome; 1 × 40. Fig. 12, the peristomial inter-ambulacral plates from a specimen measuring 5 mm. in diameter, 1 × 27. Fig. 13, the same group of plates from a specimen of $d = 12$ mm., 1 × 20. *br.n.*, branchial notch. Camera-lucida drawings.

The inter-ambulacrum of the very small *Arbacia* bears a striking resemblance to that of much larger specimens (11·5 and 17·5 mm. in diameter) belonging to the genus *Habrocidaris* Agassiz and Clark (Clark, 1908, pp. 76–81, Plate 54, figs. 1, 3, 4 and 7), and to *Podocidaris sculpta* figured on p. 77 (fig. *a*) of the same monograph.

Apparently this group of three inter-ambulacral plates (fig. 11, *a*), a transient condition in the ontogeny of *Arbacia* (*cf.* fig. 11, *a*, and fig. 14), persists in the adult *Habrocidaris*. AGASSIZ (1904, p. 54, Plate 54, figs. 2 and 5), unable to distinguish the sutures in a small urchin measuring 3·6 mm. in diameter, describes *Arbacia* as "one of the few regular Echinid genera in which the single primordial plates are not resorbed."

DÖDERLEIN* (1906, pp. 183–4), in a discussion of the relation of *Pygmæocidaris* (= *Podocidaris*) *prionigera* AGASSIZ to the Triassic *Tiarechinus*, is of the opinion that the latter is nearly allied to the Arbaciidæ. The inter-ambulacrum of *Arbacia* is, at metamorphosis, remarkably similar to that of *Tiarechinus*, but the median plate in the latter is represented as having a distinct transverse suture. In other words the fossil *Tiarechinus* is said to possess a single peristomial plate followed by three long narrow inter-ambulacral plates.

In course of time the median spatulate spine also drops off and the tubercle (t^1) to which it is attached is resorbed. A certain amount of resorption of the peristomial border also occurs, especially in the region of the developing branchial notches (*br. n.*). When the diameter has increased to 5 mm. (fig. 12) the two lateral primary tubercles (t^2) are greatly reduced, and, by the time that the test has increased to a diameter of 12 mm. (fig. 13), they have entirely disappeared. The figures show, however, that they have been resorbed to make way for the advancing branchial notches (fig. 13, *br. n.*). The actual peristomial margin has not undergone much further resorption. The outer tubercle on plate 4 is also in process of resorption.

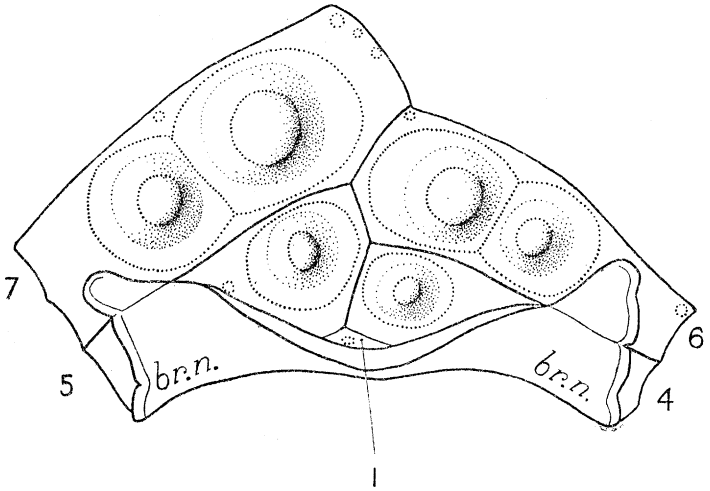


FIG. 14.—The peristomial inter-ambulacral plates from a specimen measuring 26 mm. in diameter. Camera-lucida drawing, 1 × 14.

In fig. 14 ($d = 26$ mm.) the branchial notches are much more pronounced. Only a small vestige of the initial group of plates 1, 2 and 3 now remains; the outer tubercle on plate 4 as well as that on plate 5 has gone to make way for the advancing branchial

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* See p. 305.

notches. In an adult, measuring 45 mm. in diameter, there is a slight variation in the different inter-ambulacra. In all five areas the outer tubercle on plate 6 has gone; the inner tubercle on plate 4 is still present in some areas, is undergoing resorption in others or may even have entirely disappeared. In certain cases the outer tubercle on plate 7 has also undergone resorption. Thus, during development, all the three inter-ambulacral plates which were formed in the echinopluteus disappear together with a greater or lesser proportion of plates 4 and 5.

δ. *The Buccal Membrane.*—In *Arbacia* the peristome is circular only in the smallest specimens and becomes pentagonal soon after metamorphosis. In *Echinus*, on the other hand, it is still circular in specimens measuring 3 mm. in diameter (GORDON, 1926, *a*, fig. 31, p. 298).

A few small buccal plates are laid down in the neighbourhood of the future mouth soon after metamorphosis and prior to the formation of the mouth. As the ten large buccal plates increase in size, more small buccal plates are added around the mouth. The plates surrounding the primary buccal tube-feet (the **I***b*, **II***b*, **III***a*, **IV***b*, **V***a* series*) are larger than the remaining five which as yet possess no tube-feet. By the time that the corona measures 2·76 mm. in diameter, a few small buccal plates have appeared external to the ring of large buccal plates but, as in *Echinus*, opposite the inter-ambulacra only.

The secondary buccal tube-feet undoubtedly come from the corona as is the case in *Echinus*. In a specimen just over 3 mm. in diameter, two ambulatory tube-feet belonging to the **I***a*, **II***a*, **III***b*, **IV***a*, **V***b* series were situated at a considerable distance from the margin of the corona—about mid-way between the margin and the corresponding large buccal plates. Each of the remaining three was still partially surrounded by the ambulacral plate. In the next stage all five ambulatory tube-feet were surrounded each by a buccal plate.

CONCLUSION.

Although *Arbacia* is a more primitive form of regular sea-urchin than is *Echinus miliaris*, the development of the test is very similar in both genera. The striking similarity between the development of the ambulacrum in both genera is especially noteworthy. The only fundamental difference, indeed, lies in the formation of the triad. In *Echinus miliaris* the triad consists of a diad—*i.e.*, a large primary and a small demiplate—followed by a small apicad primary (GORDON, 1926, *a*, p. 288, fig. 20). In *Arbacia punctulata*, on the other hand, a small orad primary is first formed and then a diad of the same type as in *Echinus*.

A study of the development of the test in *Arbacia* has shown (1) that in this genus also five of the buccal tube-feet are modified ambulatory tube-feet; (2) that the amount

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* In *Arbacia pustulosa* ÜBISCH (1913, Plate vii, fig. 16) represents the primary buccal tube-feet as belonging to the I*a*, II*a*, III*b*, IV*a*, V*b* series—the series which comes from the corona in *A. punctulata*.

of resorption of calcite at the actual peristomial border of the corona is slight whether the auriculæ have the form of complete arches (*Echinus*) or of incomplete* arches (*Arbacia*).

The development of the ambulacrum in *Arbacia punctulata* agrees so well with that in both *Echinus miliaris* and *Strongylocentrotus drœbachiensis* (see Gordon, 1926, *a*, p. 307) as regards (1) amount of resorption at the peristomial border, (2) arrangement of the pore-pairs in the immediate neighbourhood of the peristome, that one seems justified in concluding that the ambulacral development throughout the bulk of the regular echinoids is rather standardised. Exception must of course be made for such very primitive forms as *e.g.*, the Cidarids where the development is as yet unknown.† The grouping of the ambulacral plates into *e.g.*, triads or still more complex structures, the number of reduced plates and their arrangement within the compound structures may vary, but this variation does not seem to affect the development of the entire ambulacrum to any appreciable extent.

Although the position of plates 2 and 3 relative to plate 1 in the inter-ambulacrum of *Arbacia* is unusual, only plate 1 is in contact with the buccal membrane. Only one inter-ambulacral plate is in contact with the buccal membrane in *Echinus miliaris* also at metamorphosis (Gordon, 1926, *a*, fig. 16, p. 282). In the imago of a Spatangoid (*e.g.*, *Echinocardium cordatum*, Gordon, 1926, *b*, fig. 2, p. 262) or of a Clypeastroid (*e.g.*, *Echinarachnius parma*, fig. 16 of the present paper) a single plate is also present and persists throughout the life of the urchin. Thus the development of the inter-ambulacrum of *Arbacia* is essentially in agreement with that of other Echinoidea.

Bather (1909, p. 259) disagrees with Döderlein‡ regarding the relationship of *Tiarechinus* and *Pygmæocidaris* and writes, "Prof. Döderlein's hypothesis manifestly demands that *Pygmæocidaris* shall be regarded as the most primitive of known Arbaciidæ . . . In just those features that have given rise to the comparison with *Tiarechinus*, *Pygmæocidaris* appears to be the most specialised rather than the most primitive of the Arbaciidæ." The composition of the inter-ambulacrum of the very young *Arbacia*, resembling as it does that of the adult *Habrocidaris*, shows that the latter is the more primitive of the two. It seems to the writer that the four Arbaciid genera *Pygmæocidaris*, *Podocidaris*, *Habrocidaris* and *Arbacia* may represent a progressive

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* Macbride (1906, p. 538) writes of the family Arbaciidæ "the auricles consist of incomplete arches springing from the ambulacral plates." But in *Arbacia punctulata* the auriculæ may occasionally form complete arches, as was the case in an adult measuring 45 mm. in diameter—the specimen from which fig. 10 was obtained. In a recent paper Dr. R. T. Jackson (1927, p. 485) gives the results of a study of 300 specimens of *Arbacia punctulata*. He found that, of these, 76 per cent. had all ten auriculæ separate, 6 per cent. had all five pairs of auriculæ united in sutural contact over their respective ambulacra. In the remaining 18 per cent. either one, two, three or four pairs of auricles were in sutural contact with each other.

† A paper "On the Postlarval development of some Cidarids," by Mortensen (1927), has recently appeared.

‡ See p. 303.

series of which the first mentioned is the most primitive. DÖDERLEIN (1906, pp. 185–6) describes the inter-ambulacrum of *Pygmæocidaris* as having adorally three, adapically only two, columns of plates. There are stated to be three plates in the median column (" noch deutlich eine zusammengehängende Reihe von drei medianen Platten vorhander ist "), but in his figure 36*f*, p. 184, four out of the five inter-ambulacra are represented as having only two median plates ; in the remaining area the adoral median plate is divided by a suture. It is possible that there may be only two median plates of which the adoral one separates the first two plates of column *a* from the corresponding ones of column *b*. For AGASSIZ and CLARK (1908, p. 77), on re-examining *Porocidaris sculpta*, found that in this species the single median plate separates the first two paired* plates and encroaches upon the third pair on the exterior of the test. Seen from the interior surface, the median plate (= the unpaired or peristomial plate of other Echinoidea) only separates the first pair and encroaches upon the second pair of inter-ambulacral plates. In *Habrocidaris* the peristomial plate separates the first pair of plates and encroaches upon the second pair to a slight extent (AGASSIZ and CLARK, 1908, Plate 54, figs. 1, 3, 4 and 7). A feature characteristic of the Arbaciidæ is the tendency for the peristomial inter-ambulacral plate to extend aborally between columns *a* and *b* of the inter-ambulacrum. *Pygmæocidaris* is the only one in the series that has more than one median plate, and this tendency towards a triserial arrangement of the inter-ambulacral plates is probably a primitive feature which the other genera have lost.

The inter-ambulacrum of the Triassic fossil *Lysechinus incongruens* (GREGORY, 1896, p. 1001, and Plate LI, fig. 5) apparently consists of a peristomial plate followed by a pair of plates, above which are two series each of three plates. The arrangement of the adoral four plates recalls that found in the imago of *Echinus* (GORDON, 1926, *a*, fig. 16), and MORTENSEN (1927) found the same arrangement to hold good in the imago of *Eucidaris*. An arrangement such as DÖDERLEIN describes for the inter-ambulacral plates of *Pygmæocidaris* could be arrived at by supposing that the peristomial plate in *Lysechinus* extended aborally between the first pair of plates until it came into contact with the second median plate. Several of the differences between the inter-ambulacrum of *Pygmæocidaris* and that of *Tiarechinus*, mentioned by BATHER (1909, p. 258), do not hold in the case of that of *Lysechinus* which is a less aberrant form. It is true that the peristomial inter-ambulacral plate of *Pygmæocidaris* does not stretch across the whole area, but is limited to the part between the branchial notches. It is probable that the peristomial plate will be found to stretch across the whole inter-ambulacrum in the imago and in very young urchins.

While there is some similarity between the inter-ambulacra of *Pygmæocidaris* and of *Lysechinus*, it is quite possible that there is no phylogenetic relationship between the two, for fossil Arbaciidæ are known only from the Tertiary epoch and the latter is Triassic.

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* The inter-ambulacral plates are really arranged alternately in 2 rows.

B.—ECHINARACHNIUS PARMA, LAMK.

INTRODUCTION.

Cultures of *Echinarachnius parma*, LAMK., were started on July 28 and 29 and on August 5, 1926, at Woods Hole. The adults at that time were in very bad condition, so that large numbers had to be opened in order to find a single female with ova suitable for fertilisation. The larvæ failed to form echinus-rudiments, the larval body was abnormally large, and, during the fourth week, the larval arms commenced to shorten.

Later in August it was possible to obtain some ripe ova from the smaller females and these cultures were successful. One that was started on August 11 yielded a number of imagines on September 2—*i.e.*, in twenty-two days—and the majority of the plutei had metamorphosed ere September 14. Cultures started on August 17 and 19, respectively, did not yield imagines until September 18–20—*i.e.*, until during the fifth week.

Several large samples of sand dredged from the *Echinarachnius* grounds during September were examined in the hope of finding small postlarval stages, but in vain. The smaller specimens present in the sand were over 10 mm. in diameter and exhibited all the features characteristic of the adult. An attempt was therefore made to rear the imagines beyond metamorphosis (1) in vessels having the bottom covered with a thin layer of finely sifted sand; (2) in vessels having the sides and bottom coated with diatomaceous growth as for *Arbacia* p. 290. In both cases the majority of the young urchins were still alive at the end of September. Many had increased considerably in size but none had commenced to feed.

As the postlarval development of the test is most important, the writer returned to Woods Hole in June, 1927, in order to rear postlarval stages, as far as is possible under laboratory conditions. The sand-dollars were in good breeding condition in mid June. Larvæ from cultures started on June 15, 16 and 17 were very healthy and normal, but unfortunately the young urchins died within the echinopluteus just as they approached metamorphosis.

A small culture of *Echinarachnius parma* ova cross activated with sperm from *Arbacia punctulata*, started on June 23, gave a number of apparently normal sand-dollars on July 27. The test of such an imago was, on analysis, found to be quite normal in every respect.

Later cultures of *Echinarachnius* proved quite successful. The imagines were transferred to shallow vessels containing a small amount of a fine mud, rich in bottom-living diatoms, and sea water. The diatomaceous mud was obtained from Beaufort, North Carolina. A considerable number of the small urchins lived in this fine mud during October, November and December, 1927. During the winter growth was exceedingly slow, and, at the end of January, 1928, the largest specimen only measured 1·50 mm. in length including the spines (length of the test alone = 1 mm.). The oldest stage obtained therefore corresponds to that represented in fig. 9 (GORDON, 1926, *b*, p. 276), and is already sufficiently advanced to enable one to determine the salient differences between the early postlarval development of *Echinarachnius parma* and of *Echinocardium cordatum*.

ANALYSIS OF THE PERMANENT SKELETON IN THE ADVANCED ECHINOPLUTEUS AND IN THE IMAGO.

THÉEL (1892), in a large monograph on "The Development of *Echinocyamus pusillus*," has described much of the development of the permanent skeleton in the echinopluteus. Owing, doubtless, to the fact that the Clypeastroid larva is highly pigmented on the left side, he did not succeed in analysing the skeleton of the imago. Since the early development of the Clypeastroid skeleton is, in many respects, similar to that of a

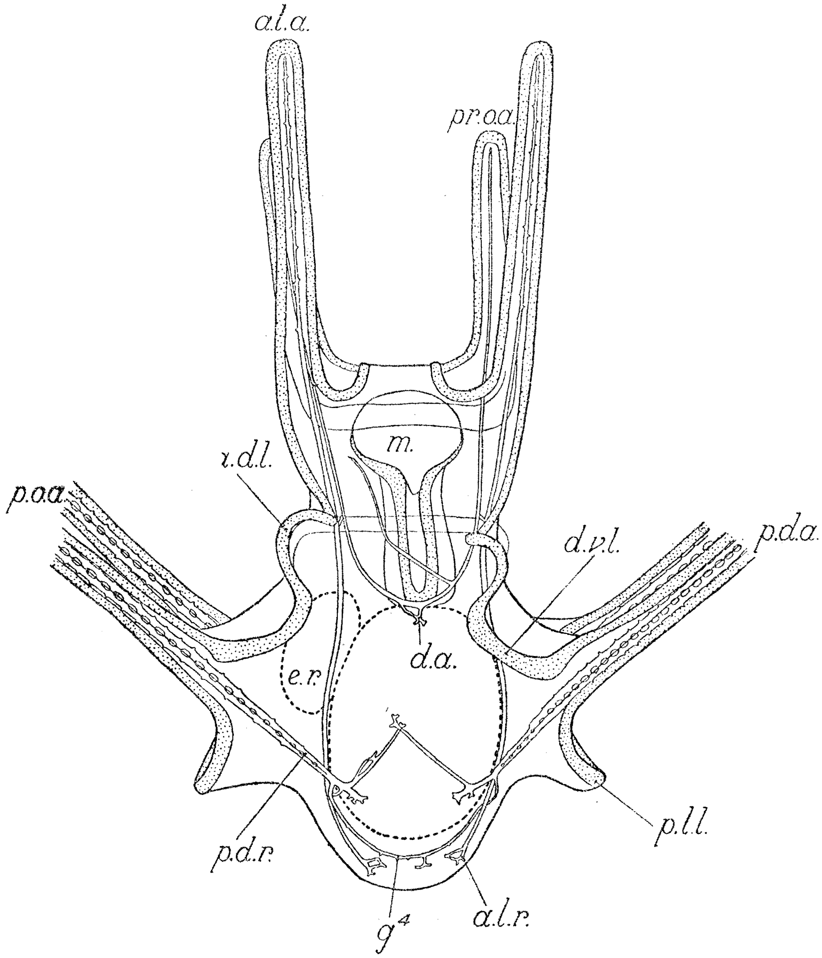

FIG. 15.—A fully developed echinopluteus of *Echinarachnius parma* seen from the dorsal surface. *p.o.a.*, post-oral arm; *a.l.a.*, antero-lateral arm; *pr.o.a.*, præ-oral arm; *p.d.a.*, postero-dorsal arm; *a.d.l.*, antero-dorsal lobe of the dorsal ciliated band; *d.v.l.*, dorsal vibratile lobe = dorsal auricular lobe of *Arbacia*; *p.l.l.*, postero-lateral lobe; *m.*, larval mouth; *d.a.*, dorsal arch; *a.l.r.*, posterior end of antero-lateral rod; *p.d.r.*, postero-dorsal rod; *e.r.*, echinus-rudiment. Camera-lucida outline.

Spatangoid (Gordon, 1926, *b*) a detailed account will not be given here. The analysis of the skeleton is all that need be dealt with.

α. *The Ambulacra.*—In *Echinocardium cordatum* (Gordon, 1926, *b*) the posterior is more highly developed than the anterior part of the corona. The reverse is true of *Echinarachnius*. Théel (1892) found that the sphæridia on plates **II***b*, **III***a*, **IV***b* appeared in advance of those on plates **I***b* and **V***a*. This is not the only difference between the trivious and the bivious ambulacra. Ambulacrum **III** develops more rapidly than the others and, at metamorphosis, there are at least three plates in each column (fig. 16). Plates 1*a* and 1*b* of area **III** are larger than the corresponding plates in the other ambulacra, and the large sphæridium (*S*) on plate 1*a* is the first to appear. Areas **II** and **IV** may, at metamorphosis, have almost as many plates in each column as has the anterior ambulacrum but the plates themselves are smaller and the sphæridia are minute (fig. 16). Soon after each ambulacral plate is formed it acquires a short spine; in area **III**, however, these spines are confined to column *b* (fig. 16).

β. The *Inter-ambulacra.*—From fig. 16 it is evident that the plates in inter-ambulacra **2** and **3** are larger and more numerous than those in the three posterior areas. For a considerable length of time areas **1**, **5** and **4** each possess only three plates (Table I, Pluteus B). In certain cases no further plates appear in these inter-ambulacra until after metamorphosis (Table I, Imago A). As a rule, however, a fourth or even a fifth plate is laid down in each of the three posterior areas in the late echinopluteus (Table I, *C*–*G*). Beyond the single peristomial plate, the plates in columns **1***a*, **2***b*, **3***a*, **4***b*, **5***b* precede the corresponding plates in columns **1***b*, **2***a*, **3***b*, **4***a*, **5***a* (see Gordon, 1926, *b*, p. 307, table 2A).

The total number of plates in the corona varies considerably as the following table shows:—

Table I.

Area :	I	II	III	IV	V	2	1	5	4	3	Total.
A. Imago	3	4	6	4	2	5	3	3	3	5	38
B. Pluteus	3	5	6	5	2	5	3	3	3	5	40
C. Pluteus	4	5	6	3	4	5	5	4	5	5	46
D. Imago*	4	5	6	6	4	6	4	4	4	5	48
E. Imago	5	6	6	5	5	6	4	4	4	5	50
F. Pluteus	5	5	7	5	4	5	5	5	5	5	51
G. Pluteus	5	6	7	5	4	6	5	5	5	5	53
Total	29	36	44	33	25	38	29	28	29	35	

* Imago D is that represented in fig. 16D and imago E is the normal imago from the same double-hydrocœle specimen. The latter, in this instance, has only two more coronal plates than the former; sometimes the difference is more marked.

Imago A, which had presumably metamorphosed prematurely, possessed only 38 coronal plates whereas the late echinopluteus G had as many as 53. Of the five ambulacra, area **III** is always the largest and most advanced. Areas **II** and **IV** are next in order, but sometimes area **II** is slightly more advanced than area **IV** (see Table I, C, E, and G). In imago D, only, it is the reverse. Area **I** may also be somewhat in advance of area **V** (Table I, A, B, F and G). Of the inter-ambulacra, areas **2** and **3** are most highly developed, but area **2** is always the first to acquire a sixth plate (Table I, D, E and G). Thus, not only is the anterior end of the test more advanced than the posterior, but the right side may be more advanced than the left. The total number of plates in areas **I**, **1**, **II**, **2**, for specimens A–G is 132 as against 122 for areas **V**, **4**, **IV**, **3**.

γ. *The Ocular Plates.*—As is the case in a Spatangoid (Gordon, 1926, *b*), the appearance of the ocular plates is delayed. Oculars **IV** and **V** are formed, after metamorphosis, from remnants of the postero-dorsal and post-oral rods, respectively (*cf.* fig. 2). The remaining three oculars arise from independent calcareous primordia ; in some instances they appear in the late echinopluteus ; in others, soon after metamorphosis.

δ. *The Genital Plates.*—Only one genital plate—the madreporite—is formed in the echinopluteus. This plate develops around the posterior end of the dorsal arch as is the case in all echinoidea so far as is known. In the imago this genital (g^2, figs. 16 and 18) is the most conspicuous of the plates on the dorsal surface. Other three genitals are present in the form of remnants of larval spicules. These are (*a*) genital **3** represented by a portion of the right postero-dorsal latticed rod ; (*b*) genital **4** represented by a portion of spicule from the posterior end of the pluteus (g^4, fig. 15 and fig. 16) ; and (*c*) genital **5** represented by a remnant of the right post-oral latticed rod. Genital **1** is absent or has not yet made its appearance.

ε. *The lantern of Aristotle.*—The development of the lantern of Aristotle is, in most respects, similar to that found in *Arbacia* or *Echinus*. The only noteworthy difference is that the rotulæ do not appear until metamorphosis is about to take place, or even until after metamorphosis. Thus, the alveoli and the epiphyses are considerably advanced before the rotulæ are laid down. In *Echinocyamus* (Théel, 1892, Plate viii, fig. 105), the rotulæ and epiphyses appear almost simultaneously. The first cone of the tooth in the imago of *Echinocyamus* (Théel, 1892, Plate viii, fig. 105, p. 56 ; Plate ix, figs. 108, 109) is markedly convex and is armed with short projecting "spines." No such thorny projections are ever developed on the first cone of the tooth of *Echinarachnius*, and the cone itself is much less convex. No trace of the compasses, which are absent in the fully developed lantern, was observed in the largest specimens, and in all probability none are ever present. Bather (1900, p. 316) states that Clypeastroids "have neither braces (rotulæ) nor compasses," and MacBride (1906, p. 546) writes, "both rotulæ and compasses are absent." This is an error, for Lovén (1893, pp. 55–73, Plates viii–xi) describes in detail the fully developed lantern in a number of genera and, in all cases, a small rotula is present (see also Müller, 1853, Plate vii, figs. 13, 14, 16).

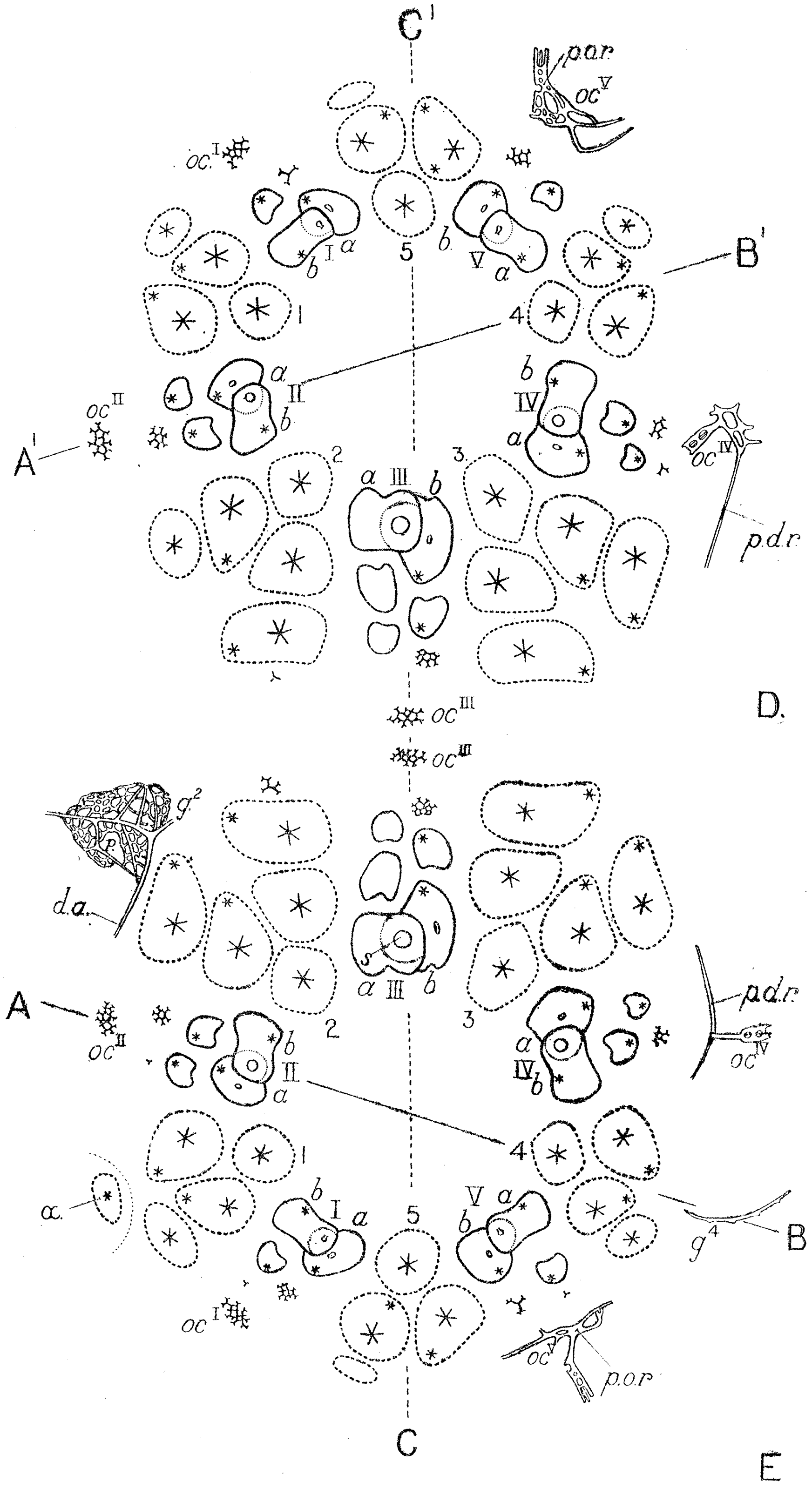

FIG. 16.—Diagram to show the complete analysis of the skeleton in a double-hydrocœle form. E, imago formed from the normal echinus-rudiment on the left side; D, imago from the right echinus-rudiment; AB and A^1B^1 the primordial plane of symmetry; C^1C, LOVÉN's plane of symmetry; I–V, ambulacra; 1–5, inter-ambulacra; oc^{I}–oc^{V}., ocular plates; g^2g^4., genital plates; *p.*, madreporic pore; *d.a.*, dorsal arch; *p.d.r.*, postero-dorsal rod; *p.o.r.*, post-oral rod. α. an additional plate not found in the imago, as a rule; it might belong to either imago D or imago E.

Form with two Water-vascular Systems.

In one culture* an unusually large number of larvæ (about 20 per cent.) each possessed a well-developed hydrocœle on the right as well as on the left side. In some instances the imago on one side metamorphosed a day or two before that on the other side.

The two imagines are placed back to back, so to speak, and the two tests are separated by a narrow band of tissue. In this tissue the remnants of larval skeleton, situated normally on the dorsal surface, are to be found. In the specimen analysed in fig. 16 the single madreporic plate (g^2) bridges the gap between column $2a$ of each imago and is pierced by a single madreporic pore (fig. 16). On the other side of the equatorial band of tissue are the remnants of the two post-oral and the two postero-dorsal spicules (fig. 16, *p.o.r.* and *p.d.r.*). The right as well as the left spicules would have given rise to ocular plates. In the space between inter-ambulacra **4** is another fragment of larval skeleton that normally forms the foundation of the fourth genital plate (fig. 16, E, g^4). The additional plate α might belong to area **1** of either imago.

From the diagram (fig. 16, D and E) it will be seen that the corona is very similar in both cases. D is, as one would expect, almost an exact mirror-image of E. No larva with a right instead of a left echinus-rudiment was observed in any of the cultures (see Ohshima, 1921). An occasional double-hydrocœle form occurred in most of the other cultures.

The Symmetry of the Imago.

Lovén (1874) emphasised the importance of the **III 5**† or antero-posterior plane of symmetry (hereafter referred to as "Lovén's plane of symmetry") in irregular sea-urchins and invariably arranged the disarticulated corona with reference to this plane in regularia as well as in irregularia. Lovén's method of representing the analysis of the test has been applied by the writer to the imago of (*a*) *Echinus*,‡ (*b*) *Echinocardium* and (*c*) *Echinarachnius* (Gordon, 1926, *a*, fig. 16; 1926, *b*, fig. 2 and fig. 16 of the present paper).

The ambulacral plates are, in nearly all echinoidea, arranged according to Lovén's

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* In this culture, also, many of the imagines had, on the dorsal surface, a balloon of larval tissue which, in some cases, disappeared a few days after metamorphosis. On macerating a few of these specimens in an 8 per cent. solution of potassium hydroxide, the remnants of larval spicules and the madreporic plate were found to be in their normal positions on the dorsal surface but masked by this surplus tissue. Sometimes two such balloons were present, one dorsally the other ventrally placed. An occasional twin form had a balloon projecting from the ventral surface of one imago.

† Lovén's notation for the ambulacra and inter-ambulacra was adopted by the author in the first paper (Gordon, 1926, *a*) and has always been used subsequently.

‡ The genital plates, however, were placed above ambulacrum III not above inter-ambulacrum 2 in *Echinus*, and the ocular plates were placed with the genitals.

law of heterotropy.† Therefore the ambulacra are not symmetrical about Lovén's plane of symmetry (fig. 17, A). Instead they are quite symmetrical‡ about the plane passing through either areas **II** and **4** or **I** and **3** (fig. 17, B and C). Of the five oculars **IV** and **V** arise in connection with larval spicules in *Echinus* (Gordon, 1926, *a*, p. 264, and in *Arbacia* (fig. 3). These are placed symmetrically about the **II 4** plane, to one side

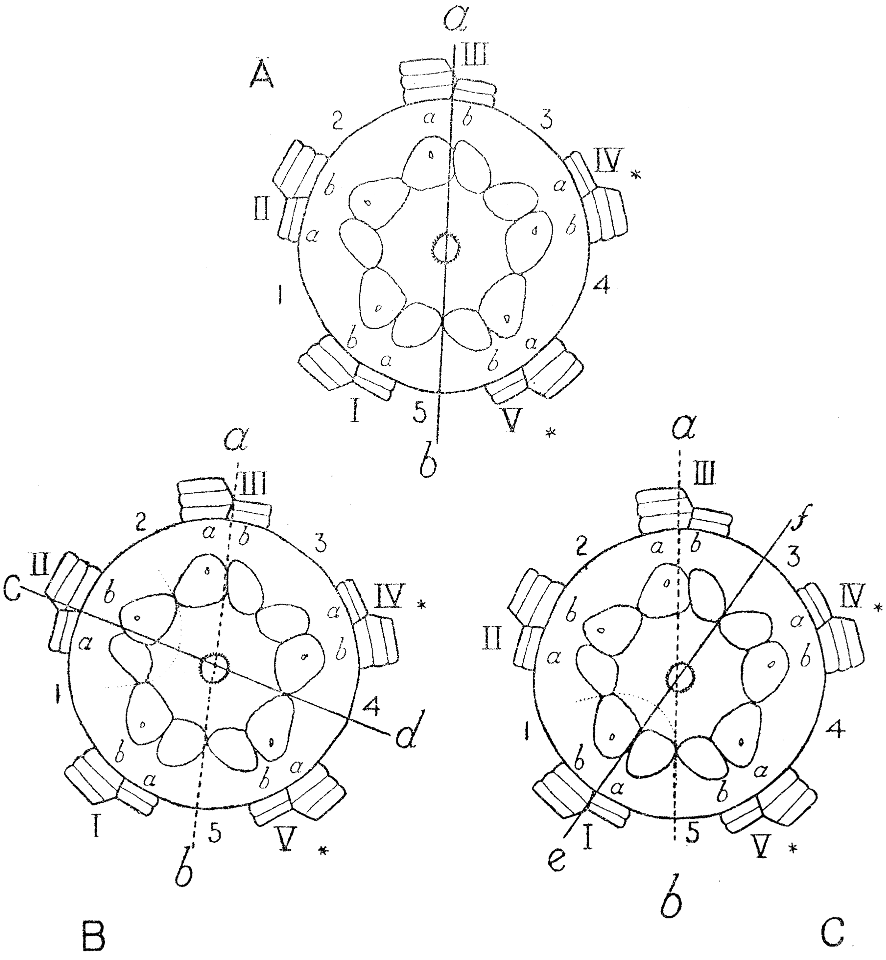

Fig. 17.—Three diagrams in oral aspect to show the arrangement of the ambulacra in a regular urchin relative to A. Lovén's plane of symmetry *ab.*; B. Übisch's primordial plane of symmetry *cd.*; C the I, 3 "Echinid" plane of symmetry *ef*. (Figures are from Gordon, 1926, *a*, fig. 31 and fig. 23.)

of the **I**, **3** plane of symmetry (* fig. 17, A, B and C indicates the ambulacra to which these ocular plates belong). In the imago of regular urchins, *e.g.*, *Echinus* (Gordon, 1926, *a*, figs. 16, 17 and 19*d*) or of *Arbacia* (fig. 3), the genital plates are symmetrical

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† See footnote on p. 281, Gordon, 1926, *a*.

‡ The symmetry is complete except for the fact that column *a* differs from column *b* in the ambulacrum through which the plane of symmetry passes—*i.e.*, it is as complete as the arrangement of the ambulacral plates in the corona permits. The same is true of the buccal plates; the two enclosed by the broken line differ from each other, the remaining 8 are symmetrical about the II, 4 or the I, 3 plane.

only about the **II**, **4** plane. In the adult regular urchin the inter-ambulacra* are not symmetrical about any plane since LOVÉN found that corresponding plates occur in columns **1***a*, **2***a*, **3***b*, **4***a*, **5***a* and **1***b*, **2***b*, **3***a*, **4***b*, **5***b*. In the imago, however, all the inter-ambulacra are alike (see fig. 3 and GORDON, 1926, *a*, fig. 16) and so do not affect the symmetry in any way.

ÜBISCH† (1913), who also adopts LOVÉN's notation, was the first to realise the importance of the **II**, **4** plane which he named "the primordial plane of symmetry." Moreover, he found that, in the echinopluteus of regular urchins the echinus-rudiment is so placed that the plane passing through areas **II** and **4** is at right angles to the plane of symmetry of the larva. This the writer has found to hold good for *Echinocardium* and *Echinarachnius* also.

The imago of *Echinarachnius* is spherical and, like that of *Echinocardium*, resembles a regular urchin in a number of ways (GORDON, 1926, *b*, p. 272). The presence of a lantern of Aristotle further adds to this resemblance. But fig. 16 shows that, in reality, the bilateral symmetry of the adult about LOVÉN's **III**, **5** plane is quite marked. This obvious bilateral symmetry masks the symmetry about ÜBISCH's primordial plane AB. This latter symmetry is, as far as the ambulacra are concerned, just as perfect as in a regular urchin (fig. 16, B), since the arrangement of the plates is the same. The symmetry about the **III**, **5** plane is therefore more apparent than real, is brought about by a difference in the size and number of the plates in the various ambulacra, and is further emphasised by a marked difference in the size of the sphæridia.

The ocular plates are symmetrical about the plane AB (fig. 16) as also are the genital plates, save that genital **1** is absent. The arrangement of the inter-ambulacral plates is, with the exception of that in area **1**, the same as in the imago of *Echinocardium* (*cf.* fig. 16, with GORDON, 1927, *b*, fig. 2). In area **1** it is reversed‡ and thus the inter-ambulacra are symmetrical about the **II**, **4** plane or about the **III**, **5** plane. The symmetry about the latter is still further emphasised by the increase in (1) size and (2) number of plates in areas **2** and **3**.

In spite of its shape, the test of the imago of a regular urchin is almost bilaterally symmetrical about the primordial plane of symmetry. This is more pronounced in the imago of a primitive form like *Arbacia* (fig. 3, *cf.* GORDON, 1926, *a*, fig. 16) than in that of *Echinus* or of *Strongylocentrotus*—or at any rate it is accentuated by the presence of the latticed rods and of the posterior transverse rod. As the young urchin increases in size the bilateral symmetry becomes less and less apparent, although still present, and the adult seems to be radially symmetrical.

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* The symmetry of the inter-ambulacra in irregularia with reference to LOVÉN's plane of symmetry has been discussed to some extent (GORDON, 1926, *b*, pp. 307–9). In the imago the inter-ambulacra already show the same arrangement of the alternating plates as in the adult (GORDON, 1926, *b*, fig. 2).

† See also ÜBISCH, 1927, in 'Zeitschr. Wiss. Zool.,' vol. 129, No. 4.

‡ See formulæ on p. 309.

The irregular urchins adhere* to the arrangement of the coronal plates inherited from their remote diademoid ancestors, and are thus also bilaterally symmetrical about the primordial plane. But already in the echinopluteus some areas develop more rapidly than the others—in *Echinocardium* the posterior, in *Echinarachnius* the anterior areas are the largest—and the test appears to be bilaterally symmetrical about Lovén's plane. As the imago increases in size this more recently acquired bilateral symmetry becomes so pronounced that the presence of the primordial symmetry is not suspected in the adult.

Hitherto the symmetry of the test alone has been discussed. When the soft parts also are considered, it is evident that the hydropore and the stone canal do not lie in either the primordial or Lovén's plane. These two planes of symmetry intersect each other at an angle of 72° and the hydropore is situated on, or slightly to one side of, the line that bisects this angle. In Irregularia the anus lies in Lovén's plane but in Regularia it is in, or near to, the **I**, **3** " Echinid " plane. Strictly speaking, a regular sea-urchin is neither radially, nor bilaterally, symmetrical. The skeletal anatomy is most nearly symmetrical about the primordial plane. Lovén's law, though not always strictly adhered to (especially as regards arrangement of the inter-ambulacral plates), is important ; Lovén's plane, however, cannot be regarded as a plane of symmetry in the Regularia.

The Early Post-larval Development of the Test.

The post-larval development of the test must be similar in many respects to that of *Echinocardium cordatum* especially as regards the surrounding of the periproct by inter-ambulacrum **5**, the backward migration of the periproct and the compacting of the apical system of plates. In Clypeastroids Lovén (1874, *e.g.*, Plate L) figures a single pentagonal plate pierced by water pores and by four genital pores. The main question demanding solution, therefore, was as follows :—Is this plate the enlarged madreporic plate (genital **2**) only, and if so what has been the fate of the other four genital plates ? Fortunately, the material available was sufficiently advanced to furnish the answer to this question.

The imago at metamorphosis is almost circular in outline, 0·4–0·43 mm. in diameter, and, owing to the fact that it possesses a lantern of Aristotle, is even more like a regular urchin than is the imago of a Spatangoid (Gordon, 1926, *b*, p. 272). Very soon the test becomes ellipsoidal (fig. 18, $l = 0 \cdot 56$ mm., $b = 0 \cdot 44$ mm.). The pentagon having at each of its apices an ocular plate occupies a large proportion of the dorsal surface. In fig. 15 it will be observed that a long, slender branch arises from the right arm of the dorsal arch. This branch is frequently present and in the large madreporic plate (g^2, fig. 18) part of the dorsal arch with just such a branch can easily be distinguished.

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* In some forms the plating in one inter-ambulacrum is reversed, *e.g.*, area 1 in *Echinarachnius*.

The presence of this branch would seem to aid but is not indispensable for the rapid backward growth of the madreporite.

To the left of the madreporic plate in fig. 18 is another plate x; several specimens show this plate which always, as an examination of somewhat younger stages reveals, arises in connection with a remnant of larval spicule. To which part of the larval skeleton this remnant belongs cannot be determined with any degree of certainty, for imagines of *Echinarachnius parma* often have a varying number of spicule remnants in addition to those which should give rise to genital or to ocular plates. To the left of and posterior to x is a remnant of the right postero-dorsal rod (g^3., fig. 18). Its identification is certain for in earlier stages part of the latticed rod is present; it is this spicule which, in *Echinocardium*, gives rise to genital **3**. Posterior to g^3. is genital **4**. In the periproct are three small anal plates (fig. 18, p.); to the left of these is a small remnant of larval spicule which is undergoing resorption. The number of plates in the

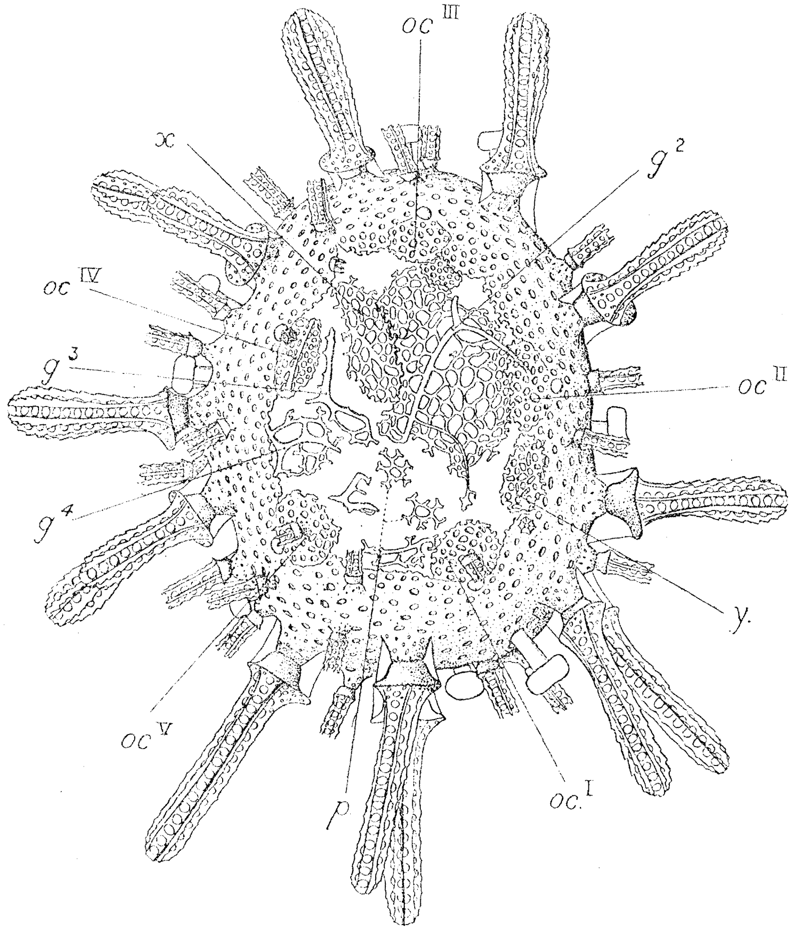

Fig. 18.—Dorsal (aboral) view of an imago of *Echinarachnius parma*. oc^{I}.–oc^{V}., ocular plates; g^2., g^3., g^4., genital plates; p., three anal plates in all probability; x., an additional plate which arises from a fragment of larval spicule; y., is not genital **1**, as a comparison with Gordon, 1926, *b*, fig. 7, g^1., would suggest, but an inter-ambulacral plate belonging to area **1**. Camera-lucida drawing, 1 × 120.

periproct varies at this stage. Some urchins have none, others show one small plate—the usual number—others two and in addition to these there may be several small pieces of larval spicule in process of resorption. The remnants of the right post-oral latticed rod, from which genital **5** should arise, is present only in the very youngest imagines. It never gives rise to a genital plate but is soon resorbed.

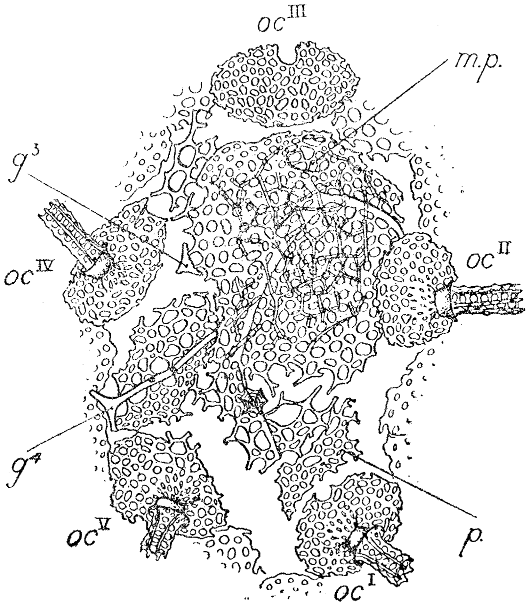

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FIG. 19.—Part of the dorsal (aboral) surface of a young urchin measuring 0·52 mm. in length. oc^{I}.–oc^{V}., ocular plates; g^3., the last remnant of the larval spicule which should have given rise to genital **3**; g^4., genital **4**; *m.p.*, water pore; *p.*, anal plate = ? suranal of *Echinus*. Camera-lucida drawing, 1 × 173.

Fig. 19 represents the plates in the centre of the dorsal aboral surface of a young urchin measuring 0·52 mm. in length. This specimen, although smaller than that represented in fig. 18, is really somewhat more advanced. Genital **4** is now a large plate, there is but one anal plate *p* in the periproct, and the madreporic plate now extends beyond genital **4** posteriorly. This specimen shows the last remnant of the right postero-dorsal rod g^3 which, instead of elaborating to form genital **3**, undergoes complete resorption. If a plate *x* (see fig. 18) is present it certainly cannot be detected as a separate plate. No suture can be made out in the large madreporite and it acts as one unit under crossed nicols. The plate *x* (fig. 18) seems too elaborate to undergo subsequent resorption; if it persists it must be incorporated into the madreporite.

Fig. 20 represents the dorsal surface of a specimen measuring 0·75 mm. in length—the second largest specimen obtained. Each of the ocular plates, with the exception of ocular **III** has now surrounded a small terminal tube-foot. One anal plate is now very large, and to one side of it two small anal plates have appeared. Perhaps this large anal plate may correspond to the sur-anal plate of *Echinus*, for in all the young specimens which are more advanced than that represented in fig. 18, only one anal plate is present, or, as in fig. 20, one anal plate is much larger than the others. In the large central plate no trace of a suture can be detected ; it acts as a single unit under crossed nicols, yet it seems as if it must include, in addition to the large madreporic plate, genital **4** (*cf.* fig. 19) and plate x when present (fig. 18). The available material included all stages between those represented in figs. 18 and 20, yet in no instance did genital **4** seem to be in process of resorption. This is the first evidence of the fusion of separate plates that the writer has met with in the course of her work on the embryology of the skeleton in Echinoidea.

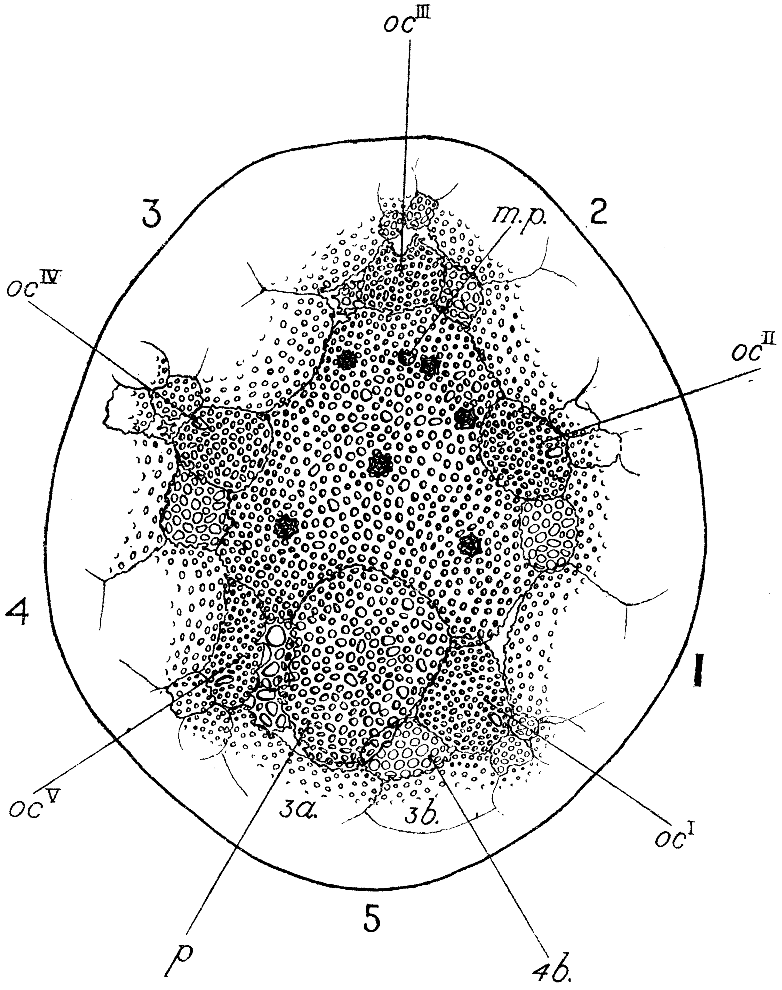

Fig. 20.—Dorsal (aboral) surface of a young urchin measuring 0·75 mm. in length. $oc^{\rm I}$.–$oc^{\rm V}$., ocular plates ; 1–5, inter-ambulacra ; *m.p.*, water pore ; *p.*, large anal plate = ? suranal plate of *Echinus*. Camera-lucida drawing, 1 × 133.

The largest specimen measuring 1 mm. in length is considerably more advanced. The pore in ocular **III** is complete ; oculars **I** and **V** have moved forward and (or) the periproct has receded until the former are opposite the anterior end of the latter (*cf.* fig. 20). There are still only one large and two small anal plates. The central plate occupies a relatively smaller proportion of the dorsal surface. Podial pores are present in the dorsal ambulacral plates in all five areas and the anterior is slightly broader than the posterior end of the test. In a very short time the periproct will be surrounded by the posterior inter-ambulacrum.

Lovén (1874, Plate L., fig. 245) figures a young *Echinarachnius parma* of 6·5 mm. in length. Already many of the characteristic features of the adult are apparent. The periproct, completely surrounded by the posterior inter-ambulacrum, is separated from the relatively small pentagonal central plate by five inter-ambulacral plates in each column. The petals, as yet inconspicuous and narrow, possess double podial pores in both columns ; area **III** is similar to the other four ambulacra in this respect (compare Gordon, 1926, *b*, fig. 14). No genital pores have as yet been formed. Another immature feature is that inter-ambulacral plate 1 is still in contact with plates 2*a* and 2*b* in each area. In the adult (Lovén, 1874, Plate L., fig. 244) plate 1 is separated from the succeeding two plates by the second pair of ambulacral plates.

In Lovén's adult specimen the periproct is surrounded by plates 4*a*, 4*b*, 5*a*, 5*b* of inter-ambulacrum **5**, in his younger specimen by plates 3*a*, 3*b*, 4*a*, 4*b* (Lovén, 1874, Plate L., figs. 244 and 245). Apparently there is some slight variation with regard to these plates. On p. 309 it is stated that, as a rule, the imago of *Echinarachnius parma* has four or five plates in the posterior inter-ambulacrum. Thus, as a rule plate 3*b*, or plates 3*b* and 3*a* are present in the imago. In fig. 20 plate 4*b* separates plate 3*b* from the periproct and doubtless would continue to do so throughout the life of the urchin. At any rate, that holds good for the corresponding plate (5*b*) in *Echinocardium cordatum* (see Gordon, 1926, *b*, figs. 9 and 5). It seems, therefore, that the periproct is, as a rule, enclosed by plates 4*a*, 4*b*, 5*a* and 5*b*. In imagines in which only plates 2*a* and 2*b* of the posterior inter-ambulacrum are present, it is possible that plates 3*b* and 3*a*, the first two plates to appear after metamorphosis, may remain in contact with the periproct. The variation in the position of the periproct may therefore be due to the fact that some imagines are less advanced than others.

When fig. 16, E, of the present paper is compared with Lovén's fig. 245 a striking difference is at once apparent. In fig. 16, E, as already described on p. 309, the anterior is much more advanced than the posterior half of the corona. In Lovén's figure (1874, Plate L., fig. 245) the corona is very regular and the posterior half of the corona is almost as well developed as is the anterior half. The following tables bring this out quite clearly ; inter-ambulacra **1**, **2**, **3** and **4** are now equally well developed,* area **5** still lags somewhat behind ; the five ambulacra are equally well developed. It seems therefore that the corona with large anterior and small posterior areas is characteristic only of the imago and of very small urchins. During development this condition is gradually altered so that in the adult all the ambulacra and all the inter-ambulacra are almost equally well developed (Lovén, 1874, Plate L., fig. 244).

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* These areas agree not only as to number but also as to size of the plates.

TABLE II.

Area	1		2		3		4		5	
Column	*a**	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
No. of Plates	11	11	11	11	11	11	11	11	9	9

* The unpaired inter-ambulacral plate is regarded as belonging to both column *a* and column *b* and is included in each of the numbers.

TABLE III.

Area	I		II		III		IV		V	
Column	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*	*a*	*b*
No. of Plates	18	18	18	17	18	17	18	18	18	18

CONCLUSION.

Although the development of the Clypeastroid *Echinarachnius parma* is in many respects similar to that of the Spatangoid *Echinocardium cordatum*, it nevertheless exhibits some important differences. In the imago of *Echinocardium* (GORDON, 1926, *b*, fig. 2) the posterior inter-ambulacrum possesses four unusually large plates (3*a*, 3*b*, 4*a*, 4*b*). Areas **I**, **1**, **V** and **4** are somewhat more advanced than areas **II**, **2**, **III**, **3**, and **IV** in that they possess 1–3 additional plates, but there is no increase in the size of any of the plates. In *Echinarachnius*, on the other hand, the anterior is more highly developed than the posterior end of the test at metamorphosis. Areas **2** and **3** possess larger and more numerous plates than do the three posterior inter-ambulacral areas. The anterior ambulacrum is most advanced and has the largest individual ambulacral plates. The plates in areas **II** and **IV**, though approximately equal in number to those of area **III** are somewhat smaller in size ; those in areas **I** and **V** are fewer in number and still smaller in size, (fig. 16).

As development proceeds, the difference between the posterior and the anterior half of the test becomes more and more pronounced in the case of *Echinocardium* (GORDON, 1926, *b*, fig. 5). In *Echinarachnius* the reverse is true, and the corona in the adult, when drawn according to LOVÉN's method (LOVÉN, 1874, Plate L., figs. 244 and 245), is very regular although the position of the periproct serves to accentuate LOVÉN's plane of symmetry somewhat.

Echinarachnius agrees with *Echinus* and *Arbacia*, but differs from *Echinocardium* in that oculars **IV** and **V** arise each in connection with a remnant of larval spicule. Genital **5** is not transformed into an anal plate as in *Echinocardium*, but is entirely lost, as are also genitals **1** and **3**. The fusion of genitals **2** and **4** is unusual and is confined apparently to the Clypeastridæ; no evidence for any fusion of plates is at present forthcoming either in the Regularia or in the Spatangoidæ.

Regarding the problem of evolution within the class Echinoidea, some of the facts brought forward in the papers on *Echinocardium* (GORDON, 1926, *b*) and on *Echinarachnius*, particularly those concerning the apical system, are not quite in keeping with the conclusions arrived at from the palæontological approach as to the phylogenetic relations of the Irregularia, especially of the Clypeastroida. These will be discussed below. The writer, having no first-hand knowledge of palæontological data, is not in a position to make any very definite contributions to the problem of the internal evolution of the class, and can only venture to submit a few tentative suggestions as to the possible phylogenetic significance of some of the embryological data.

HAWKINS (1912, *a*, 1912, *b*), in his work on the apical system in the Holectypoida, seems to have made use of two postulates that, in the light of embryological data now at hand, prove to be erroneous. In the first place, it is assumed that genital **5** is entirely absent in Spatangoids. Secondly, it is assumed that the plate in the centre of the apical system of Clypeastroids is derived from the coalescence of all five genital plates (1912, *b*, p. 481). HAWKINS' hypothesis of the evolution of the apical system may be summarised as follows. The apical system became disorganised due to the breaking through of the periproct. "In *Pygaster* sens. str. the first stage of the disruption is still visible. The posterior genital plate is entirely absent, and the remaining four genitals are grouped in a roughly semi-circular order around the anterior edge of the periproct" (p. 478). Evolution within the Holectypoida proceeded along two lines. "In one line (*Pygasteridæ* and *Conulidæ*) the apical system never fully regained, and finally lost, the posterior genital plate" (p. 487). From this line HAWKINS thinks that the type of apical system found, *e.g.*, in *Spatangus* or in *Echinocardium* was derived through some such form as *Anothopygus*, while the elongate apical system of a *Pyrina* or a *Holaster* can readily be derived from that of *e.g. Conulus*. The embryological evidence is not in any respect at variance with this theory, if it is assumed that the fifth genital plate did not disappear but was incorporated into the periproct, and that no attempt was made to replace genital **5** in the apical system.

"In the other line (the Discoidiidæ) the fifth genital plate was early redeveloped and later regained its function while the system as a whole became circular in shape" (p. 487). "It seems probable that this new genital plate is a specialised member of the anal series which has become incorporated into the apical system" (p. 480). In *Discoidea* genital **5** is as large as genitals **1**, **3** or **4** and sometimes has a genital pore (HAWKINS, 1912, *b*, fig. 59 G), sometimes has no pore (BATHER, 1900, fig. XI, 4). In the former figure all the genitals are pierced by water pores, and HAWKINS regards this as "the preliminary stages of the assimilation of the genitals—a phenomenon that is preparatory to their coalescence and fusion in the Clypeastroida" (p. 481).

Two facts tend to support HAWKINS' view that the Clypeastroid apical system evolved from that of, *e.g.*, *Discoidea*, namely, (1) that some Clypeastroids, *e.g.*, *Echinarachnius*, possess four genital pores, while some, *e.g.* *Clypeaster* and *Echinanthus*, have five; (2) genitals **4** and **2** ± plate x do seem to fuse to form the pentagonal plate in the apical system of *Echinarachnius*. But his hypothesis is considerably weakened by the following facts. (1) Genital **5** is absent in the Clypeastroid which has been studied —the spicule from which it should develop is, of course, present since it is essential to the larva throughout its free swimming life, but it is resorbed with surprising rapidity at metamorphosis. This seems to show that genital **5** disappeared early in the phylogenetic sequence. (2) Genitals **1** and **3** have also disappeared. It is unlikely that genital **5**, once lost as HAWKINS postulates, should have been reacquired only to be lost again.

HAWKINS realised that his hypothesis was confronted with some difficulties. He writes (1912, *b*, pp. 470–471), "The greatest difficulty that appears when an attempt is made to trace a phylogenetic sequence from the Holectypoida to the Clypeastroida is the presence in the latter group of a few large ambulacrals in the adoral part of the area, with no signs of plate crushing. Can a compound plate be resolved by evolution into its constituent primaries, or is the simplicity of the Clypeastroid ambulacral only apparent, being in reality the result of the fusion of the components of a compound plate, followed by atrophy of two of the three pore-pairs?" While he does not commit himself to either alternative he says, in support of the latter, that "in Clypeastroids the pore-pair of each large polygonal ambulacral is situated near the adoral margin of the plate, leaving a high non-poriferous region along the rest of the adradial margin." This does not necessarily support the latter alternative, however, for in regular urchins the podial pore, which later becomes a pore-pair, is always situated on the adoral transverse border of the ambulacral plate (GORDON, 1926, *a*, figs. 20, 21 and 22). In the younger stages of *Echinus* there is a considerable non-poriferous zone along the adradial margin in spite of the possibility that there may be ontogenetic acceleration of the triad formation. Rather would it point to a primitive condition suggesting a reversionary tendency in Clypeastroids similar to that which HAWKINS believes to have occurred in the case of *Echinocardium*.

In a later paper HAWKINS (1920, pp. 461–462) again emphasises the close similarity between the apical systems, and the marked dissimilarity between the ambulacra, of the Discoidiidæ and the Clypeastroida. He then proceeds to show how the ambulacra of the Clypeastroida may have evolved along two different lines from the Discoidiidæ, concluding with these words, "the anomalous scattering of the podial pores in the Clypeastroida is ascribed to the destruction of their containing plates by an over development of "plate complexity" and the apparently "Bothriocidaroid" ambulacrals of their adoral surfaces are thus not analogous with the similar plates in other

Irregular groups" (1920, p. 470). As Hawkins predicted (p. 465, 1920), no trace of this supposed destruction of the Discoidiid ambulacral plates is found in the ontogenetic study. As far as the embryological evidence goes, the adoral ambulacral plates may quite easily be analogous with the corresponding plates in *e.g. Echinocardium.*

In a phylum in which such a complete metamorphosis occurs the question arises whether or not the larval structure can throw light on the internal evolution of the group. Within the order Diademoida* of the class Echinoidea there is, on the one hand, the rather complex echinopluteus of *Arbacia* with its six pairs of larval arms and its latticed skeletal rods, on the other hand, the simple echinopluteus of *Psammechinus* or of *Strongylocentrotus* with its four pairs of arms and its simple rods. That there may have been, within the order, a gradual process of simplification is suggested by an examination of the numerous figures of echinoplutei given by Mortensen (1921). Such a process may have occurred in this way: (*a*) gradual reduction of the antero-dorsal arm and rod to the type found, *e.g.*, in the larva of *Echinometra* or of *Lytechinus* (see p. 292, section A) ending ultimately in the complete disappearance of both; (*b*) a gradual shortening of the postero-lateral arm and rod to the type found in the larvæ of the two genera just mentioned, followed by complete disappearance of the posterior transverse rod (*a* and *b* would have occurred simultaneously). Prenant (1926, figs. 3 B, 5 and 9; pp. 533 and 538) found that in *Paracentrotus* and *Psammechinus* there are, at the posterior end of the echinopluteus, mesenchyme cells corresponding to those which are instrumental in forming the posterior transverse rod in the echinopluteus of *Echinocardium.* These cells do not form an independent spicule but the calcite secreted by them goes to enlarge the posterior extremities of the two lateral larval spicules. In *Arbacia* genital **1** arises in connection with the right antero-lateral rod and is one of the first genital plates to appear; in *Echinus* it arises as an independent spicule and appears at a considerably later period. At some point in the series the antero-lateral rod ceased to give rise to genital **1** and the formation of that genital plate was delayed.

The larval skeleton of Echinoidea has not been studied from this aspect and a careful comparative study of many echinoplutei might yield interesting results.

The discovery of a pair of true antero-dorsal arms in the echinoplutens of *Arbacia* reveals the very close similarity between this form and the typical Spatangoid echinopluteus, and is quite in keeping with the theory of the descent of the Spatangoids from some diademoid ancestor. Genital **1** is not formed from the antero-lateral rod in *Echinocardium,* but its appearance is only slightly delayed.

As already stated (p. 292, section A), the echinopluteus of *Echinarachnius* is somewhat more simple than that of the genus *Lytechinus.* Both the antero-dorsal and the postero-lateral rods are absent, but there are distinct antero-dorsal and postero-lateral lobes on the ciliated band. The spicule that seems to correspond to the posterior

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* The classification given by Bather (1900) is here followed.

transverse rod is fused to a small branch from one of the "lateral" latticed rods. Unfortunately no note was made whether or not it arose as an independent spicule, but in all probability it did not.

Perhaps the ancestors of the Clypeastroida did not separate from the diademoid line until a considerably later period than those of the Spatangoids. Two embryological facts seem to be in keeping with such a suggestion. (1) There is in the young *Echinarachnius* a plate which probably corresponds to the suranal plate of *Echinus*. No suranal plate is present in the *Arbaciidæ* but it occurs in the higher Diademoida, especially is it characteristic of the young urchins (GORDON, 1926, *a*, fig. 19). The presence of a so-called suranal plate in the Saleniidæ (BATHER, 1900, p. 306, fig. XIX) seems at first sight to be a serious objection to the statement that the suranal is characteristic of the young forms of the higher Diademoida. But AGASSIZ (1904, pp. 39 and 40) has shown that the so-called suranal plate of *Salenia* is intercalated into the apical system and never becomes part of the anal system proper. Thus this plate is not homologous with the suranal of young Echini. (2) That genital **1** is absent in *Echinarachnius* is in keeping with the tendency for the formation of that genital to be delayed.

On the other hand, there may have been, within the Irregularia, a gradual simplification of the echinopluteus along similar lines, resulting in a loss of the same two pairs of larval arms as in the Diademoida—a case of parallel evolution in the two groups.

C.—LEPTASTERIAS ÆQUALIS, STIMPSON.

INTRODUCTION.

The most complete description of the development of the skeletal elements in an Asteroid is that given by FEWKES (1888) for Asterias. The early developmental stages have also been described in *Asterina gibbosa*, FORBES, by LUDWIG (1882) and in *Solaster endeca*, FORBES, by GEMMILL (1912). FEWKES' account of the development of the skeleton of *Asterias* has been confirmed by the writer. A small culture of *Asterias Forbesii*, DESOR, was started at Woods Hole on June 23, 1927; the adults spawned in the laboratory and the larvæ were remarkably healthy. A number of larvæ were observed in process of fixation on July 19 and four days later the imagines detached themselves from the stalks. The larval development was thus completed in thirty days. GEMMILL (1914, p. 226) found that metamorphosis occurred during the eighth or ninth week in the case of Asterias rubens L.

A number of young stages of *Leptasterias æqualis*, STIMPSON, were obtained through the kindness of Dr. W. K. FISHER, Director of Hopkins Marine Station, Pacific Grove, California. In the genus *Leptasterias* the ova are very yolky and, during the early stages of development, they are attached in clusters to the buccal membrane of the parent. The material was fixed in 70 per cent. alcohol, and, while the spines could be distinguished as short rounded prominences, the calcareous plates could be seen only with difficulty, if at all. Clearing in xylol was sufficient to bring out the calcareous elements in the older stages. For younger stages maceration in a 10 per cent. solution of potassium hydroxide was sometimes used, as it gave better results than clearing.

SHORT DESCRIPTION OF THE LARVA AND OF THE IMAGO.

The larvæ are massed together in clusters somewhat resembling bunches of grapes. Fig. 21 represents the dorsal view of one of the youngest larvæ. Already the aboral primordia of the six arms (**I–VI**, fig. 21) are apparent. Above area **I** and **VI** is a large sucker-like portion (*s.*) which serves as the point of attachment and corresponds to the præoral lobe in the larva of *Asterina* (LUDWIG, 1882, Plate V, fig. 66) or of *Solaster* (GEMMILL, 1912, Plate I, fig. 3). On the ventral surface the first pair of tube-feet has appeared in each of areas **III**, **IV** and **V**.

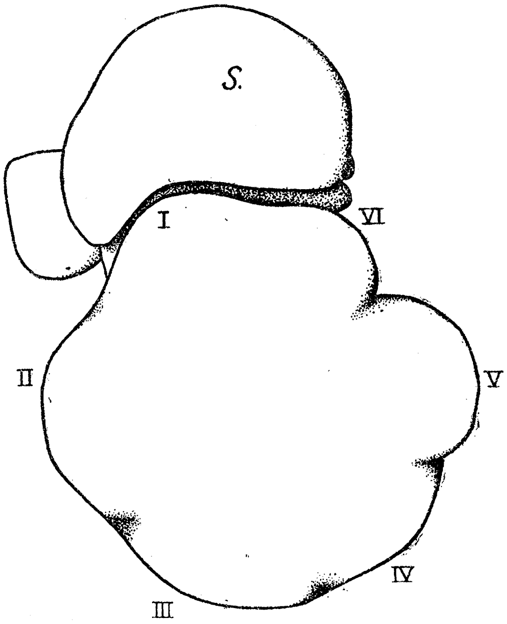

FIG. 21.—Dorsal (aboral) aspect of a young larva of *Leptasterias æqualis*. *s.*, sucker; I–VI, aboral primordia of the six arm. Camera-lucida drawing, 1 × 63.

Fig. 22 represents the ventral (oral) surface of a more advanced larva. The sucker is much less conspicuous and the tube-feet in areas **II–V** are quite prominent. In area **I** the radial water vessel and the tube-feet are considerably smaller and no radial water vessel has as yet been formed in area **VI.** At this stage calcification commences on the dorsal surface.

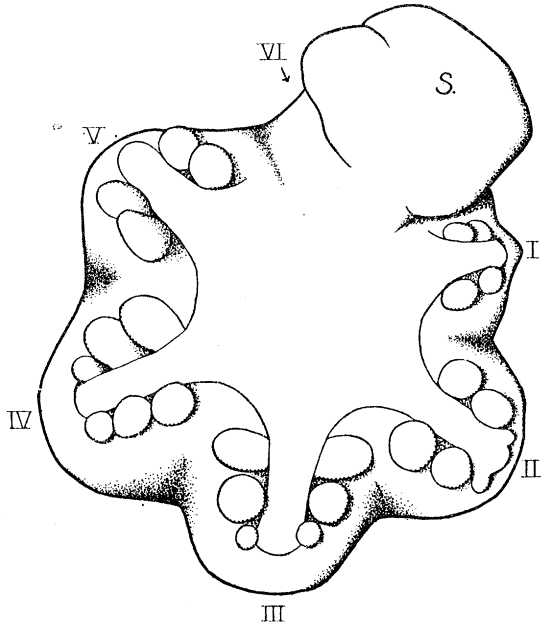

FIG. 22.—Ventral (oral) aspect of an older larva; calcification has just commenced on the dorsal surface. Camera-lucida drawing, 1 × 63.

Fig. 23 represents the ventral aspect of an imago which is about to commence, or has just commenced, an independent existence. The mouth (*m*) is open, the sucker (*s.*) is very much reduced, and the tube-feet, spines and skeletal plates are well formed. The calcareous spines can be seen only faintly through the ectoderm and have been omitted in the diagram. Of the plates on the ventral surface, only the inter-brachial thickened ends of the oral ambulacrals are discernable in the angle between each pair of adjacent arms (fig. 23, *i.br.*). On the dorsal surface the spines only are visible unless the specimen is cleared in xylol.

DEVELOPMENT OF THE CALCAREOUS ELEMENTS.

(A) *On the Dorsal* (*Aboral*) *Surface.*—Once calcification commences the thirteen plates, represented diagrammatically in fig. 24, appear in quick succession. The terminal plates are the first to appear and those belonging to areas **II–V** are slightly in advance of those in areas **I** and **VI**. At the same time as the latter two, or immediately afterwards, some of the genital plates are laid down (fig. 24, g^1., fig. 25, A, *g*). The median plate, the dorso-central (fig. 24, *d.c.*) is formed at the same time as the last two genital plates. This order is not always followed for, in the specimen represented in fig. 22, three of the terminals, one genital and the dorso-central were apparently laid down simultaneously. Thus, in this instance, the dorso-central preceded three of the terminals and five of the genitals.

In the imago (fig. 25, A) twelve spines are associated with each terminal plate. These are arranged in a definite manner thus :—(*a*) four rather large spines situated on the anterior lateral margin* of the terminal and directed slightly towards the ventral surface (these alone have been represented in fig. 25, B, as they are the only ones visible from the ventral surface as a rule) ; (*b*) two median spines the inner one of which is always the last of the terminal spines to be formed ; (*c*) three spines on either side within the large outer set. From fig. 24 it will be seen that these spines appear in the following order :—(1) the four large outer ones, (2) the inner of the lateral group of three followed almost immediately by (3) the outer median one, (4) soon afterwards the remain-

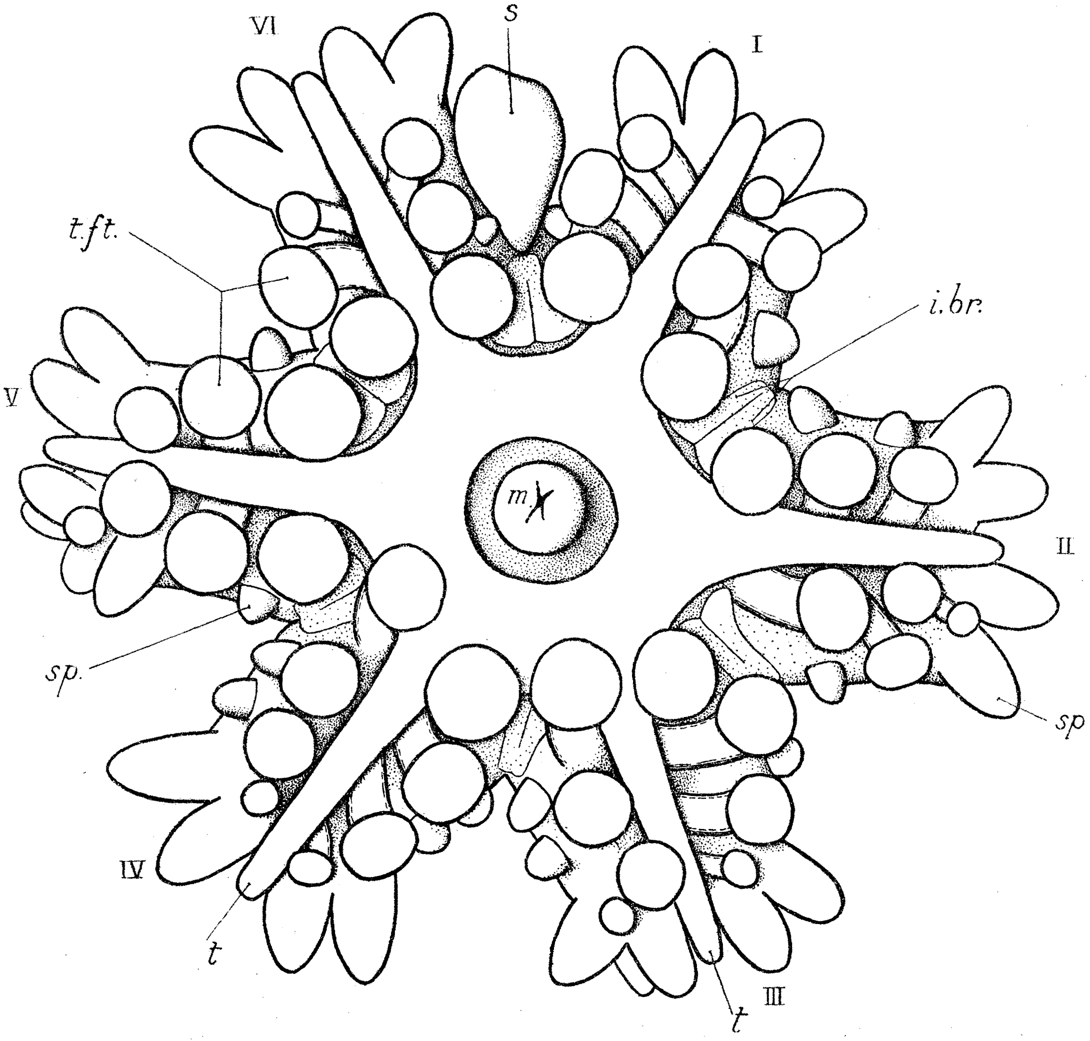

FIG. 23.—Ventral view of an imago. *m.*, mouth ; *sp.*, ectoderm over spine ; *s.*, sucker ; *t.-ft.*, tube-foot ; *t.*, terminal tube-foot ; *i.br.*, inter-brachial expanded ends of the oral ambulacral plates ; I–VI, arms. Camera-lucida drawing, 1 × 100.

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* Fig. 25, A and B, were made from an imago which had been macerated in a 10 per cent. KOH solution and the spines had become separated from the terminal plate.

ing two on either side are formed, and, lastly, towards the end of the larval period, the inner median one.

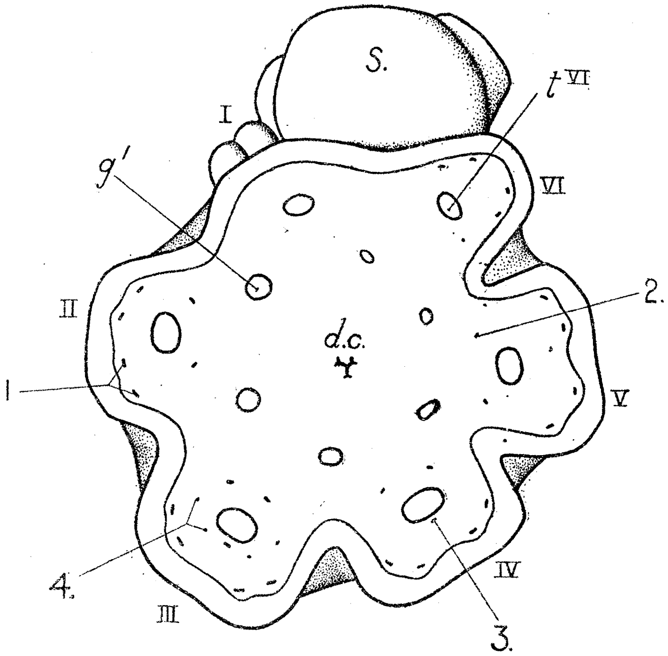

FIG. 24.—Dorsal aspect of a larva, which had been macerated for a short time in a 10 per cent. KOH solution, to show the skeletal elements. *s.*, sucker; *t.*^{VI}, terminal plate of the sixth arm; *g*^{1}., first genital plate; *d.c.*, dorso-central; 1, 2, 3, 4 show the order in which the terminal spines appear. Camera-lucida drawing, 1 × 63.

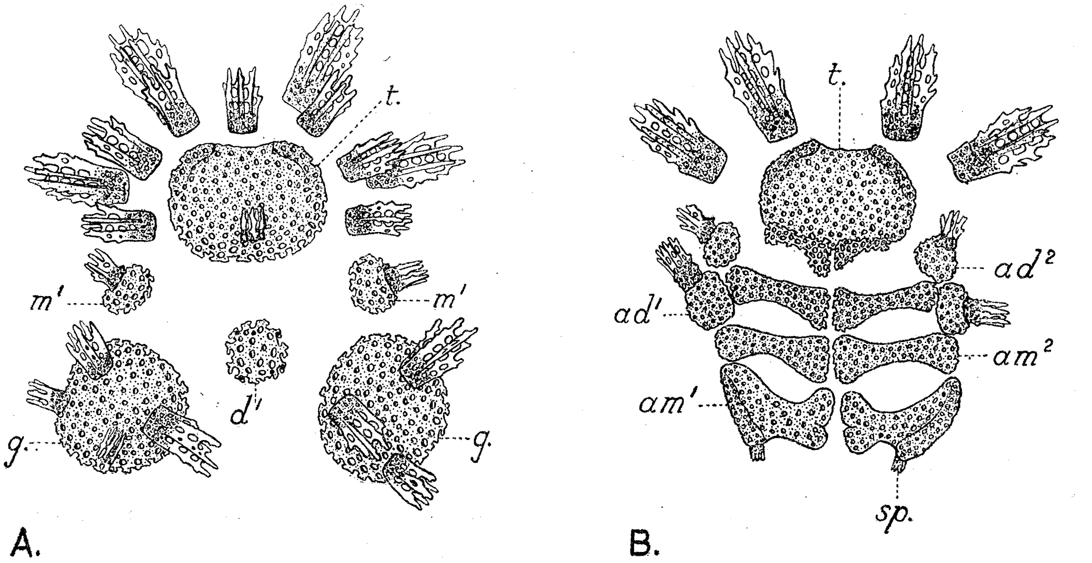

FIG. 25.—A. Plates and spines from the dorsal surface of one arm of an imago together with the two adjacent genital plates. *t.*, terminal plate; *m*^{1}., first marginal; *g.*, genital plate; *d*^{1}., first dorsal plate. B. Plates from the ventral surface of an arm of the same imago together with the terminal plate and four of the terminal spines. *t.*, terminal; *ad*^{1}., first adambulacral plate; *ad*^{2}., second adambulacral; *am*^{2}., second ambulacral plate; *am*^{1}., oral ambulacral plate; *sp.*, "tooth." Camera-lucida drawings, 1 × 100.

As the genital plates increase in size three or four spines are formed above each (fig. 25, A, *g*), and, in the imago, there are also two spines above the dorso-central. Just prior to the formation of the mouth, three small plates make their appearance in the angle between each terminal plate and the two adjacent genital plates. Of these the median plate, known as the first dorsal plate (fig. 25, A, d^1), is slightly in advance of the lateral ones or first marginals (fig. 25, A, m^1). A short spine is formed above each marginal plate.

(B) *On the Ventral* (*Oral*) *Surface.*—In *Asterias* the first pair of ambulacral plates is laid down before any tube-feet have been budded off from the radial water vessel. In *Leptasterias*, on the other hand, areas **II–V** each possess at least three pairs of well-formed tube-feet before the oral ambulacral plates appear. The oral ambulacral plates are laid down on the inner (oral) side of the first pair of tube-feet and are at right angles to the radial water vessel, not parallel to it, as is the case in *Asterias* (see FEWKES, 1888, Plate I, fig. 3, *a.m.*). The second pair of ambulacral plates appears very soon after the oral ambulacrals, and it in turn is succeeded almost immediately by the third pair. In the specimen represented in fig. 24, areas **III**, **IV** and **V** each possessed three pairs of ambulacral plates, of which the third pair was, in each case, very minute; area **II** had two pairs, and areas **I** and **VI** had each only one pair. In the imago (fig. 25, B) the first three pairs of ambulacral plates are well formed and the fourth pair is present in most, if not all, of the areas.

In *Solaster* GEMMILL (1912, p. 41) found that "the first pair of adambulacrals appears in each interradium at much the same time as the second ambulacrals in the adjacent rays" . . . they "are much longer than the others and form the teeth." LUDWIG (1882, Plate VII, fig. 97) also figures an adambulacral ossicle at the outer extremity of an oral ambulacral plate in *Asterina gibbosa*. In *Leptasterias* as in *Asterias* no separate adambulacral plate is formed in the neighbourhood of the oral ambulacral plate. Instead, the outer extremity of each oral ambulacral plate is greatly enlarged and thickened. This inter-brachial thickening bears a very short spine or "tooth" (fig. 25, B, *sp.*). The oral ambulacral plate differs from all the succeeding ambulacrals (*a*) in being more massive, (*b*) in being bifurcated at the inner and expanded at the outer extremity. The first adambulacral plate on each side is laid down at the same time as the third ambulacral plate and bridges the gap between the outer ends of ambulacrals 2 and 3. The second pair of adambulacrals are also present in the imago and each bears a short spine (fig. 25, B, *ad.*^{1}, *ad*^{2}.).

(C) *The Development of a Spine.*—In *Asterina* the spines are simple and develop in a regular though simple fashion (LUDWIG, 1882, Plate VIII, fig. 100); the base is always a regular triradiate which later becomes hexaradiate. In *Leptasterias* it is a curious fact that the part which is first formed is not the true base, but the part marked *x* in fig. 26, *c*. The primordia of four different spines from the same larva are represented in fig. 26 *a* and *b* to give some slight idea of the great irregularity which prevails. The majority are either somewhat irregular six-rayed stars or tri- or tetraradiates. A number of vertical prongs, as a rule six or seven, are sent out from *both sides* (fig. 26, *c*). The prongs on the lower side—*i.e.*, those directed towards the plate to which the spine will later become attached—remain relatively short, are joined by cross bars and elaborate to form the compact basal portion of the spine. The upper prongs grow to a much greater length and are united by cross bars at more or less regular intervals. The spine bears more resemblance to a typical echinoid spine than to the spine of *Asterina*. Fig. 26, *d*, represents a spine from an imago of *Asterias Forbesii*; its development is rather similar to that of the spines in *Asterina*.

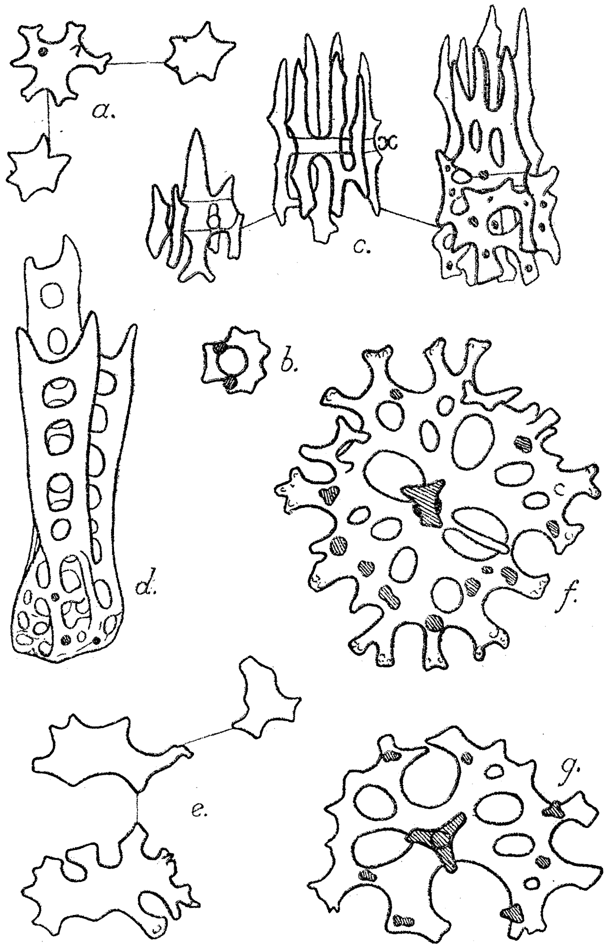

Fig. 26, *a* and *b*.—The primordia of four spines from the same specimen. *c*. Three early stages in the development of a spine. *d*. A spine from an imago of *Asterias Forbesii*. *e*. The primordia of three ambulacral plates. *f*. A developing genital plate. *g*. The dorso-central from the same specimen as *f*. Camera-lucida drawings, 1 × 426.

(D) *Note on the Early Development of the Plates.*—The primordia of the ambulacral plates are irregular scale-like structures instead of the usual regular triradiate spicules (fig. 26, *e*). The plates on the dorsal surface are very compact with but few meshes (fig. 26, *f*, *g*). From the centre of each a short vertical prong arises, and from the distal end of the prong a triradiate is formed in a plane parallel to that of the plate. Many similar prongs are formed around the periphery of the plate and in course of time the branches from these meet to form a much more open meshwork overlying the compact plate.

THE DEVELOPMENT OF THE SKELETON IN *Leptasterias* AND IN *Asterias* CONTRASTED.

The development of the skeleton of *Leptasterias* is essentially similar to that of *Asterias*, especially as regards the order in which the plates appear. The differences are mostly in keeping with the fact that in the latter genus there is a long free-swimming larval period, whereas in the former the ova are yolky and the larval development is greatly modified. The chief differences are as follows :—

(*a*) In *Asterias* the plates are large and very openly meshed in the imago ; in *Leptasterias* the plates are of small size and very compact.

(*b*) In *Asterias* there is a marked tendency for the plates to crowd together and even to overlap in the imago ; in *Leptasterias* the plates are quite separate from each other as a rule.

(*c*) The spines of *Leptasterias* are much more solid than those of *Asterias*.

(*d*) The most marked difference is to be found in the terminal plates. In *Asterias* the terminal is large and prominent, for it protects the sides of the arm as well as the dorsal surface. The adambulacral plates are laid down along the ventral border of the cup-shaped terminal. In *Leptasterias* the terminal is relatively small and is confined to the dorsal surface of the arm.

As regards (*a*), (*b*) and (*d*) the skeleton of *Leptasterias* closely resembles that of *Asterina* (LUDWIG, 1882) in which also the ovum is yolky and the larval development is much modified.

SUMMARY.

A.—*Arbacia punctulata*, GRAY.

A complete analysis of the test in the imago is given. The test is bilaterally symmetrical about ÜBISCH's primordial plane of symmetry.

The post-larval development of the test is essentially similar to that in *Echinus miliaris*. Approximately the same amount of resorption of the peristomial margin of the ambulacrum occurs. The young arbacioid triad consists of an orad primary followed by a diad—*i.e.*, a large primary and a demiplate. The orad primary is later reduced to a demiplate.

The inter-ambulacrum of the imago consists of one row of three plates ; the median one alone is in contact with the buccal membrane. The inter-ambulacrum of the imago is therefore similar to that of the Triassic *Tiarechinus*, except that a transverse suture is absent from the median plate. The young *Arbacia* possesses an inter-ambulacrum similar to that of the adult *Habrocidaris*. The first three plates, together with a small portion of the succeeding pair, are resorbed during development.

B.—*Echinarachnius parma*, LAMK.

A complete analysis of the test in the imago is given. At metamorphosis, the anterior is more advanced than the posterior half of the test and there may be a few more plates on the right than on the left side of the corona. This is a passing phase in the development, for in the adult all five ambulacra are almost equally well developed, as also are the five inter-ambulacra. Genital **1** is absent; the larval spicule which should give rise to genital **5** disappears immediately after metamorphosis, and that which should develop into genital **3** is resorbed at a somewhat later stage. Only genitals **2** and **4** therefore are present, but these seem to fuse at a comparatively early stage to give rise to the pentagonal central plate. Sometimes an additional plate x seems also to enter into the formation of the central plate.

C.—*Leptasterias æqualis*, STIMPSON.

A short description of the larva and of the imago is given. The order in which the calcareous elements appear is similar to that in *Asterias*. *Leptasterias* agrees with *Asterina* and differs from *Asterias* in having smaller, more compact plates, each quite separate from the others, and in having the small terminal plate confined entirely to the dorsal surface of the arm. The spines are more compact and develop in a different way from those of *Asterias*.

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