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The Development of the Calcareous Test of Echinus miliaris

Isabella Gordon

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VII. *The Development of the Calcareous Test of* Echinus miliaris.

By Miss Isabella Gordon, *B.Sc.* (*Kilgour Scholar, Aberdeen University*).

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

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Contents.

Introduction.

This investigation was suggested to the writer by Prof. E. W. MacBride, F.R.S., who kindly provided for study a large number of young imagos and a slightly more advanced urchin. These had been reared by him in the summer of 1924 and preserved in absolute alcohol. All stages from small specimens of about 3 mm. in diameter (including the spines) up to the fully-grown urchin were obtained from Plymouth.

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The material for studying the development of the permanent skeleton in the pluteus could not be procured until the spring of 1925. Then, an abundant supply of material, representing all stages, was obtained from some splendid cultures which Prof. MACBRIDE had succeeded in rearing. So healthy were these cultures that many metamorphosed in 24-26 days into perfectly normal imagos. From the same cultures, the few early stages required to complete the study of the development of the corona were also obtained. It was necessary to rear these stages in the laboratory as they were too young to rely upon material brought up in dredgings.

To Prof. MACBRIDE, F.R.S., the writer is deeply indebted, not only for having made it possible to obtain material, but also for much valuable advice and criticism. Thanks are also due to Dr. H. GRAHAM CANNON for his interest in the work, and for much helpful advice.

PREVIOUS WORK.

Regarding the development of the permanent skeleton in the pluteus of *Echinus*, our knowledge, up to the present, is very fragmentary. In 1889 BURY, working on the pluteus of *E. microtuberculatus*, showed that certain plates which develop immediately over the right enterocœl are genital* plates of the imago, and that the madreporic plate (genital 2) is formed as a meshwork round the median (posterior) arm of the so-called " dorsalbogen." In a later paper (1895, Plate 7, fig. 3) he gives a figure of the plates found in the imago of the same species, but was not able to trace their development. 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 of *Strongylocentrotus lividus* and *Arbacia pustulosa*. He also figures the dorsal, ventral and lateral aspects of the imago of *Strongylocentrotus*, together with the ventral and dorsal views for *Arbacia*, and the dorsal view for *Echinus microtuberculatus*. But in none of these cases does he go into the development of the plates which are laid down in the " echinus-rudiment."

Since the skeleton of the imago is very simple compared with that in the adult, one would naturally suppose that many interesting points would be met with in a study of the growth of the test after metamorphosis. But nothing seems to have been done previously except by LOVÉN (1874), who gives a series of figures illustrating the growth and development of the ambulacral area in " *Toxopneustes* " *drœbachensis*, commencing with that of a young individual measuring 3 mm. in diameter (Plate XVII). From these figures it appears that only a relatively small amount of resorption takes place round the peristome in this species. Two sphæridia are transferred to the peristome from each ambulacral area, one spine boss is resorbed in each row of ambulacral plates, while no tube-feet pores appear to be entirely lost.

The apical region seems to have attracted more attention. LOVÉN (1874, Plate XXI) gives six stages in the development of this region in " *Toxopneustes*," while BURY

* The basals of other writers.

(1895, Plate 8, figs. 36-38) gives three stages for *E. microtuberculatus*. In a later paper Lovén (1892) deals with a number of young echinoid forms, but certain points brought forward in this work of Lovén will be dealt with later on.

In the present paper all the permanent skeletal elements laid down in the Echino pluteus have been traced from the very beginning. The entire development, from the condition found in the imago* to that of the adult, is also described. While the post-larval development in *E. miliaris* agrees well with what Lovén has shown to take place in "*Toxopneustes*," several important points, especially relating to the buccal plates and the buccal tube-feet, are here brought forward for the first time.

Methods.

The development of the calcareous elements in the "echinus-rudiment" has probably remained undescribed for so long, chiefly because of the difficulty of clearing the larvæ. Bury (1895, p. 78) says of these elements, "they are most difficult to study in the pluteus, and I have not yet determined, in spite of much time spent on them, their order of development." The Echinopluteus is, when living, rather transparent, and the developing genital plates can readily be made out. The rudiment, however, is situated more in the interior of the larva, and, especially if the stomach is full of *Nitzschia*, the calcareous elements can only be faintly discerned. When fixed in absolute alcohol, the pluteus becomes much more opaque, and clearing in clove oil gives very poor results. Even when the rudiment is dissected out, and cleared separately, the developing plates, spines, etc., do not show up very well, especially in the more advanced stages and under high magnification. Further, the large amount of pigment present in the pluteus of *E. miliaris* adds to the difficulty.

Since this method, which apparently gave quite good results in the case of *Asterias*, Fewkes (1888) proved inefficient, the following method was employed. The plutei were brought down through the various grades of alcohol to water, and treated for a short time in a very weak solution of NaOH.† The time required varied according to the size of the "echinus-rudiment," but all specimens were carefully watched under a dissecting microscope. Care had to be taken not to allow the maceration to proceed too far, or the calcareous elements became displaced. Even after this treatment, in the larger plutei the plates on the right side sometimes interfered with the examination of the elements in the "echinus-rudiment," and so the latter were dissected out and treated separately.

After maceration, the specimens were transferred to water and gradually brought into a strong solution of glycerin in water (by adding a drop of glycerin to the water every half-hour). They were then mounted in pure glycerin, orientation being carried

* The term "imago" is used to describe the young urchin immediately after the completion of metamorphosis.

† A 4 per cent. solution of sodium hydroxide may be allowed to act over night or even longer in the case of advanced plutei, if the strength be raised to 8% a few hours will suffice.

out under a dissecting microscope. Such preparations were very transparent and the calcareous parts stood out very clearly, especially when examined in artificial light.

This maceration has one great advantage, namely, that a large amount of the pigment present in the ectoderm is removed. Its great disadvantage, of course, is that it is unsuited for histological work. That there is still much of the latter work to be done is admitted, but that is outside the scope of the present paper.

The imagos were mounted entire ; clearing in clove oil gave quite good preparations, but slight maceration in dilute NaOH prior to clearing gave much better results. Many of the imagos in the 1924 cultures had died, and, the tissues having disintegrated, these skeletons were used whenever dissections were required.

Larger specimens were treated in various ways. A graded series of denuded tests was obtained by maceration in NaOH. As the plates of the apical region were apt to loosen, these were carefully removed by means of a pipette on to a slide, washed with water, and brought up through the alcohols to clove oil. This was then drained off and the specimens covered with a drop of clove-oil celloidin.* Under a high-power dissecting microscope the separate plates were then carefully arranged in their proper relative positions, and the celloidin hardened in chloroform vapour for one hour. The hardened block was then trimmed, cleared in xylol to which a trace of phenol had been added, then in xylol, and mounted in Canada balsam.

A graded series of denuded coronas was prepared to give permanent preparations for the study of the ambulacral and inter-ambulacral plates. By gently pressing on any one of these specimens with a fine needle the median suture of one of the inter-ambulacral areas could be made to give way. Then, by gently pulling in opposite directions with two needles, the corona could be divided into two without damaging or dislodging any of the plates. One half was kept entire, the other was transferred to a slide, and four rows of plates (two ambulacral and two inter-ambulacral) were mounted in clove-oil celloidin.

In making permanent preparations of the oral region, as many as possible of the spines in the neighbourhood of the mouth were removed. The test was then gradually cut away, starting from the apical region and working in a series of circles downwards towards the peristome. This was found necessary, because if a single cut was made through the equator the test invariably cracked.

After removing the lantern and remaining parts of the viscera, the specimens were macerated for a short time in dilute NaOH. While this was taking place, as much of the muscle on the inside and as many of the remaining spines and tube-feet as possible were removed without damaging the delicate peristomial membrane. The

* A stock solution of celloidin was made up as follows :—

$$\left.\begin{array}{ll}\text{Celloidin} & \\ \text{Absolute Alcohol} & 3\\ \text{Ether} \quad \ldots & 1\end{array}\right\}\ 3 : \text{Clove Oil } 2.$$

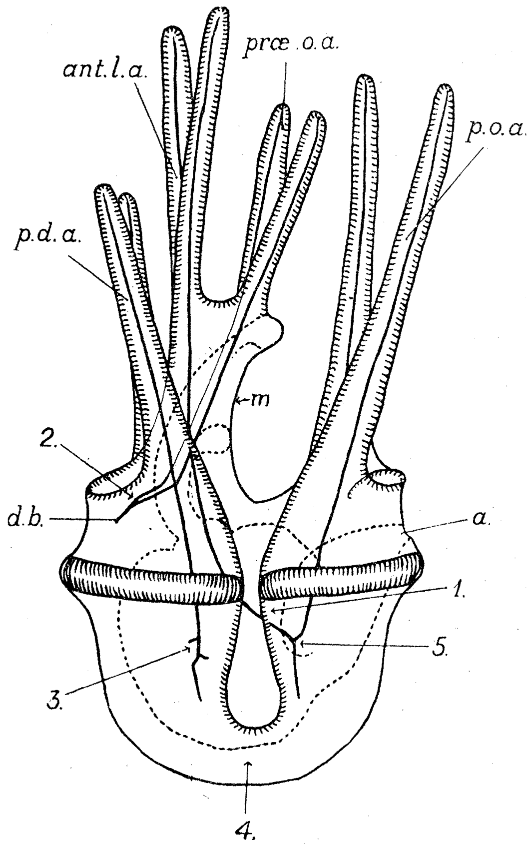
preparations were then transferred to pure glycerin by the method already described and mounted in glycerin jelly. Mounting in this medium gave excellent results, although it proved too drastic for the delicate plutei.

Part I.—Development of the Skeletal Elements laid down in the Pluteus.

In describing the development of the skeletal parts of the imago which are laid down in the Echinopluteus, it is proposed to give (*a*) a general account of the order in which the various parts make their appearance, and (*b*) a more detailed account of the development of the spines, sphæridia, pedicellariæ, tube-foot discs, and the rudiments of the lantern of Aristotle.

(*a*) *The Order in which the various Elements appear.*

When the Echinopluteus has reached approximately the stage figured by MacBride (1899, Plate 33, fig. 4), *i.e.*, when all the eight larval arms have been acquired and the "echinus-rudiment" is small, each arm is supported by a slender calcareous rod or spicule. The two præ-oral arms are supported by a single U-shaped spicule with a short, median, posterior arm (fig. 1, *d.b*). Übisch has named this the "dorsalbogen." The other spicules are in reality longer posteriorly than MacBride has shown in the figure already referred to. The spicule supporting the left antero-lateral arm bends round posteriorly to join that which supports the left post-oral arm, the "echinus-rudiment" being situated in the fork. The posterior end of the postero-dorsal rod is also in contact with the rudiment. On the right side one of the groups of ectoderm cells, which are budded off to form pedicellariæ, is situated above (*i.e.*, exterior to) the post-oral rod, near the point where it is joined by the antero-lateral (fig. 1, 5); the other is immediately above the postero-dorsal rod (fig. 1, 3). Later on part of the calcite is resorbed, with the result that the antero-lateral spicule is separated from the post-oral. The position of these larval spicules has been dealt with here in order to simplify description later on (p. 267).



Text-fig. 1.—Diagram of pluteus viewed from right side, to show larval spicules. *p.d.a.*, postero-dorsal arms; *ant.l.a.*, antero-lateral arms; *præ.o.a.*, præ-oral arms; *p.o.a.*, post-oral arms; *m.*, mouth; *a.*, anus; *d.b.*, "dorsalbogen"; 1, 2, 3, 4, 5, indicate relative positions of the genital plates.

At this stage three small particles of calcite, measuring 1—2μ in diameter, are laid down in the primordium of each pedicellaria (fig. 11, *r.bl.*). Each particle develops into a single blade, but as yet there is no trace of the future axial rod, nor of the genital plate to which it will become attached later on.

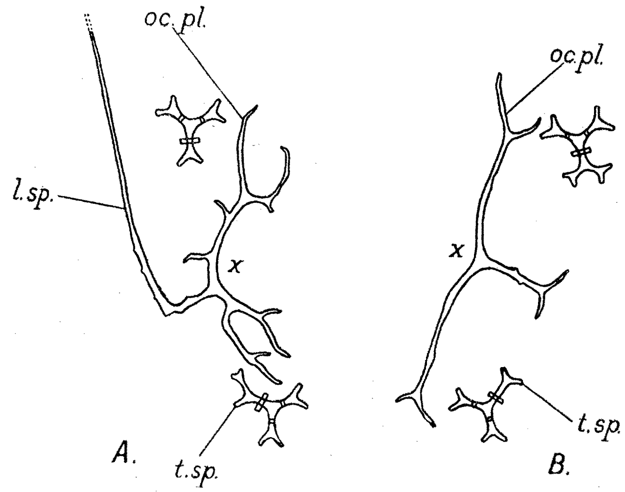
Soon afterwards calcification commences in the " echinus-rudiment." The first plates to make their appearance are the oculars which are laid down external to the developing terminal tube-feet (" primartentakel "). Almost at the same time a single plate is laid down in each inter-ambulacrum ; and shortly afterwards two other inter-ambulacral plates appear, one on either side of and external to the first. As a rule one of these is slightly in advance of the other and, occasionally, that one may be contemporaneous with the first plate. Later still, a fourth plate is developed external to the other three, being situated opposite the first plate and practically on a level with the oculars (fig. 3).

The development of the individual skeletal plates of Echinoderms is already well known, having been described by FEWKES (1888), THÉEL (1892), BURY (1889), and others. The earliest form observed is that of a small spherical granule, and, briefly, this soon becomes triangular and later triradiate. Each ray soon branches dichotomously, and, by repeated branching, an open meshwork results. WOODLAND (1905–6) found that each granule is laid down in the interior of a single cell (scleroblast) and that the young triradiate originates in a " clear pseudopodial clump " formed by the fusion of the ectoplasm of three or more cells.

Of the oculars only three, I, II and III, appear to be laid down in the " echinus-rudiment " as triradiate spicules. The other two, IV and V, arise in connection with the left post-oral and postero-dorsal larval spicules. For some considerable time these two oculars can be distinguished from the other three because of the striking difference in shape which exists between the two types. (Compare fig. 2, A, and 2, B.) Although these two plates originate as branches of larval spicules still, while the branches are elaborating to form the usual meshwork, the posterior portions of the larval spicules in question are undergoing resorption, and, in course of time, their connections with the ocular plates are lost.

While the last formed inter-ambulacral plate is assuming the triradiate form, two small granules appear external to, and slightly more superficial than, each ocular plate. These are the rudiments of the two tetraradiate spines which are present on the oculars at metamorphosis. Soon afterwards the rudiments of the inter-ambulacral spines are laid down, each being situated some little distance above the centre of a developing inter-ambulacral plate. The development of these two types of spines will be described in detail later on.

The calcareous discs of the five terminal tube-feet next appear as small triradiate spicules. When these have reached the stage shown in fig. 12, *b*, the rudiments of the first pair of ambulacral plates are present in each ambulacrum. Of these the series I*a*, II*a*, III*b*, IV*a*, V*b* (which is termed the first series) is laid down slightly in advance of the series I*b*, II*b*, III*a*, IV*b*, V*a*. Soon afterwards the rudiments of the ten large buccal plates make their appearance. These are not, as one might anticipate, ambulacral but inter-ambulacral in position, being situated opposite the two "lateral" rays of the

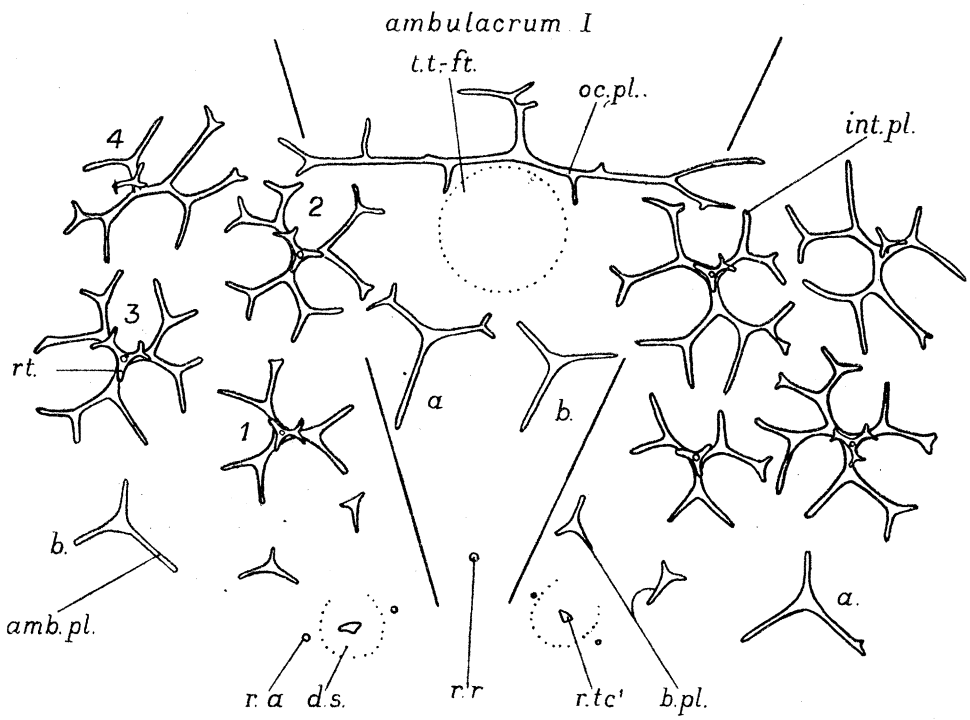


TEXT-FIG. 2.—(A) An early stage in the development of ocular V to show its attachment to a larval spicule (*l.sp.*); *t.sp.*, base of a developing tetraradiate spine—the vertical processes are indicated diagrammatically. (B) Another ocular plate from the same pluteus for comparison with A. All the oculars (I, II and III) which arise as independent triradiate spicules are similar to *B*. X indicates the position of the terminal tube-foot. Camera lucida drawings, 1 × 466. (Original 1 × 700.)

first formed inter-ambulacral plates (fig. 3, *b.pl.*). In most cases these ten rudiments appear simultaneously, though occasionally one rudiment may be slightly in advance of the other in some areas. When this occurs, however, it is irregular and it is impossible to say that one series precedes another.

A careful examination of a large number of slides shows that there is considerable variation in the order in which the various elements appear. The above account may be taken as typical, but an occasional specimen may have, for example, both ambulacral and buccal rudiments present before there is any trace of the discs of the terminal tube-feet. Sometimes, too, the buccal plates appear almost at the same time as the ambulacral series I*b*, II*b*, III*a*, IV*b*, V*a*, while in other cases that series may be present as large, well-formed, triradiate spicules when the buccal plates are just beginning to assume the triangular shape.

When the rudiments of the buccal plates have just become triangular, a single particle of calcite is laid down in each "dental sac"—the rudiment of the first or primordial "cone" of the tooth (see fig. 14, *a*). Shortly afterwards the alveoli appear as two small granules one on either side of the "dental sac" (fig. 3, *r.a.*). About this time also, or in some cases a little later, the rudiments of the rotula and the epiphyses are to be found in each ambulacral area, while in the dental sac the rudiments of the first pair of lamellæ appear, one slightly after the other (see figs. 14, *b*, *c*). Contemporaneously, the primordia of the discs of the ordinary tube-feet appear but only in the case of those belonging to the first series of ambulacral plates (I*a*, II*a*, III*b*, IV*a*, V*b*). Although the second series of plates appears very soon after the first, calcification does not commence in the second series of tube-feet until some considerable time after it has started in the



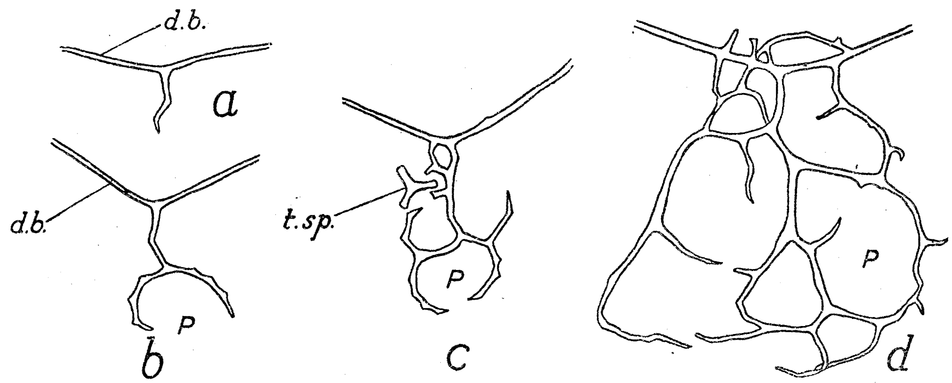
TEXT-FIG. 3.—Developing plates in "echinus-rudiment" soon after calcification commences in the lantern of Aristotle. (All spines have been omitted.) *oc.pl.*, ocular plate; *t.t.ft.*, indicates position of terminal tube-foot; *amb.pl.*, ambulacral plates (also $a + b$); *int.pl.* and 1, 2, 3, 4, inter-ambulacral plates; *r.t.*, an early stage in the formation of a spine boss; *b.pl.*, buccal plates; *r.t.c'.*, rudiment of first cone of tooth; *d.s.*, dental sac; *r.a.*, rudiment of alveolus; *r.r.*, rudiment of rotula. Camera lucida drawing, 1×466.

first series. Indeed, the discs in the case of the first series generally reach stage four in their development (fig. 13, *d*) when the discs of the second series have only reached stage one (fig. 13, *a*).

About the same time as the rudiments of the second series of tube-foot discs appear, the development of the sphæridia commences. With regard to these THÉEL (1892) writes, "It ought to be kept in mind that they do not become visible all simultaneously, but that those of the trivious ambulacra first arise, the frontal portion of the young being thus clearly marked," while the rudiments of the sphæridia rarely appear simultaneously in *E. miliaris* it cannot be said that those of the trivious ambulacra are always the first to appear.

Having thus followed the order in which the calcareous elements are laid down in the "echinus-rudiment," it is necessary to go back and trace the development of the five remaining plates—the genitals. ÜBISCH (1913) has described this for *Strongylocentrotus* *lividus*, but as his description is brief, and these plates, in the case of *E. miliaris*, are much further advanced ere metamorphosis is reached, a detailed account of their development will be given here.

Soon after the three calcareous particles are laid down in each pedicellaria (see p. 275), the small median projection at the posterior end of the "dorsalbogen" begins to lengthen (fig. 4, *a*). In a short time it divides, the two branches growing round, roughly in a circle, towards each other to surround the water pore P (fig. 4, *b*—*d*). Soon another calcareous rudiment appears. When this was first observed as a triradiate spicule (fig. 4, *c*) it was naturally assumed to be the beginning of the madreporic plate. Later stages, however, showed conclusively that it developed into a tetraradiate spine. Meanwhile other branches arise in the down-growing portion of the "dorsalbogen," and, in course of time, a meshwork results which is genital 2 (the madreporite). The madreporic plate thus formed is markedly convex as, after a time, the rather slender branches bend inward especially in the neighbourhood of the water pore.



TEXT-FIG. 4.—*a*–*d*, four early stages in the development of the madreporic plate (genital 2). *d.b.*, posterior portion of the "dorsalbogen"; P., indicates position of the water pore; *t.sp.*, developing base of a tetraradiate spine. Camera lucida drawing, 1 × 466.

At the same time, both the postero-dorsal and the post-oral spicules on the right side of the pluteus begin to send out branches, so that gradually a meshwork is formed below each pedicellaria, these are genitals 3 and 5. While this is taking place a second pedicellaria may be formed, sometimes above one plate, sometimes above both, so that a large percentage of larvæ have three or even four pedicellariæ before metamorphosis is reached. Two tetraradiate spines also develop above each of these plates while, in rare cases, a third may be found on one of them.

When the buccal plates are small triradiate spicules, and the first traces of the lantern are being laid down in the "echinus-rudiment" (see p. 265), a small triradiate spicule is formed slightly anterior to genitals 3 and 5 and somewhat nearer the latter. (Fig. 1, 1.) This is the rudiment of genital 1. Almost immediately another triradiate spicule, a rudiment of a tetraradiate spine appears above genital 1. Soon afterwards another pair of triradiate spicules are laid down near the posterior end of the pluteus also on the right side (fig. 1, 4). These develop into genital 4 and its associated spine. By the time metamorphosis is reached this plate, the last of the genitals to appear, and consequently the smallest, consists of a number of open meshes.

Thus three of the genitals (2, 3 and 5) develop simultaneously and may be said to arise as proliferations of larval spicules. Neither Bury (1889) nor Übisch (1913) mention this in connection with genitals 3 and 5, while the former states that the madreporic plate is formed round the posterior portion of the " dorsalbogen." The figure given by Übisch (*op. cit.*, Plate 6, fig. 3) suggests that genitals 3 and 5 are formed in connection with larval spicules in *Strongylocentrotus* also. This figure likewise shows that, although nearing metamorphosis, the genital plates in *Strongylocentrotus lividus* are far behind those of *E. miliaris* in their development. The posterior process of the " dorsalbogen " is still practically simple, genitals 1 and 4 are merely triradiate spicules, while genitals 3 and 5 are also comparatively small and simple. These differences are all the more striking as the spines on the inter-ambulacral plates, though rather short, suggest that the calcareous elements in the " echinus-rudiment " are well developed.

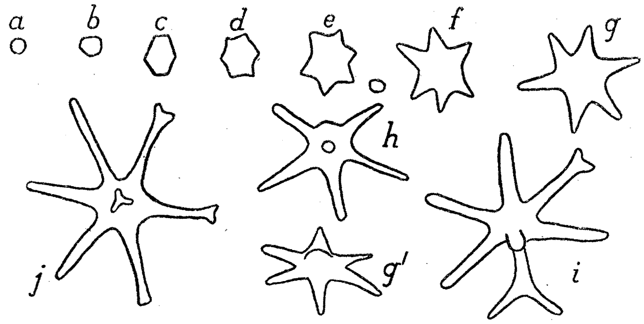
The genital plates of *E. microtuberculatus* figured by Bury (1889, Plate 38, fig. 10) are much more advanced and approach more closely to those of *E. miliaris* in degree of complexity. However, he says that, at the posterior end, a " small calcareous nodule, the remnant of the posterior end of one of the larval skeletal rods . . . . appears to develop later into a plate " (the third basal, *i.e.* genital 4). In *E. miliaris* there is no such nodule, nor has Übisch figured one in *Strongylocentrotus*.

In *Echinocyamus* Théel (1892) found that the plate formed at the posterior end of the " dorsalbogen " also surrounds the water pore and, at metamorphosis, occupies practically the whole dorsal surface of the imago.

(*b*) *More detailed Account of the Development of* :—

1. *The typical echinoid spine and its tubercle.*—Up to the present the development of two types of Echinoderm spines have been described, viz., those of an Asteroid *Asterina gibbosa* Ludwig (1882) and of an Echinoid *Echinocyamus pusillus* Théel (1892). Although two types of spines are present at metamorphosis in the latter, Théel does not mention whether their mode of formation is similar or not. His figure (Plate 9, fig. 107), however, suggests that the short spines are similar to the longer ones, being merely somewhat modified at their extremities. The development of the inter-ambulacral spines in the Echinopluteus of *E. miliaris* closely resembles that described for *Echinocyamus*.

Although the primordia of these spines are laid down a short time after those of the spines on the ocular plates they soon exceed them in size. These rudiments do not appear simultaneously so that all stages from *a*–*j*, fig. 5, may be found in the same Echinopluteus. Théel mentions that the six-rayed star (a form early assumed by the developing rudiment) arises from a small triangular deposit or " tetrahedron " by the division into two of the three angles. The very early stages in the " echinus-rudiment " of *E. miliaris* have been carefully examined under high magnification ($\times$ 1800) and no such triangular stage has been found. The earliest stage observed is that of a small spherical grain measuring 2 μ in diameter. As the granule increases in size, it gradually assumes a hexagonal outline (*see* fig. 5, *a–c*) without first becoming triangular as is usually the case in other skeletal elements. The six angles gradually grow out to form six rays though



TEXT-FIG. 5.—*a–j*, early stages in the formation of the base of a typical echinoid spine, showing the gradual transition from a spherical granule to a hexagon which develops into a six-rayed star. *e* shows an additional granule close to a small star. Camera lucida drawings, 1 × 1200. (Original 1 × 1800.)

occasionally, only five or even four of these rays may develop. LUDWIG (1882) appears to have found a definite small triradiate spicule which he has figured, and also one in which one ray appears to have divided into two. It would seem, therefore, as if the six-rayed star is derived from a triradiate spicule in the case of *Asterina*. In *Echinocyamus*, however, the shape of the granule figured by THÉEL is not very definite, and it is probable that the star is formed, in this genus also, in the manner described and figured here for *E. miliaris*. In any case the primordial granules are by no means regular. The majority approach the spherical shape, and it is possible that THÉEL may have mistaken a stage in the transition from a somewhat spherical granule to a hexagon, for the triangular form generally assumed.

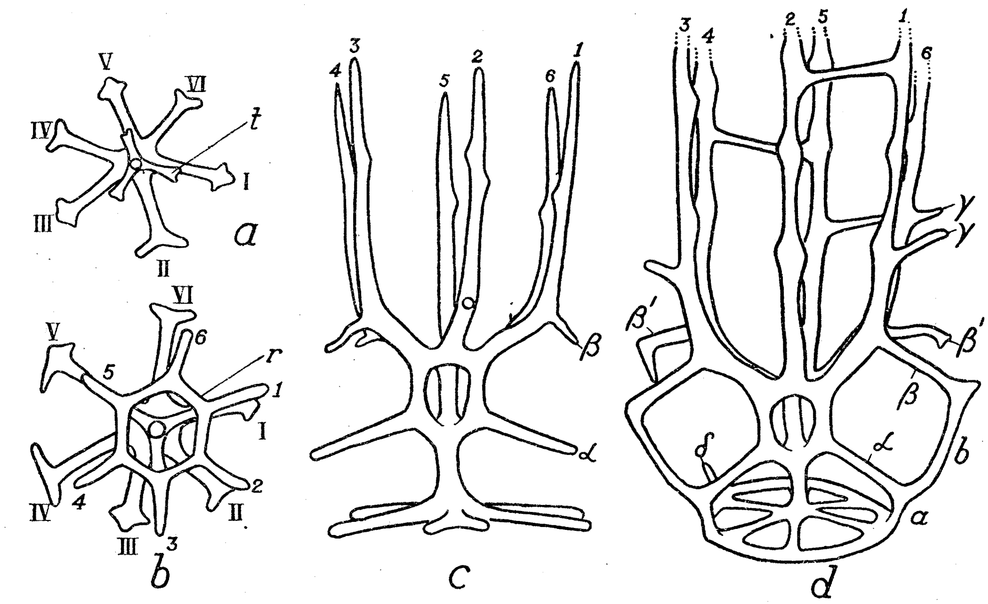
In a number of cases two granules are formed quite close to each other above a single inter-ambulacral plate. One of these fails to increase much in size and, though it occasionally persists for some time (fig. 5, *e*), is probably resorbed. WOODLAND (1905) found that, in the very early pluteus of *E. esculentus*, "isolated granules, rods and (occasionally) triradiates arise independently in other regions of the skeletal area marked out by scleroblasts." He thinks it "probable that these independent deposits largely contribute to the small processes and other irregularities characterising the adult larval skeleton." These granules situated close to the developing inter-ambulacral spines* are practically the only additional particles found in the "echinus-rudiment," and these do not appear to persist. Additional calcareous deposits on the right side of the larva give rise to pedicellariæ or tetraradiate spines.

To continue with the development of the spine, the arms of the star elongate much more than appears to be the case in the developing spines of *Asterina*. In course of time

* Sometimes an additional granule is also found close to the rudiment of a sphæridium.

each divides at its extremity ; the branches grow out to meet those from the two neighbouring rays, and so a complete ring is formed (fig. 6, *a*, *b*, *d*) that constitutes the base of the spine. As shown in the same figure, a third branch arises from the extreme end of rays I, III and V.

Meanwhile a process grows vertically upward from the centre of the star (fig. 5, *g′*, *h*, *i*). Soon this gives rise to three branches (figs. 5, *j*, and 6, *a*) which grow outward and



TEXT-FIG. 6.—Early stages in the development of an inter-ambulacral (typical) spine. *a*, base of spine, a six-rayed star, viewed from above ($d = 20 \cdot 5\mu$), showing a small triradiate immediately above rays I, III, V. *b*, later stage from same aspect showing ring *r*., to which the triradiate *t*., has given rise ; from this ring six processes are sent out, one above each basal ray (*d* of base $= 25\mu$). *c*, a somewhat later stage—lateral aspect (total height, 50μ). *d*, basal portion of a still later stage. Camera lucida drawings, 1×1200.

upward for a short distance and then divide, one branch continuing the upward course, the other α growing outward and slightly downward towards the base (process α, fig. 6, *c*). Then each of the three upward growing processes divides at its extremity into two branches which grow out to meet each other, fusing to form a hexagonal ring in a plane practically parallel to that of the base (fig. 6, *b*, *r*). From this ring six processes (one opposite each ray of the base) grow outward and upward. These soon bend rather sharply upward giving off a down-growing branch β at the angle, and continue to grow rapidly upward sending out, at intervals, lateral processes which fuse to form horizontal bars (fig. 6, *d*). While this is taking place process α grows out till it extends a short distance beyond the base and then it branches, one process growing downward and inward to meet a short process from the rim of the base [the median branch given off by the rays I, III, V] forming the bar *a* (fig. 6, *d*), the other growing outward and upward to fuse ultimately with a down-growing process from β forming the bar *b* (fig. 6, *d*).

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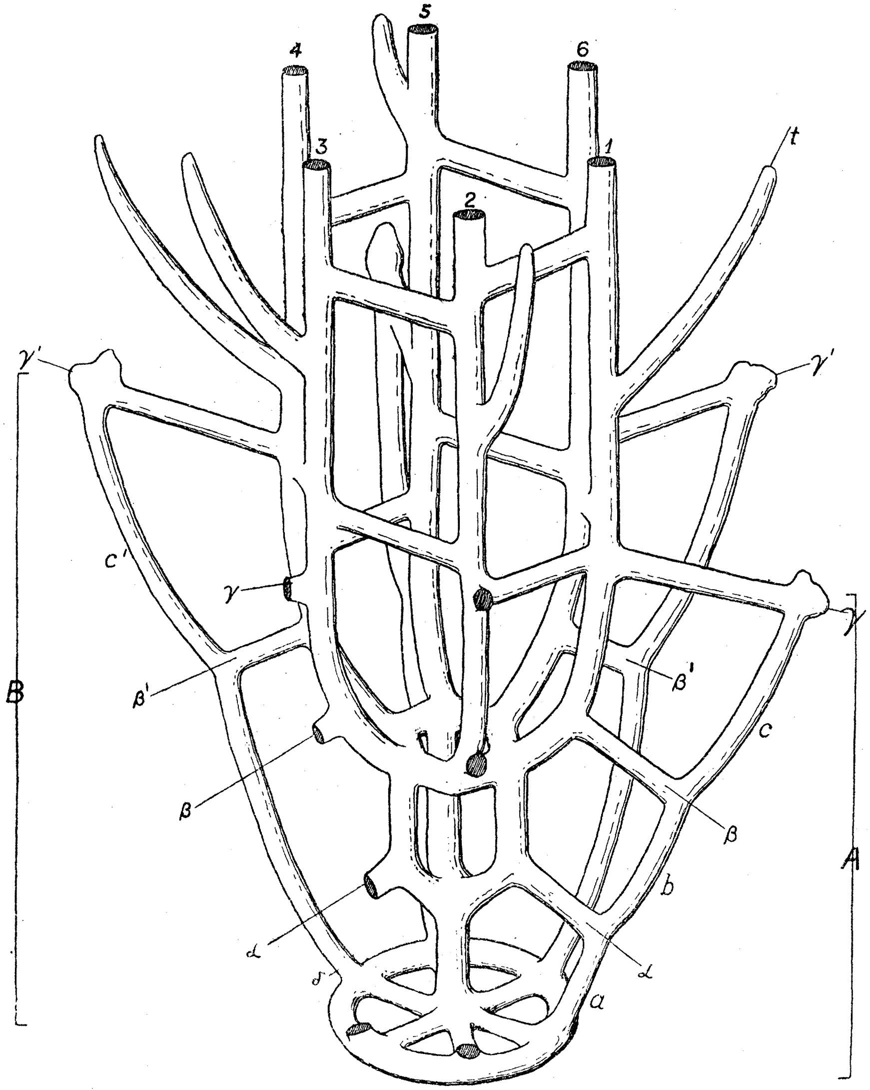
Branches β′ similar to β also grow out from the prongs which are opposite rays II, IV, VI of the base, but as there are in these areas no processes corresponding to α these branches are met by processes δ sent up from the rim of the base (fig. 6, *d*). Each prong soon sends out another lateral branch γ, γ′,* which ultimately send down a branch to meet an



TEXT-FIG. 7.—Drawing of basal portion of a spine in an advanced pluteus to show the structures formed from (A) the processes α, β and γ in series 1, 3, 5; (B) the processes β′, γ′, δ in series 2, 4, 6. (Drawn by Dr. H. GRAHAM CANNON.)

up-growing one from β, β′, forming the bar *c*, *c′* (fig. 7). The result of all this is represented in fig. 7. Thus the foundation of the enlarged basal portion of the spine is laid down.

The rest of the development may be stated very briefly. The spine increases rapidly in length, and, in addition to the cross-bars, short branches are sent out from each prong

* γ being that on prongs 1, 3, 5; γ′ that on prongs 2, 4, 6.

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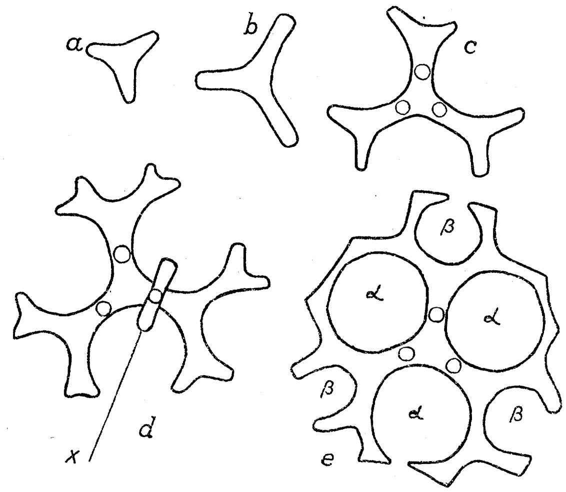
to develop later into the thorny projections along the outer margin (fig. 7, *t*). About the time metamorphosis occurs each of the structures A and B (fig. 7) send out lateral branches so that a meshwork is built up over the foundation to form the expanded basal portion of the spine. The spine itself lengthens considerably after metamorphosis, then the six prongs bend towards each other and fuse, the spine ending in a point of solid calcite.

Meanwhile the tubercle is being formed on the underlying plate. About the time that the rudiments of the ambulacral plates appear, a vertical process grows up from the centre of each inter-ambulacral plate. Later, this process sends out three branches in a plane parallel to that of the developing plate (fig. 3, *r.t.*), and these branch dichotomously. This second triradiate is situated immediately below the developing spine, and is the foundation of the future spine boss. While the branches of this triradiate are elaborating, small processes begin to grow upward from the branches of the plate itself, and these are met by descending processes. Regarding the formation of the tubercle THÉEL (1892, p. 52) merely says that, while the plate is developing, "*arms* also begin to grow in a vertical direction from the central part of the plate in order to raise the tubercle of calcareous network." It would seem, therefore, as if he had been unaware of the fact that the single vertical process which he figures (Plate 7, fig. 97) represents the first stage in the formation of the tubercle.

2. *The Tetraradiate Spine.*—It has long been known that, at metamorphosis, the young urchin (imago) possesses two types of spines, viz.:—tetraradiates which somewhat resemble those of an asteroid and are transient, and typical, permanent ones. As the tetraradiates differ so markedly from the inter-ambulacral spines it would naturally be concluded that their mode of development would also differ.

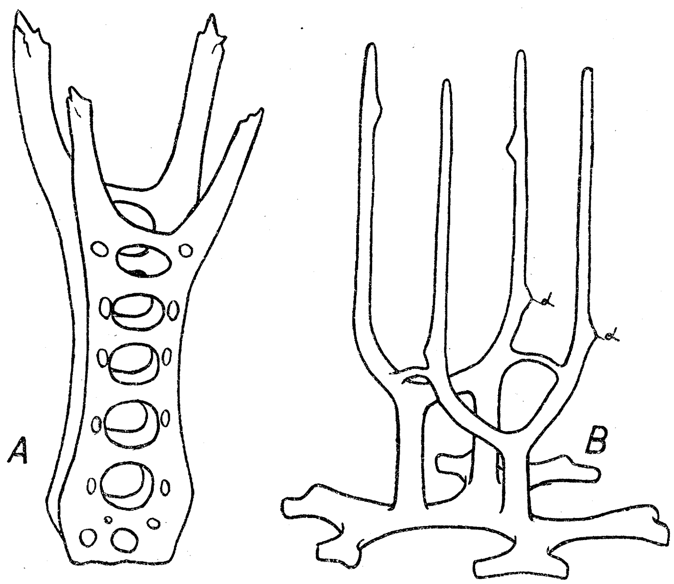
Although, in the development of a tetraradiate, there is a certain amount of resemblance to that of an inter-ambulacral spine, the differences are indeed profound and striking. Instead of a six-rayed star, a typical triangle is formed which then develops into an ordinary triradiate spicule. This elaborates comparatively simply as shown in fig. 8, *a*–*e*, to form the base of the spine. In fig. 8, *e*, the process has almost been completed. The interesting point, however, in the development of the spine is the method by which the tetraradiate symmetry arises from this triradiate. From *each of the three primary rays*, a short distance from the centre of the spicule, a vertical process arises (fig. 8, *d*). Two of these grow straight up for a time, and soon become connected by a horizontal bar (fig. 9, B). Then they bend outward and grow up as prongs similar to those found in the other type of spine. *But the third process soon divides into two.* Each branch forms a prong, and these two, together with the two just described, constitute the four prongs of the spine. They develop in the manner described for the typical spine, only less rapidly, and they also diverge at the top to form the four characteristic prongs from which the spine gets its name (fig. 9, A). Meanwhile a single process α (fig. 9, B) grows down from each prong to meet the base.

No definite tubercle is formed on the ocular and genital plates as the spines are so transient. In a large number of cases only three prongs are formed. Although this suggests that the third vertical process has failed to divide, such is not always the case. In one specimen at least this process gave rise to two prongs, but one of the other simple



TEXT-FIG. 8.—*a–e*, five stages in the development of the base of a tetraradiate spine. When completed all the spaces ααα, βββ are completely enclosed. X indicates the position of the third vertical process which forks to give rise to two prongs (see fig. 9). Camera lucida drawings, 1 × 1200.

processes failed to develop. In another case, after the division of the third process had taken place, one branch remained abortive. Occasionally spines with five or



TEXT-FIG. 9.—(A) Camera lucida drawing of a tetraradiate spine, 1 × 466. (B) Lateral view of an early stage in the development of a tetraradiate spine.

even six prongs occur on some of the genital plates, but no preparations show the early stages of these. Perhaps this result is due to one or both of the simple vertical processes becoming bifurcate.

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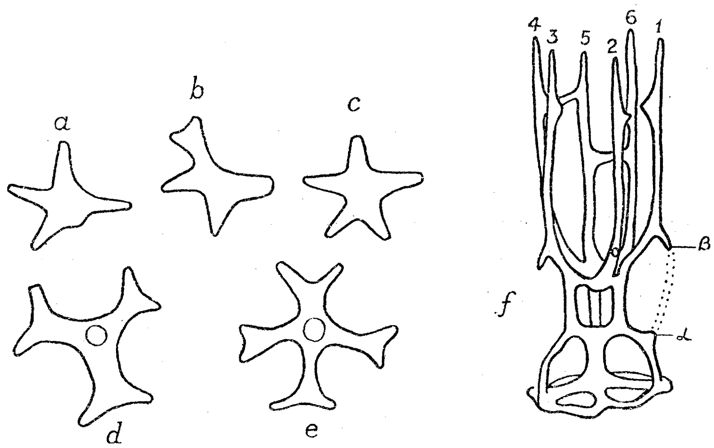
3. *The Sphæridium.*—The fact that each ambulacrum bears, at metamorphosis, a single sphæridium has been overlooked by MacBride (1903) in the case of *E. miliaris*, although he was aware of their presence in *Echinocardium cordatum.* Théel (1892) found five sphæridia of a somewhat different type in the imago of *Echinocyamus* and described their development. Übisch (1913), on the other hand, figures no sphæridia in the imago of *Strongylocentrotus lividus*.

A developing sphæridium looks almost exactly like a miniature inter-ambulacral spine. The basal portion, however, is very irregular in striking contrast to the great regularity exhibited by that of the spine. (Fig. 10, *a–e*, compare with fig. 5.) As a rule only four



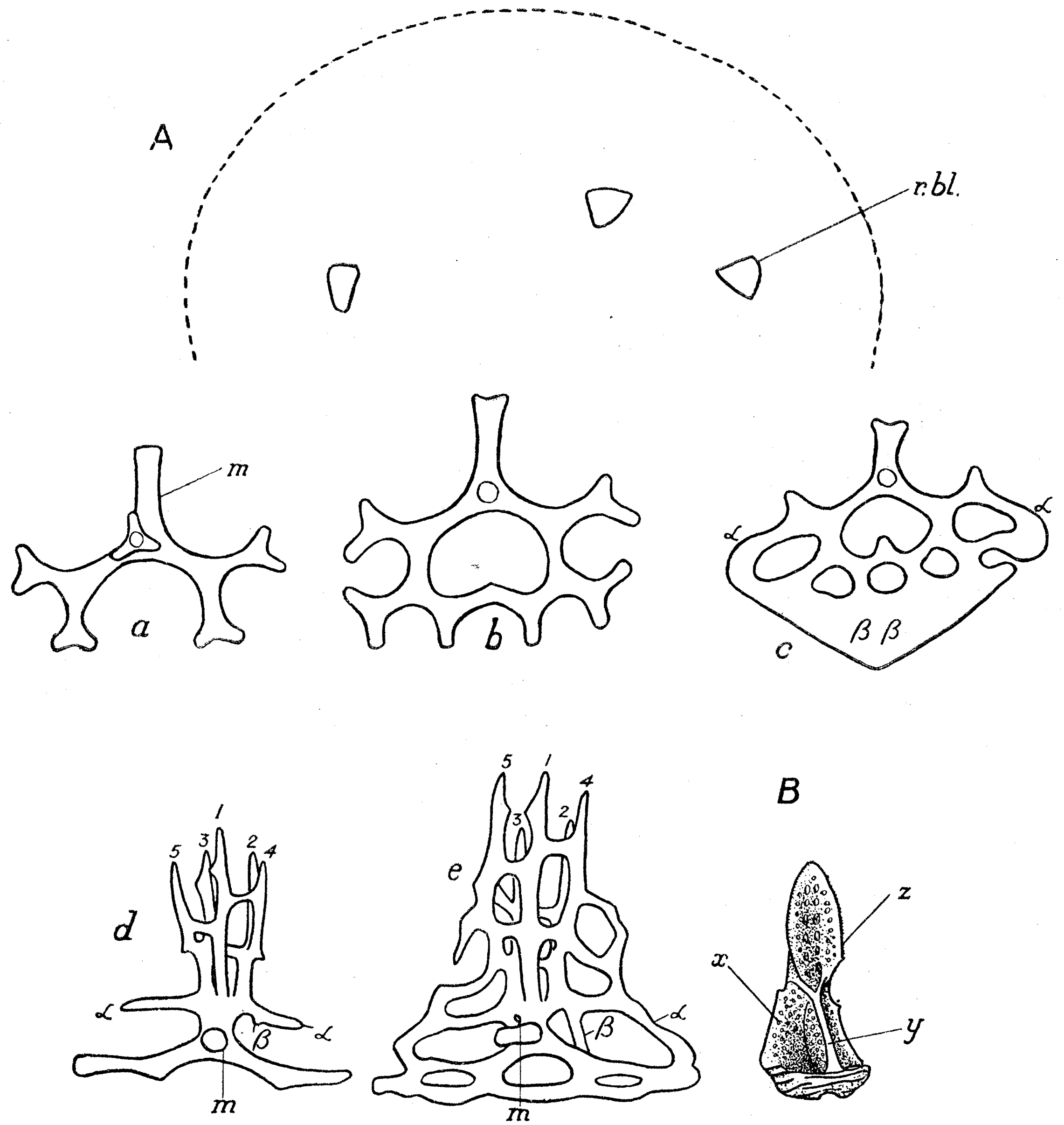
Text-fig. 10.—*a–e*, early stages in the development of a sphæridium, showing the irregularity of the basal portion. Camera lucida drawings, 1 × 1350. *f*, lateral view of a developing sphæridium. Camera lucida drawing, 1 × 1350. (Original 1 × 1800.)

or five rays are developed, although, in rare cases, all six are equally developed or only three may be present. The vertical portion is quite regular except that an occasional one has only five instead of six prongs. These are always short and soon bend inwards to fuse with each other distally. As in the case of the typical spines three processes α (fig. 10, *f*) are sent down to meet the base, but the prongs themselves only send down one other process β, β′. In series 1, 3, 5 this process (β) is met by an up-growth from α, while β′, in the series 2, 4, 6, is met by an up-growth from the base. These structures form the foundation of the stalk of the sphæridium and soon send out a few lateral branches to meet with those from neighbouring ones.

In *Echinocyamus* [Théel (1892, Plate 9, fig. 110)] the base appears to be quite regular, as no departure from the six-rayed star is mentioned. The single vertical process soon divides into three branches, which grow upward as three curved rods, which soon bend inwards and unite. The tip of each, moreover, swells considerably, so that three spherical bodies "closely united and with a minute hole in the middle" are formed. Meanwhile only one process grows down from each rod to unite with the base.

4. *The Pedicellaria.*—In the early pluteus, soon after the primordia of the pedicellariæ

have been budded off from the ectoderm, three calcareous rudiments are laid down in each. Fig. 11, A, shows these rudiments at the stage when they become triangular.



TEXT-FIG. 11.—(A) *r.bl.*, rudiments of the three blades laid down in a single pedicellaria. *a–c*, three stages in the development of the base of a single blade; *m.*, the "median" ray, never divides; α and β indicate the points where the down-growing processes α and β (fig. 11, *d*, *e*) meet the base; *d*, *e*, lateral aspect of two early stages in the development of a blade. Camera lucida drawings, 1 × 1350. (B) A diagram of a fully-formed blade (after MORTENSEN).

Each develops into a triradiate spicule, and two rays, which may be called "lateral," branch dichotomously, and by repeated branching form the somewhat curved base of a single blade (fig. 11, *a-c*). The "median" ray (*m*) fails to develop after a time. While

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this is taking place a single vertical process arises from the centre of the triradiate spicule and soon gives rise to three short branches, one opposite each ray of the original triradiate (fig. 11, *a*). Branch 1 (fig. 11, *d*), that immediately above the abortive " median " ray of the base, grows continuously upward, giving off lateral branches at intervals. Branches 2 and 3 each send out a lateral branch α, which grows outward and downward to fuse with the base. Close to its point of origin α sends down another branch β (fig. 11, *d* and *e*), which ultimately fuses with the base near the margin and practically *opposite* the stunted basal ray *m* (β, fig. 11, *c*).

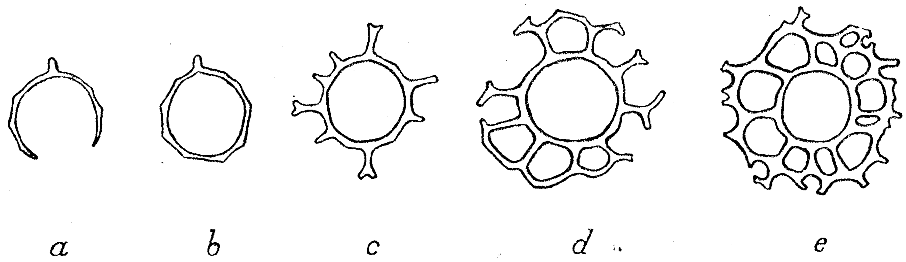
Meanwhile branches 2 and 3 continue their upward course, each soon sending off another vertical branch 4 and 5. These latter continue to grow parallel to branch 1, but do not lie quite in the same plane as 1, being somewhat nearer to that of branches 2 and 3. They soon become connected to 1 by a number of transverse bars, and each also sends out a number of lateral processes (fig. 11, *e*), which grow down to join α and ultimately form the wings marked *x* in the fully formed blade (fig. 11, B). Branches 2 and 3 also become connected by a few horizontal bars to each other and to 4 and 5. But they soon become lost in a number of branches; some of these join branches 4 and 5, others grow outward and downward to meet up-growths from β and so, in course of time, form the median portion *y* of the blade. The remaining branches 4, 1, 5 continue to grow upward for some time and, in addition to the transverse processes connecting these, outgrowths arise from the lateral edges of branches 4 and 5. By further division of these the upper portion of the blade (*z*) is formed. A short process is also sent down from branch 1, near its point of origin, to meet the short " median " basal ray.

As the blades elongate the bud itself becomes trifid, and the axial rod is laid down a short distance below the developing blades. In the pedicellariæ formed in the Echinopluteus this rod is but poorly developed and they are almost sessile. All the pedicellariæ formed in the pluteus are ophiocephalous, and, when fully formed, the margin of *z* in each blade consists of a rather broad band of solid calcite beset with numerous minute teeth. The " ring " on the base of one of the blades with which the other blades articulate is formed by a secondary down-growth of solid calcite.

Since the three other types of pedicellariæ which occur on the test of *Echinus* do not develop until after metamorphosis, it is difficult to detect the very early stages of these. An examination of the numerous figures of pedicellariæ given by MORTENSEN (1913, Taf. 4 and 5) shows that, however modified the blades may be, there is a certain fundamental structure which is common to all. It may be that in the various types the development is similar to that of the ophiocephalous type, but with more or less modification.

5. *The Disc of a Terminal Tube-foot* (" *Primartentakel* ").—In the somewhat expanded portion towards the tip of each terminal tube-foot, one small triradiate spicule is laid down. Two of the rays grow rapidly round towards each other, the ends fusing to form a complete circle (fig. 12, *a b*). The notches which occur at intervals on the outer

edge of each rapidly growing ray suggest that this circular form is the result of repeated attempts at division, one branch always growing much more rapidly than the other. While the circle is being formed the growth of the "median" (third) ray is retarded, but, once the circle is completed, this ray elongates and soon branches dichotomously at

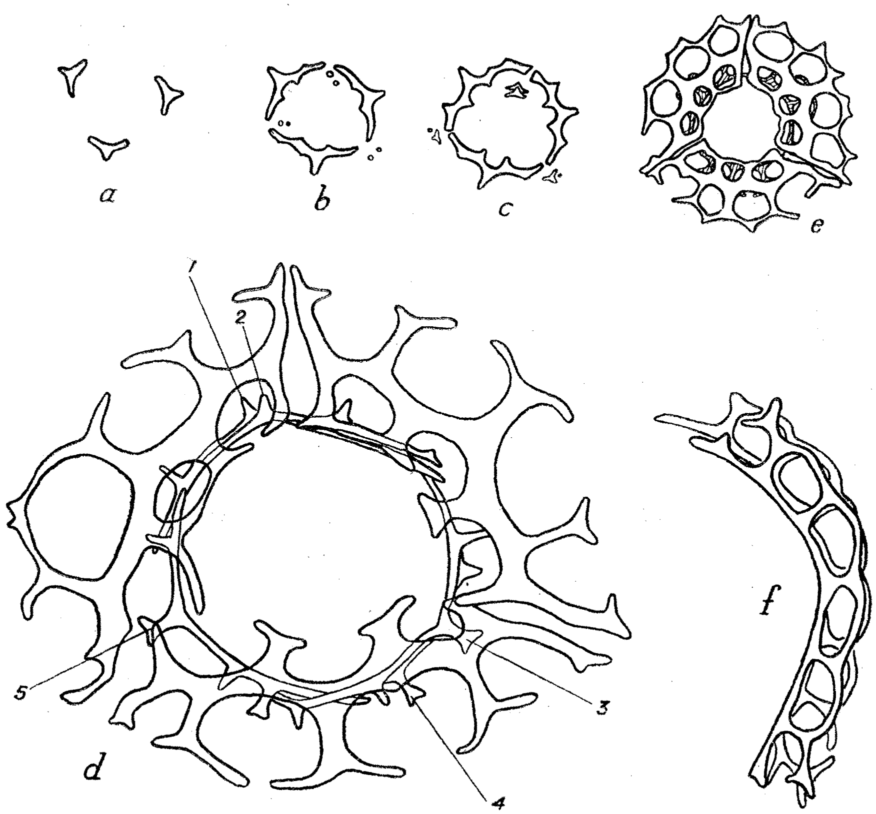


TEXT-FIG. 12.—*a–e* stages in the formation of the disc of a primary tube-foot. Camera lucida drawings 1 × 525. (Original 1 × 700.)

the end. At the same time, the notches already referred to give rise to similar rays, which also divide (fig. 12, *c*). These branches soon meet and, in course of time, a disc similar to that shown in fig. 12, *e*, results.

6. *The Disc of an Ordinary Tube-foot.*—Mention has already been made of the fact that a pair of tube-feet is present in each ambulacral area in the imago of *E. miliaris*. In the terminal portion of each tube-foot three separate rudiments are laid down. The two "lateral" rays in each triradiate develop more rapidly than the "median" one, giving off branches which elaborate until, in the late pluteus, the condition shown in fig. 13, *e*, is reached. Meanwhile a number of calcareous granules appear at a somewhat lower level than, and alternating with, the original three triradiates (fig. 13, *b*). Six additional elements, in all, are present, but, in some cases, all six are formed almost simultaneously, in others only three or four appear at first, and, when these have developed into small triradiate spicules, the remaining three or two are laid down (fig. 13, *c*). Each of these rudiments develops into a slender triradiate spicule (fig. 13, *d*), the two "lateral" arms of which grow rapidly, sending off branches at intervals on the outer edge only. Each branch soon divides again and, in course of time, the structure shown in fig. 13, *f*, results.

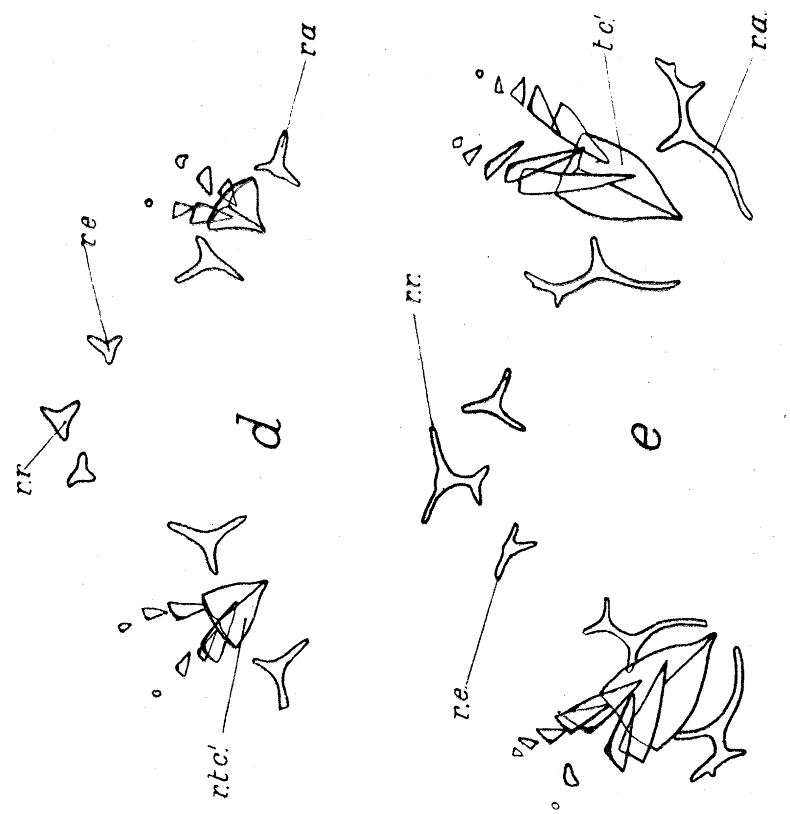
Thus, below the compound disc formed from the three primary rudiments there are, at metamorphosis, six of these structures in two sets of three, one slightly above the other (fig. 13, *f*, shows two of these). The free ends of these elements are situated practically opposite the centres of the three primary elements of the disc, and, at metamorphosis, there is just a hint that the branches at these points grow slightly further out than the rest of the structures. As the imago grows the discs enlarge and become more compact, the six secondary structures appear to fuse together to form a somewhat hexagonal ring (beneath the three primary pieces) from which three short processes are sent out below the central portion of each primary component.

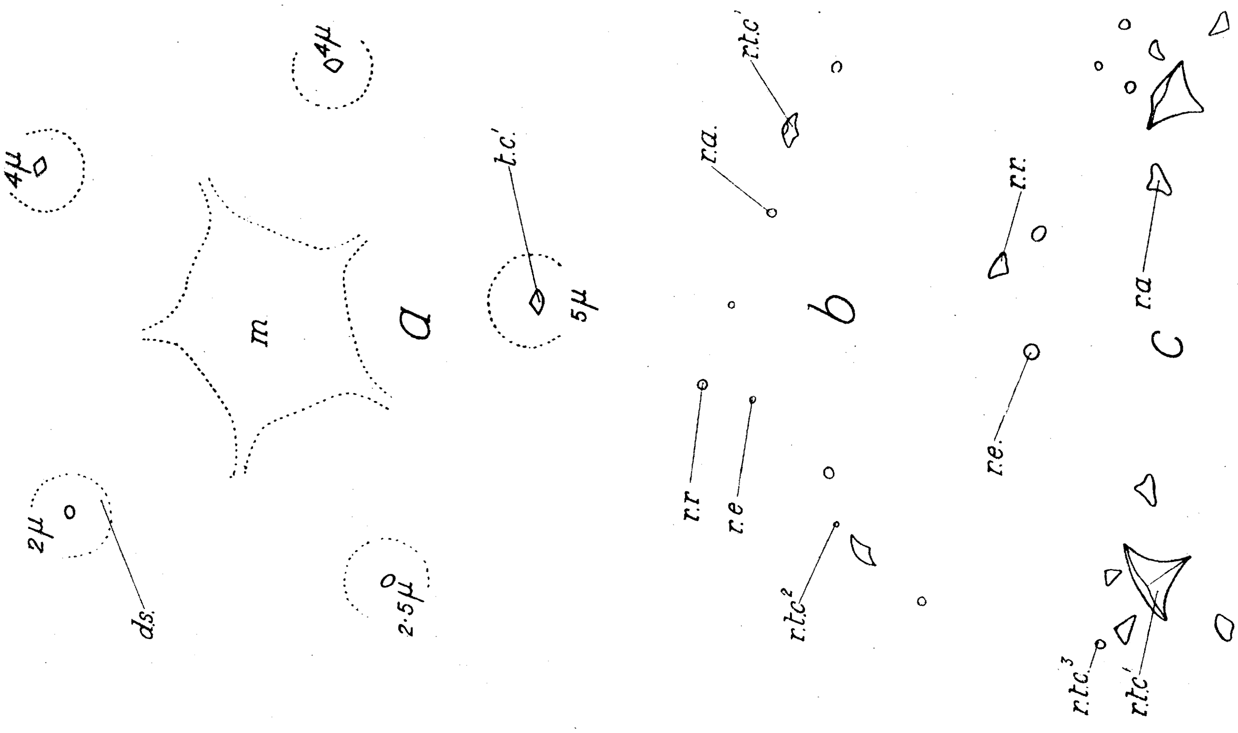


TEXT-FIG. 13.—*a–e* stages in the formation of the disc of an ordinary tube-foot. *a, b, c, e.* 1 × 525. *d* shows 5 of the 6 secondary elements 1–5. 1 × 1350. *f* shows two of the structures which arise from the secondary elements. 1 × 1350. Camera lucida drawings.

7. *The Early Stages in the Development of the Lantern.*—The development of the lantern of Aristotle has been worked out by DEVANESEN (1922), but, as he commenced with plutei about to metamorphose, it is necessary to describe here the earlier stages in order that the account may be complete. The earliest stage found shows, in three of the five "dental sacs" (those in inter-radii 1, 3, 5), a single particle of calcite measuring about 1 μ in diameter, the other two have not yet appeared. This, the rudiment of the first "cone" of the tooth, is laid down very soon after the rudiments of the ten buccal plates. The granule soon assumes a somewhat triangular outline, the apex being directed towards the oral region while the base is slightly convex (fig. 14, *a* and *b*). The apex lengthens rapidly while a ridge is formed across the base (fig. 14, *c*), and soon a keel is also formed stretching from the centre of the basal ridge to the apex. Thus, as THÉEL (1892) found to be the case in *Echinocyamus*, the first "cone" gradually assumes the shape of an "isosceles triangle," the inwardly directed surface of which is concave (fig. 14, *e*).

While this is taking place the rudiments of the alveoli (*r.a.*) next appear, one on either side of the "dental sac," together with the rudiments of the rotulæ (*r.r.*) and the epiphyses (*r.e.*) which are situated radially (ambulacrally) and more in the interior of the "echinus-





TEXT-FIG. 14.—*a–e* early stages in the development of the lantern of Aristotle. *d.s.*, dental sac; *r.a.*, rudiment of alveolus; *r.e.*, rudiment of epiphyses; *r.r.*, rudiment of rotula; *r.t.c*¹., rudiment of first cone of tooth; *r.t.c*²., one rudiment of second cone; *r.t.c*³., one rudiment of third cone. Camera lucida drawings *a–c* 1 × 700. (Original 1 × 1400.) *d–e* 1 × 448. (Original 1 × 560.)

rudiment." The order in which these granules appear varies somewhat even in the same larva. Sometimes those of the alveoli and the rotula are laid down simultaneously to be followed slightly later by those of the epiphyses (figs. 3 and 14, *b*). In some cases the rotula and the epiphyses appear simultaneously soon after the alveoli, while, in rare cases, the epiphyses precede the rotula. All these elements pass through the usual triradiate form. Meanwhile in the "dental sac" the secondary "cones" of the tooth are laid down one after the other. These differ from the first or primordial "cone" in having a double origin, *i.e.*, in arising from two separate rudiments, one of which is, as a rule, slightly in advance of the other (fig. 14, *b*-*e*). These rudiments develop into lamellæ.

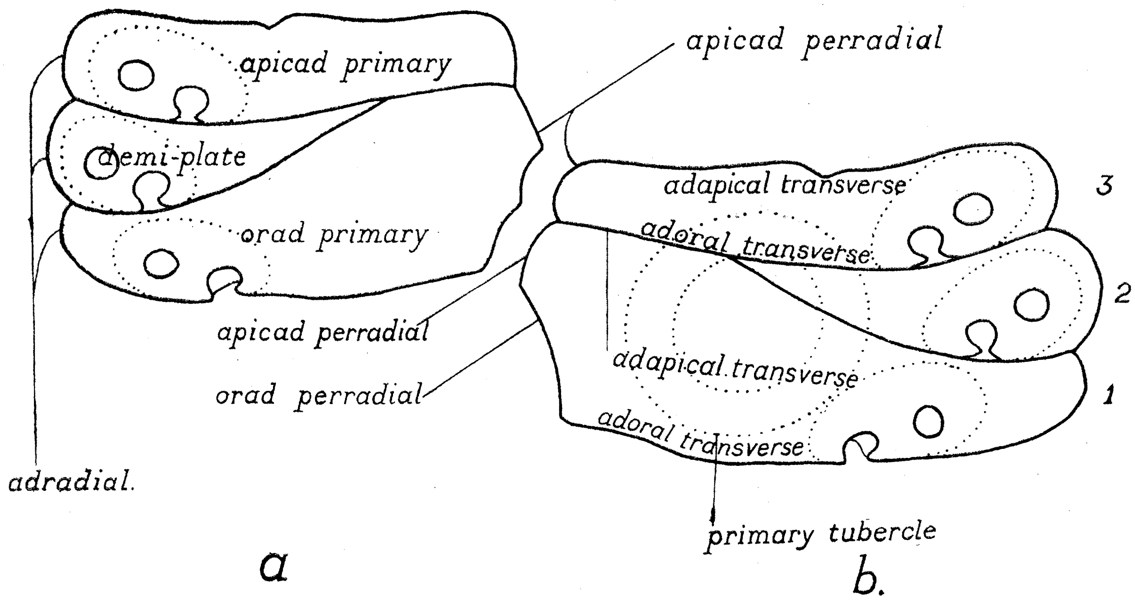
Since DEVANESEN (1922) started with a comparatively late stage, he was naturally unaware of the fact that, in *E. miliaris*, the first "cone" differs from all succeeding ones in having a simple origin. As all subsequent ones are formed from a pair of lamellæ, he writes, "one may therefore reasonably infer that each of these five (primordial) cones also arises in the same way from a pair of lamellæ," and these he termed the "pair of primordial lamellæ." The larger lamella of the second "cone" almost equals the first "cone" in length in advanced Echinoplutei (see fig. 14, *e*, also Plate 11, fig. 1 given by DEVANESEN). This, together with the fact that the two lamellæ of "cone" 2 are still far from fusing might have suggested that the first "cone" is either simple from the beginning, or, if double, the lamellæ must fuse very early. Besides this, he cites THÉEL'S paper (1892), and he must have been aware of the fact that THÉEL describes the first "cone" in the tooth of *Echinocyamus* as arising from a single "tetrahedron."

PART II.—THE POST LARVAL DEVELOPMENT OF THE TEST.

The test of *Echinus* may conveniently be divided into three parts: (*a*) the apical system of plates, consisting of the periproct plates and the genitals with which the oculars may be grouped, although really belonging to the corona; (*b*) the corona, and (*c*) the plates in the buccal membrane or peristome.

In an adult *E. miliaris* the apical system occupies only a relatively small area in the centre of the dorsal surface. The periproct is covered with numerous small plates, one of which is somewhat larger than the others [this plate is variously known as the "central-plate" (LOVÉN), the "dorso-central" (BURY) and the "sur-anal" (MORTENSEN)]. The anus is slightly excentric.

The corona consists of ten longitudinal meridians, five radial or ambulacral areas characterized by the presence of tube-feet, and five inter-radial or inter-ambulacral areas. Each meridian consists of two columns of alternating plates, those in the inter-ambulacra being simple, those in the ambulacra compound plates known as "Echinoid" triads. In the present paper LOVÉNS' system of numbering the elements of the corona is used; the five ambulacral areas are denominated thus I, II, III, IV, V, the inter-ambulacral areas thus 1, 2, 3, 4, 5, while the two columns in each area are marked *a* and b*; the triads are numbered A, B, C, D, E† . . . while for the individual plates and the pores for the tube-feet smaller numbers are used, thus 1, 2, 3, 4, 5, . . . The genital plates are numbered in the same way as the inter-ambulacra, the oculars in the same way as the ambulacra. The nomenclature of the plates (and their sutures) of a triad is summarized in the following diagram. The perignathic girdle, which also belongs to the corona, is of the continuous type.



TEXT-FIG. 15.—Diagram to show terminology of the sutures and plates of an "Echinoid" triad. The two triads are drawn from a young urchin 12 mm. in diameter.

A short distance from the mouth is a ring of ten large buccal plates, each bearing a buccal tube-foot. There are also numerous small buccal plates in the peristome.

A. *Description of the Imago.*

The imago, which measures approximately 1 mm. in diameter including the spines (that of the test alone is only 0·45 mm.‡), differs markedly from the adult. Fig. 16 is a diagram to show the relation of the component parts of the test, above is the apical region, below the disarticulated corona with, in the centre, the plates of the peristome. Figs. 17 and 18 give a dorsal and a ventral aspect of a slightly more advanced imago.

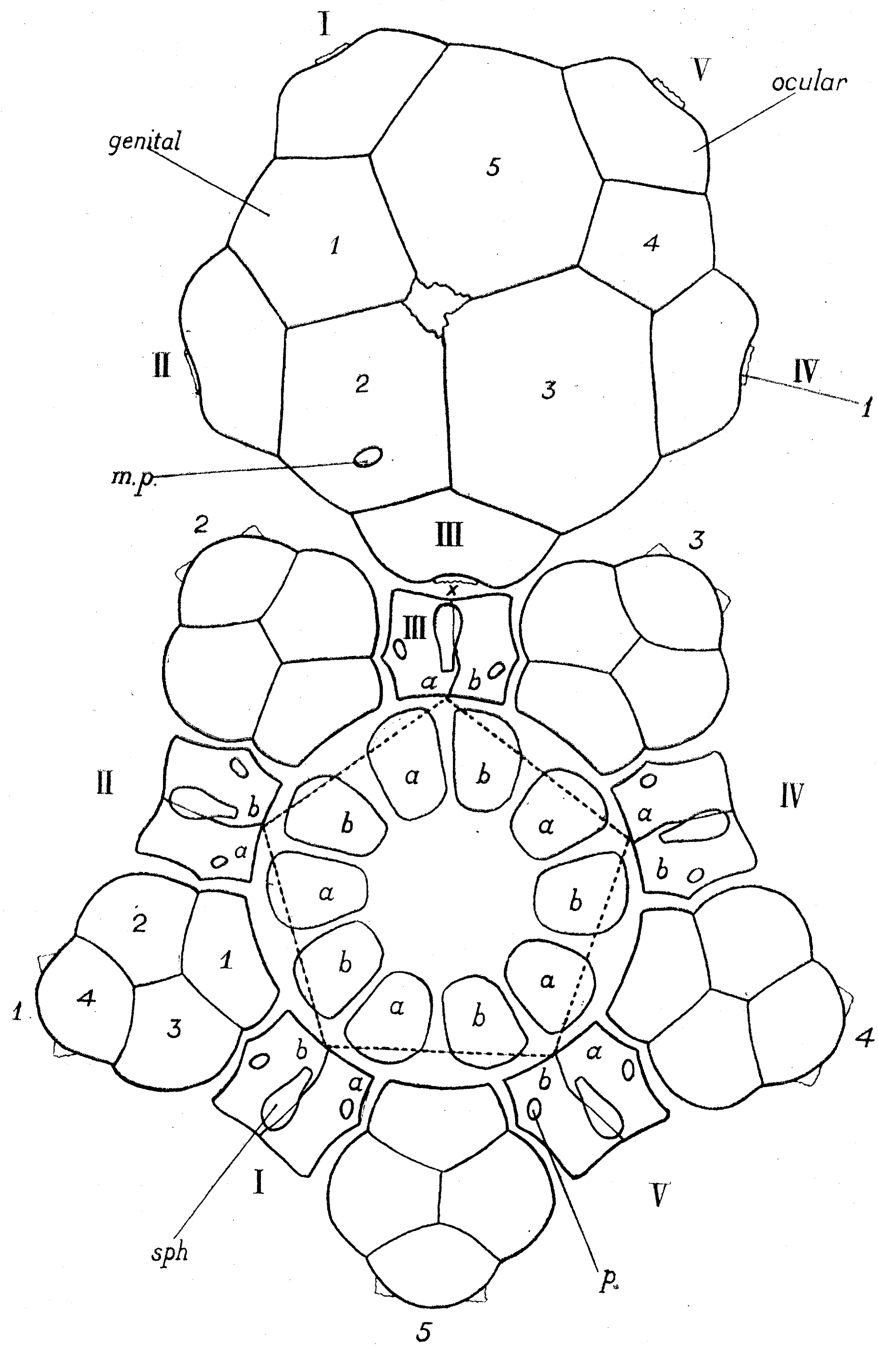
(*a*) *The Apical System of Plates.*—In the imago the apical region is considerably larger than the peristome, occupies practically the whole of the dorsal surface and consists

* The columns are lettered *a* and *b*, clockwise when viewed from the ventral surface, counter-clockwise when viewed from the dorsal surface. The plate next the peristome in column *a* always differs from that in column *b*; the corresponding ones in the five ambulacra being arranged in two series thus: (1) I*a*, II*a*, III*b*, IV*a*, V*b*, the "first series," and (2) I*b*, II*b*, III*a*, IV*b*, V*a*, the "second series" (LOVÉN'S *Law of Heterotropy*).

† As suggested by HAWKINS (1919, p. 395).

‡ The diameter given throughout is always that of the denuded test unless otherwise stated.

only of the five genital and five ocular plates (fig. 16). Each ocular bears two tetraradiate spines (*t. sp.*), which have been omitted in diagram 16 (see, however, figs. 17 and 18).



TEXT-FIG. 16.—Diagram to show the relation of the component parts of the test in the imago. *m.p.* madreporic pore; *sph.*, sphæridium; *p.*, pore for tube-foot; 1–4, the four plates in the inter-ambulacrum; I–V, ambulacra and ocular plates; 1–5, inter-ambulacra and genital plates; *l.*, ledge on ocular plate.

At metamorphosis the genitals, which are now delicate reticulate plates somewhat irregular in outline, assume the adult position relative to the oculars but are not yet in

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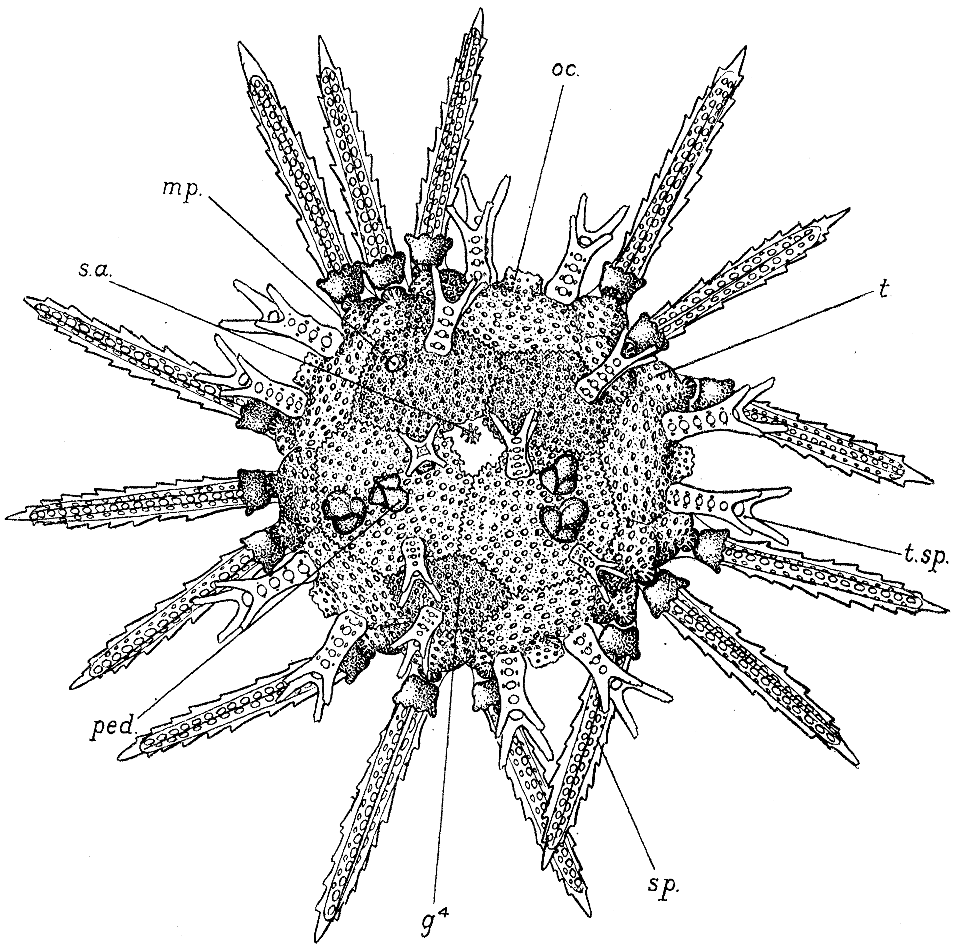
contact with the corona. Growth at this point is, however, rapid, so that they soon assume a more definite shape and come into contact with the corona and with each other, interlocking to form typical sutures. Each plate bears one or more tetraradiate spines. Genitals 3 and 5 each bear one (or two) ophiocephalous pedicellariæ, are larger and more openly meshed than the other three (fig. 17) and meet to exclude genital 4 from the centre. Genital 2 is pierced by a single, rather large water-pore, but the genital pores are not



TEXT-FIG. 17.—Imago a short time after metamorphosis, dorsal aspect. *sp.*, typical spines; *t.sp.*, tetraradiate spines; *t.*, tubercle to which typical spine is attached; *oc.*, ocular plate; g^4., 4th genital plate; *ped.*, pedicellaria; *m.p.*, madreporic pore; *s.a.*, sur-anal. (Magnification 1 × 100.)

yet formed. The small central space surrounded by genitals 1, 2, 3 and 5 corresponds to the adult periproct, but has as yet no calcareous plates and no trace of the adult anus.

(*b*) *The Corona.*—Each ambulacrum consists simply of two plates, one in each column *a* and *b* (fig. 16). The plates in the second series I*b*, II*b*, III*a*, IV*b*, V*a* are somewhat larger than those of the first series, and each bears a single sphæridium. These sphæridia, which measure approximately 0·032 × 0·014 mm., still show traces of the vertical

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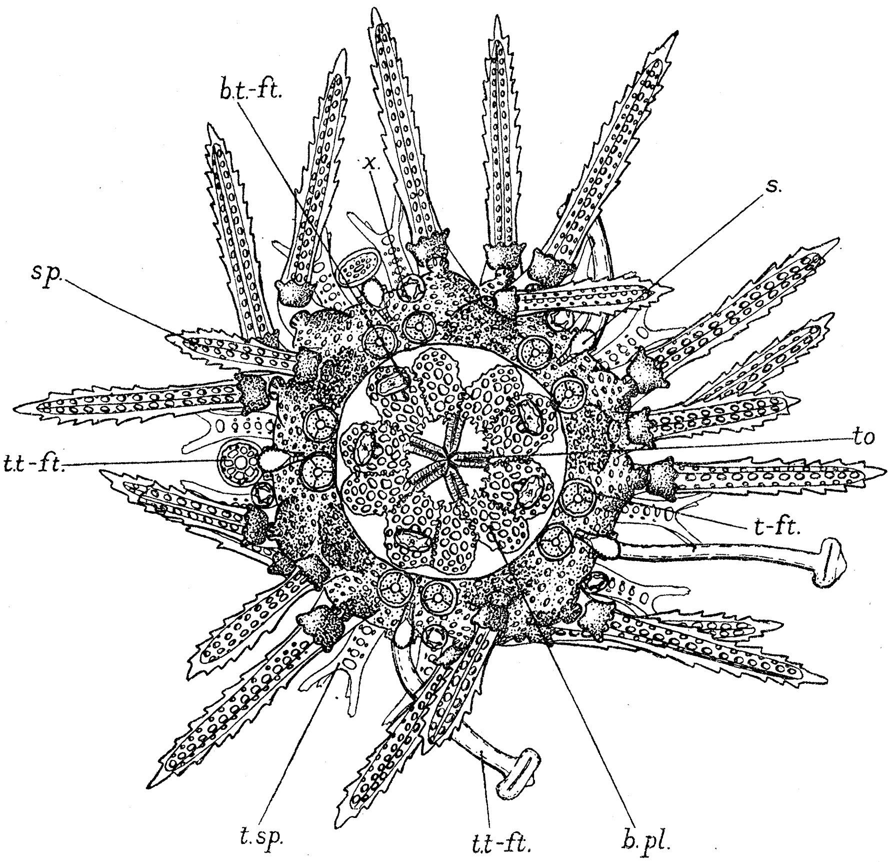
prongs but deposition of solid calcite on the external surface has commenced. In each ambulacral plate is a simple pore through which an ordinary tube-foot passes. The pores in the first series of plates I*a*, II*a*, III*b*, IV*a*, V*b* are somewhat nearer the peristome than those in the other series. Each ambulacrum terminates in an ocular plate, and from a large oval pore (*x* fig. 16), bounded dorsally by the ocular plate, ventrally by both ambulacral plates, a terminal tube-foot emerges. At this stage the terminal tube-



TEXT-FIG. 18.—Imago a short time after metamorphosis, ventral aspect (slightly schematised). *t.t.-ft.*, terminal tube-foot; *t.-ft.*, ordinary (ambulatory) tube-foot; *to.*, tooth; *s.*, sphæridium; *b.t.-ft.*, buccal tube-foot (primary series). X. a developing tube-foot—one of the series *a a b a b*. The other series has not yet appeared; *sp.*, typical spine; *t.sp.*, tetraradiate spine. (Magnification 1 × 90.)

feet are capable of much extension and aid locomotion (fig. 18 *t.t–ft.*). Besides possessing a peculiar type of calcareous disc (fig. 12) they differ from the ordinary tube-feet in ending in a small cone which is probably sensory.

The inter-ambulacrum, which at this stage is much higher than the ambulacrum, is a lozenge of four plates (fig. 16). Next the peristome is a single median plate (1) followed by two lateral plates (2 and 3) of almost equal size; the fourth plate, which is also median, extends on to the dorsal surface to meet the genital plate (fig. 17). Each of these four plates bears a large tubercle to which a long, typical spine is attached (figs. 17 and 18, *sp.*).

The peristomial margin of the corona is thus composed of 15 plates, two in each ambulacrum, one (No. 1) in each inter-ambulacrum (fig. 16). This Lovén stated to be the case in all the young Echinoid forms which he studied.

(*c*) *The Plates in Buccal Membrane.*—In the buccal membrane only 10 delicate, very openly reticulate plates are present (fig. 16). These are the 10 large buccal plates of the adult. None of the buccal tube-feet have as yet appeared, and the adult mouth is also absent. The alveoli and the teeth can be seen through the buccal membrane projecting slightly beyond the buccal plates.

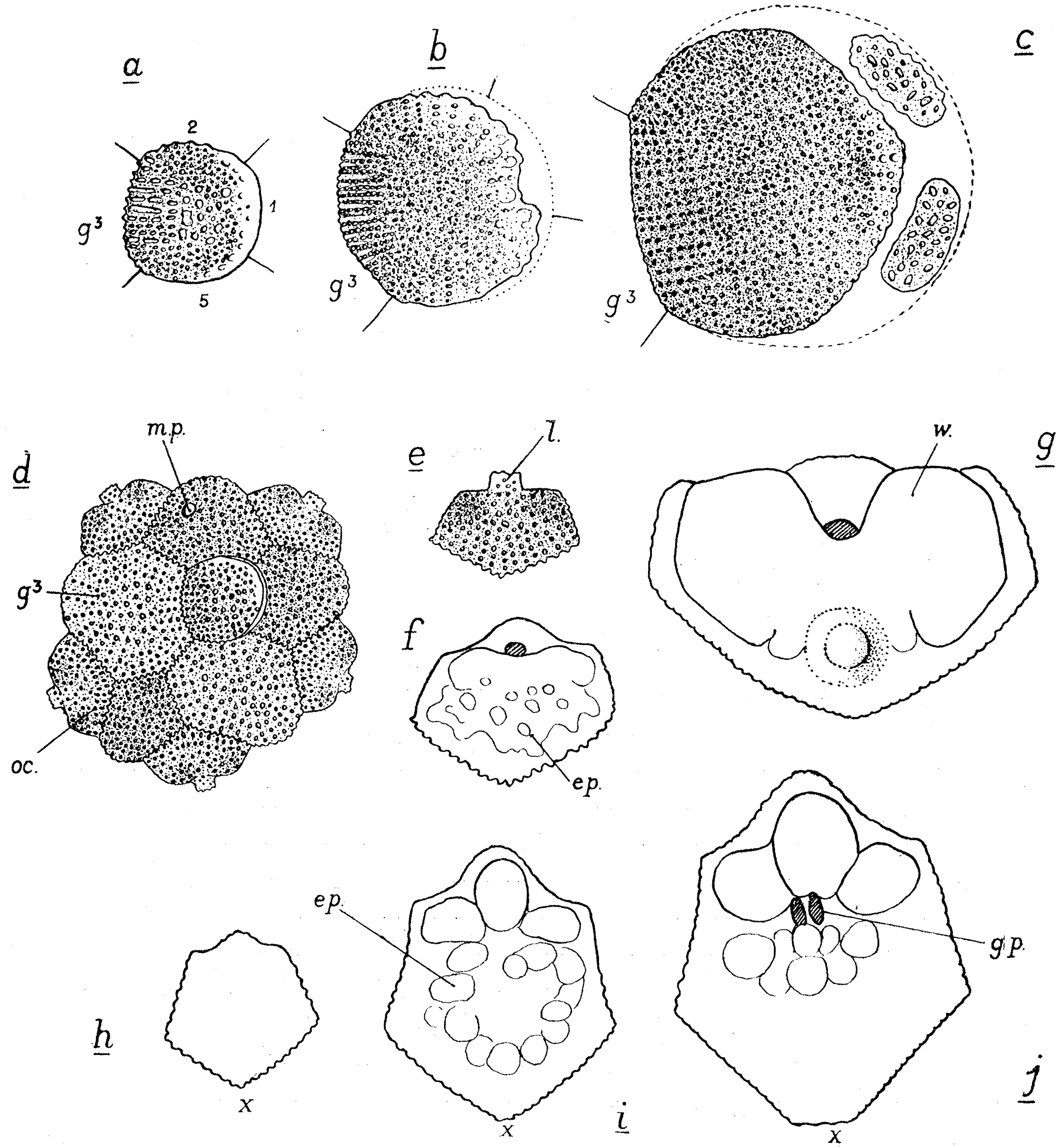
B. *Further Development of the Young Urchin.*

(*a*) *The Apical Region.*

As the young urchin grows additional plates are continuously added to both ambulacra and inter-ambulacra. The plates in the apical region increase in size and become more and more compact. As a result of the comparatively rapid growth in the 10 meridians, the diameter of the apical system becomes proportionately smaller and smaller until the adult condition is reached.

α. *The Periproct Plates.*—Very soon after metamorphosis the "sur-anal" ("dorso-central") plate begins to develop in the periproct (fig. 17, *s.a.*). It soon grows out to meet the genitals 1, 2, 3, and 5. It is never definitely pentagonal in shape, as is the case, for example, in the young *Goniocidaris canaliculata*, Lovén (1892, Plate 2, fig. 6), where it is bounded by all five genitals. As it enlarges it becomes more and more circular except along its junction with genital 3, where it remains almost straight (fig. 19, *a–c*, also *d*). Very soon resorption sets in along the edge which is in contact with genital 1 and part of genitals 2 and 5, resulting in a narrow gap in this region (fig. 19, *d*). Although resorption commences when the diameter of the test is only 0·6–0·7 mm., the sur-anal plate continues to increase in size, and even when the diameter has increased to 2·5 mm. it still occupies the entire periproct except for the narrow gap. Then it begins to recede from genitals 2, 1, 5 more rapidly. Soon a small additional plate is laid down in the gap, and as this space increases in size more and more small plates are laid down in it. Text-fig. 19, *c*, shows two of these, but the sur-anal plate is still contiguous with genital 3. Meanwhile the sur-anal plate is increasing in size (fig. 19, *a–c*, shows three stages in the development of this plate), and owing to the fact that the calcite is undergoing rapid resorption, the rim of the plate which is in contact with genitals 2, 1, 5, becomes thin and transparent (fig. 19, *d* and *a*). Then the margin itself becomes jagged and the plate gradually assumes approximately the shape found in the adult (fig. 19, *c*). It retains its connection with genital 3 for a long time, but as more plates are laid down in the periproct it is ultimately separated completely from the genital ring. However, even in the adult it remains in the neighbourhood of genital 3.

It has been stated that no trace of the adult anus can be seen before the urchin has reached a diameter of 6 mm. (this probably includes the spines). Once, while a living



TEXT-FIG. 19.—Post-larval development of the apical region. *a–c*, three stages in the development of the sur-anal plate. *d*, apical system of plates of a young urchin; *d*, of test = 0·68 mm.; *d*, of apical region = 0·64 mm. *e–g*, three stages in the development of an ocular plate. *h–j*, three stages in the development of genital 4. g^3., genital 3; *m.p.*, madreporic pore; *oc.*, ocular plate; *l.*, ledge; *w.*, wing; *ep.*, epistroma; *g.p.*, genital pore.

urchin (diameter, including the spines, 4·5 mm.) was being observed, it was seen to raise the sur-anal plate slightly opposite genital 1 for the purpose of ejecting fæcal pellets. It would appear, therefore, as if the adult anus opens underneath this plate practically as soon as the adult mouth opens in the peristome.

β. *The Genital Plates.*—It has already been mentioned that genital 4 is at first excluded from the periproct. As it enlarges, however, it gradually grows more and more towards the centre, the suture between genitals 3 and 5 decreasing the while, until by the time the diameter of the test has increased to 3–4 mm., it succeeds in separating these two plates entirely. Once it reaches the periproct, resorption sets in (compare X, fig. 19, *h–j*), and it soon assumes the shape common to all the other genitals.

Meanwhile, the outer border of each genital (*i.e.*, that which articulates with the inter-ambulacrum), which is at first almost straight (fig. 17), becomes somewhat convex (fig. 19, *d*), and then the central portion grows rapidly outwards (compare fig. 19, *h–j*). The new inter-ambulacral plates are laid down one on either side of this rounded apex, between it and the adjacent ocular plate. While this is taking place, globules of calcite (epistroma) are laid down on the outer surface of both genital and ocular plates, these globules being characteristic of this species.

The tetraradiate spines, as well as the ophiocephalous pedicellariæ which are laid down in the larva, soon fall off and short permanent spines appear, first on plates 1 and 5 or 2 and 5, followed soon afterwards by others on plates 2 and 3 or 1 and 3. Thus, when the diameter measures approximately 3·75 mm. these four genitals each bear a short, stout spine. That on genital 4 is not formed till later on.

The madreporic pore (*m.p.*) which is simple in the imago (figs. 17 and 19, *d*) soon divides, and by the time the test measures 1·6 mm. in diameter two or three pores are usually present. In rare cases the pore may be still simple when the diameter has reached 2·5 mm. Gradually the number of these apertures increases until, in the adult, practically the whole surface of genital 2 is perforate. When the diameter has increased to 4·5—5·5 mm., the genital apertures are formed by resorption of part of the calcite from within. Some of these pores are at first double (fig. 19, *j*) but this condition is transient.

Figs. 17 and 19, *d*, show that, in very young urchins the two large genital plates (3 and 5) differ from the others in texture. This curious difference persists for a long time, being quite marked even when the diameter of the test measures 5 mm., but as the plates become thicker and more compact it disappears entirely.

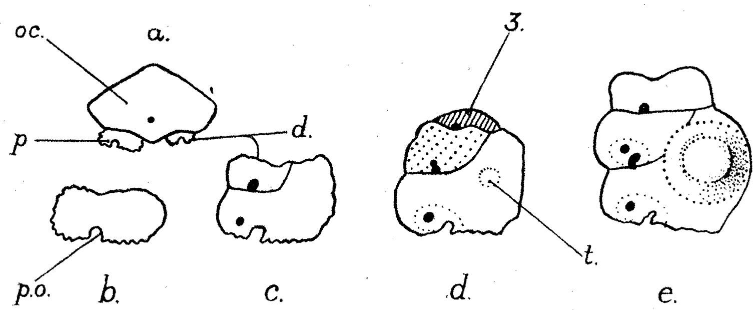
γ. *The Ocular Plates.*—Immediately after metamorphosis a ledge (*l*) begins to grow out from each ocular plate over the base of the terminal tube-foot. The oculars in fig. 16 show the rudiments of these ledges which soon become quite prominent (figs. 17 and 19, *d, e*). The terminal tube-foot soon becomes reduced to a small nodule, the so-called "eye" of the adult. As it is dwindling the ocular plate grows out to surround it and a definite ocular pore is formed (fig. 19, *f*). The projecting ledge (*l*) probably represents the initial stage in this process.

No definite tubercles are formed to afford attachment for the transient tetraradiate spines, broken remnants of which may still be present in specimens measuring 2 mm. in diameter, but the calcite is slightly raised in the parts which are in contact with the spine-bases. These parts gradually become more and more prominent and soon form strong wing-like elevations (fig. 19, *g*, *w.*), the new ambulacral plates being laid down in contact with the ocular immediately beneath these wings (fig. 20, *a*).

Soon each ocular bears one (in some cases two) ophiocephalous pedicellaria, which also appears to be transient, while the external surface becomes partially overlaid by globules of the epistroma (fig. 19, *f*, *ep.*). Even before the last remnants of the tetraradiate spines have fallen off, a typical spine begins to develop on first one of the oculars (ocular I) and then on the others until, by the time the diameter of the corona measures 3 mm. each bears a short stout spine. As each plate increases in size still more spines are formed.

(*b*) *The Corona.*

α. *The Ambulacrum.*—Soon after metamorphosis new plates are laid down one by one in each ambulacrum. These are formed beneath the wing-like upgrowths of the oculars, the plates (and the tube-feet) in the series I*a*, II*a*, III*b*, IV*a*, V*b* appearing slightly in advance of the other series (see fig. 18 which shows the developing tube-feet of the former series, those of series I*b*, II*b*, III*a*, IV*b*, V*a*, have not yet appeared). From the very beginning the plates are, in most cases, grouped in threes in each column, the triads being (with one exception) formed in the following manner. The first (orad) plate is always laid down as a "primary," *i.e.*, it stretches from the adjacent interambulacrum to the median or perradial suture (fig. 15) of the ambulacrum to which it belongs While the second plate is being formed the first one grows upward along the perradial border to exclude it from the median suture. The second plate is therefore termed a "demiplate." Fig. 20*a* shows two developing plates in contact with an ocular plate; that



TEXT-FIG. 20.—The formation of an "Echinoid" triad. *a*, inner view of an ocular plate (*oc.*) to show where the additional ambulacral plates are laid down. *b*, an isolated primary plate the first of a triad. *c*, the first primary together with the demiplate. *d*, a triad just being completed, the third plate (3) is still very small. *e*, a triad when completed. *p.*, primary plate; *d.*, demiplate; *po.*, pore; *t.*, first hint of the primary tubercle.

on the left being a "primary," that on the right a "demiplate." Fig. 20, *b*, shows an isolated "primary," the first plate of a triad. Fig. 20, *c*, this plate together with the "demiplate." The third plate is similar to the first. Fig. 20, *d*, shows a triad which has just been completed (the third plate is still very small) as it appears under crossed nicols.

Once the three plates have been laid down a primary tubercle, which soon extends over on to the "demiplate," is formed on the perradial up-growth of the orad plate. When the "demiplate" is first laid down it separates readily from the orad "primary," but by the time the third plate is formed, it is more closely associated with the first plate and the third separates readily from the other two.

Each plate is laid down on the aboral side of a developing tube-foot, the latter being bounded adorally by the preceding plate (fig. 20, *a*—*e*). The pore, which is at first simple, elongates obliquely, the plate meanwhile undergoing resorption to accommodate the enlarging tube-foot (see the pore in the "demiplate," fig. 20, *d*). Soon calcareous processes grow out from either side cutting the single pore into two distinct pores. In course of time each pair so formed becomes surrounded by a definite peripodium and represents a single tube-foot. The suture always passes through the lower border of the peripodium (fig. 20, *c*—*e*) so that, when the triads are separated, the lower pore in the orad plate is incomplete.

As new triads are gradually added to each column of plates, not only is the apical system raised higher and higher above the peristome, but the rapid production of new plates also exerts a certain amount of pressure ("growth pressure") on the plates which have been previously formed. These tend to be pushed towards the peristome where a certain amount of resorption takes place. After it has been laid down each triad and, indeed, each member of a triad, continues to grow, and this expansion of the plates undoubtedly produces much strain. As a result of all this the triads, which are at first much higher than broad (fig. 20, *e*), undergo a marked change in shape as well as in size. The three pore pairs (podia) in each triad, at first situated one above the other, become displaced and, towards the peristome, they become greatly reduced in size, and in some cases the upper pore may disappear entirely. In the region of the peristome also, the sutures between the plates tend to become obliterated. These changes can best be followed if the development of a single ambulacrum (say ambulacrum I) be studied in detail.

In the imago (fig. 16) column *a* and *b* each consists of a single plate. Fig. 21 (p. 291) shows ambulacrum I a short time after metamorphosis, when four plates (all primaries) are present, two in each column. Plate 1, *b*, is now considerably larger than 1, *a*, having extended aborally, while plate 2, *a*, was being laid down slightly in advance of 2, *b*. It may be noted also that pores 1, *a*, and 1, *b*, differ from the others in being bounded on all sides by the same plate. The tube-feet which pass through these are formed in the Echinopluteus and are, ere metamorphosis, completely surrounded by the ambulacral plates.

The next three plates which are added to column *a* are laid down in the typical manner already described, and constitute an "Echinoid" triad. Thus, as the urchin grows and more plates are added, column *a* in area I consists of two "primaries" nearest the peristome followed by a number of triads. In column *b*, however, the arrangement near the peristome is somewhat different. While the third plate (a "primary") is being laid down a tubercle is formed on the second plate, which latter bulges out slightly in the neighbourhood of the perradial suture. The base of the tubercle soon spreads over on to plates 1 and 3, and plates 1, 2 and 3 become grouped together into a triad which consists of *three "primaries*." After this, the plates are laid down in typical triads.

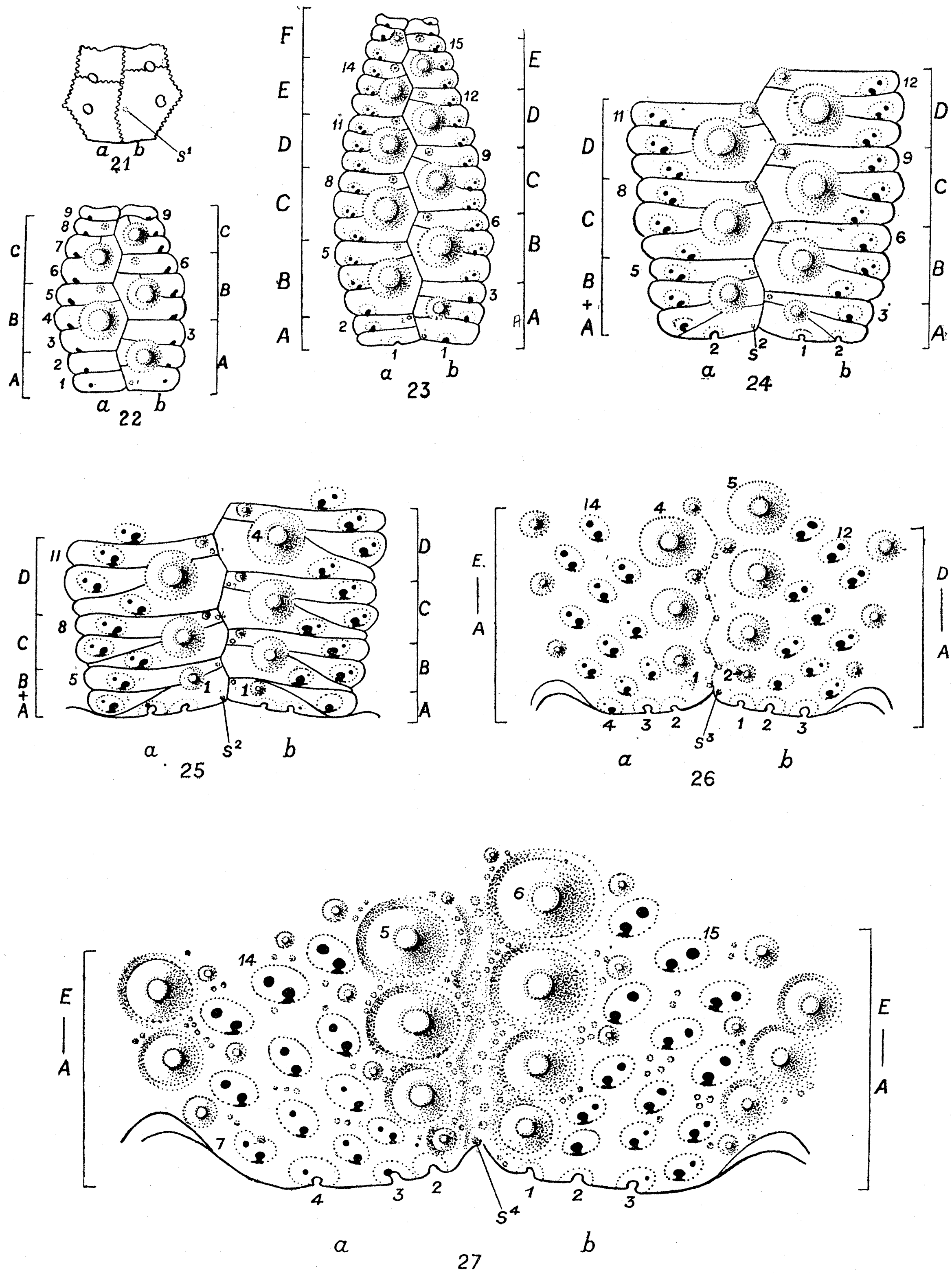
The next figure (fig. 22) represents ambulacrum I of a specimen in which the diameter of the test measures 1·3 mm. In column *a* the plates, nine in number, are grouped as follows: A, the two "primaries" next the peristome, succeeded by two typical "Echinoid" triads B and C, the last plate being the first (orad) plate of the next triad D. The tubercle on B has now spread over a short distance on to the apicad plate, while there is also a small secondary tubercle on the apicad plate of triads B and C. In column *b* the plates, also nine in number, are grouped into three triads, A, B and C, the first of which consists of three "primaries." The apicad plate of triad B also bears a secondary tubercle. Only one sphæridium* is present, namely, that on plate 1, *b*, which was laid down in the Echinopluteus. All the triads are, at this stage, high, and the pores in each column are arranged in a single row. All the pores are, moreover, still simple although a number are elongated and just about to divide. A small amount of resorption has taken place at the peristomial margin; this results in pores 1, *a*, and 1, *b* becoming relatively nearer to the peristome. When the diameter has increased to approximately 1·6 mm., the pore 1, *a*, has reached the margin, the lower (orad) border having undergone resorption.

By the time that the diameter measures 2·3 mm. the number of plates in each column has increased to seventeen (fig. 23). In column *a* the two "primaries" (A) are still distinct plates, but the pore in the lower one has almost gone, and when the diameter has reached approximately 2·6 mm. it has entirely disappeared. Thus, since all five ambulacral areas are undergoing resorption simultaneously five pores are lost (those belonging to the series, I*a*, II*a*, III*b*, IV*a*, V*b*) and five tube-feet are entirely expelled from the corona. The fate of these tube-feet will be dealt with later (p. 300). Two sphæridia are now present, the second one being on plate 2, *a*. In column *b* the first pore has now reached the peristomial margin, while the sphæridium has also descended to the edge of the plate.

The pores are still arranged in a single row in each column. The two last formed ones (those nearest the apex) are still simple, but all the others are now double, except pores 1, 2 and 3 in each column. These, it is interesting to note, never divide as a rule; in a few cases the third may divide later on, but only in one case has the second been observed to undergo division.

In fig. 24 only the adoral part of the ambulacrum is represented. The diameter of the test has now increased to 5 mm., and many more triads have been added. Four sphæridia are now present, but the first one has become detached from the corona

* In the series of figures given (figs. 21—27) only the granules to which the sphæridia are attached are represented.



TEXT-FIGS. 21–27.—A series of figures illustrating the development of ambulacrum I. (*s*., sphæridium).

together with a small flake of calcite, and has passed on to the buccal membrane. Pore 1, *a*, has, of course, gone by this time and plate 1, *a*, has entirely disappeared, as also has part of plate 2, *a*, for the second sphæridium is now quite near the margin (compare with the preceding figure). The orad border of pore 2, *a*, has been resorbed and the suture between plates 2 and 3, *a*, slopes obliquely towards the tubercle. The third pore has moved downwards towards the peristome, and now lies externalto and almost on a level with the second pore with the result that the adradial* border (*i.e.* that in contact with the adjacent inter-ambulacrum) of plate 2, *a*, has disappeared entirely. Thus the lower compound plate in column *a* consists of triad B together with the remaining portion of the second "primary" of A.

The lower triad in column *b* has undergone considerable reduction also. The adradial border of plate 1 has disappeared while plate 2 has been reduced on the perradial side and is now a "demiplate." The second pore has reached the peristome and been partially resorbed. The perradial* border of plate 3 is also considerably smaller and the tubercle binding the three plates together has also decreased in size.

Hitherto all the triads have been high (*see* previous two figures) and have not undergone very much alteration in shape since their inception. But now the succeeding triads as well as the plates in the immediate neighbourhood of the peristome have become considerably reduced in height, and the pores are beginning to be displaced from the uniserial arrangement. This displacement commences near the peristome and gradually extends towards the apex. Already pores 6, *a*, and 4, *b*, have been forced towards the perradial suture as also have 9, *a*, and 7, *b*, though to a lesser extent. Meanwhile the individual triads are increasing in breadth and the ambulacrum is thus gradually widening out near the peristome.

The next figure (fig. 25) shows the peristomial plates of ambulacrum I of a specimen 12 mm. in diameter. Although the diameter of the corona has increased to more than twice that of the preceding specimen, resorption at the actual margin has not proceeded much further, but the reduction in height of the triads and the displacement of the pores (podia) has been much more rapid.

In column *a* the compound plate A + B is still more reduced. The suture between plates 2 and 3 has been almost completely obliterated. The "demiplate" 4 has now descended adradially to the margin so that the adradial border of plate 3 has also disappeared, while pore 3 has been partially resorbed. The tubercle on A + B has become greatly reduced in size, but the second sphæridium is still attached to the corona. The next triad (C) is also very low and the adradial border of the orad plate has almost disappeared. The pore (7) in the "demiplate" has descended until it is practically on a level with pore 6 which latter has moved still nearer to the median suture. The next triad (D) has not been reduced to such a marked extent, but the adradial suture of the orad plate (9) is considerably smaller than in the previous figure and the podium (9) has been displaced from the adradial border.

* *See* Text-figure 15, p. 281.

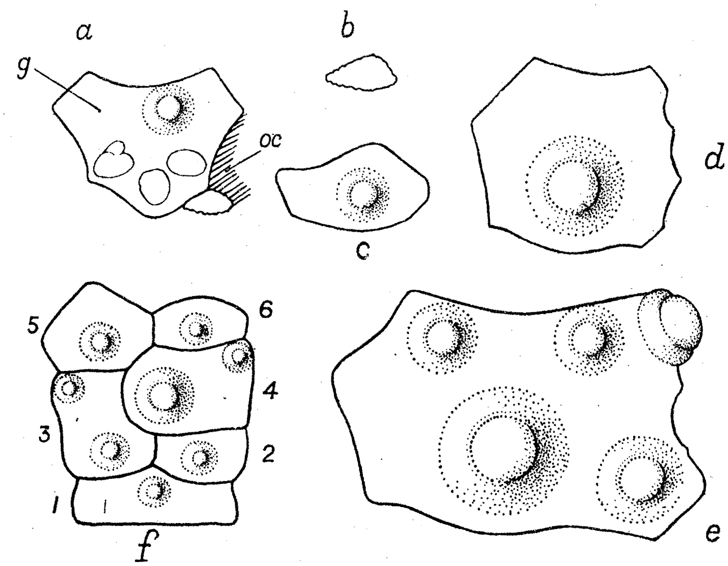
In column *b* similar changes have occurred. Triad A is greatly reduced, the suture between plates 1 and 2 having disappeared while the adradial border of plate 2 has also gone. The third plate has undergone reduction perradially and is now a "demiplate," while pore 3 has descended almost to the margin. [In this ambulacrum pore 2 has divided—the only instance of this observed.] The adradial border of the orad plate in triads B and C is greatly reduced. The upper pore of each pore-pair becomes smaller as it approaches the peristome, that in podium 4 in each column being now very small. The number of sphæridia has increased to eight.

This "plate-crushing" and pore displacement continues with the result that the sutures near the peristome tend to disappear almost entirely. Soon they cannot be made out in denuded tests but will show up if the ambulacra are stained and etched. In the next figure (fig. 26, $d = 15$ mm.) they have been omitted as they could not be seen in the denuded corona from which the drawing was made. In column *a* pores 2 and 3 are still present, and these always persist on the peristomial margin (as also do pores 1, 2 and 3, *b*), the tube-feet which pass through them being bounded orally by the buccal membrane. The fourth podium has just reached the margin. The second sphæridium has passed on to the buccal membrane. The first primary tubercle has practically disappeared, as also has the secondary one which was present in triad C in the previous figure, while the second primary tubercle is also relatively smaller. In column *b* the third pore is now partially resorbed and the upper pore in podium 4 has entirely gone. The first primary tubercle has also disappeared, the second one is greatly reduced, and the small secondary tubercle on B has vanished, while that on C is reduced to a mere granule.

Fig. 27 represents the adult condition ($d = 40$ mm.). Although the diameter is almost three times that of the previous specimen resorption along the actual peristomial margin has been slight. In column *a* podium 4 has undergone partial resorption, the first primary tubercle has entirely disappeared, while the second one is small and two secondary tubercles have also gone. In column *b* the third sphæridium has passed on to the peristome and the second primary tubercle has disappeared, the one nearest the peristome being the third tubercle (that on triad C of previous figures). The podia are now arranged in almost horizontal rows of three, those nearest the peristome being considerably smaller than those higher up. The number of sphæridia has greatly increased, while numerous additional granules and secondary tubercles are present, the latter being confined chiefly to the "pore-field."

In the course of development resorption at the peristomial margin proceeds at first rapidly with the result that, in each ambulacrum, a single pore entirely disappears while a few others undergo partial resorption. Later on this process of resorption proceeds much more slowly, and by the time the diameter has increased to 15–20 mm. the adult condition has practically been reached. Regarding the change undergone by the triads the opposite is the case. For a considerable time these remain relatively high but later become rapidly smaller and smaller from above downwards. The two up-growing processes on the interior peristomial border of each ambulacrum (see page 296) fuse, when the diameter of the test measures approximately 7 mm.,* to form a complete arch. The perignathic girdle is thus now continuous and probably retards the downward movement of the plates. Meanwhile new plates continue to be added and those already formed continue to grow with the result that "growth-pressure" is now particularly powerful in the neighbourhood of the peristome. The plates must of necessity undergo reduction in size, the calcareous meshwork (stereom) being rapidly resorbed. This "plate-crushing" results in a marked crowding of the podia which commences at the margin (next the buccal membrane) and gradually extends upwards towards the apical region. While this is taking place the sutures are at first quite distinct as might be expected, since the placogenous membrane separating the individual plates is used in the resorption as well as in the deposition of the calcite. In course of time, however, this membrane becomes more and more attenuated, the sutures becoming fainter and fainter, but the placogenous membrane probably does not entirely disappear even in the fully grown adult.

β. *The Inter-ambulacrum.*—New plates are added to the ambulacrum in the imago before the inter-ambulacrum begins to extend, so that when the former consists of three



TEXT-FIG. 28.—*a–c*, stages in the development of an inter-ambulacral plate. *f.*, an early stage in the development of the inter-ambulacrum; *g.*, genital plate; *oc.*, ocular plate.

plates in each column the latter is still a lozenge of four plates. Soon afterwards a fifth plate is laid down, and, as it is being formed, one of the lateral plates of the lozenge (which may be termed plate 3) extends aborally to meet the new plate, the up-growing portion developing a small tubercle (see fig. 28, *f*). This up-growth serves to displace plate 4 slightly to one side. As plate 5 is increasing in size another plate (6) is laid

* In series of figs. (21—27) resorption is very slow and the triads alter rapidly at a stage intermediate between figs. 24 ($d = 5$ mm.) and (25 $d = 12$ mm.).

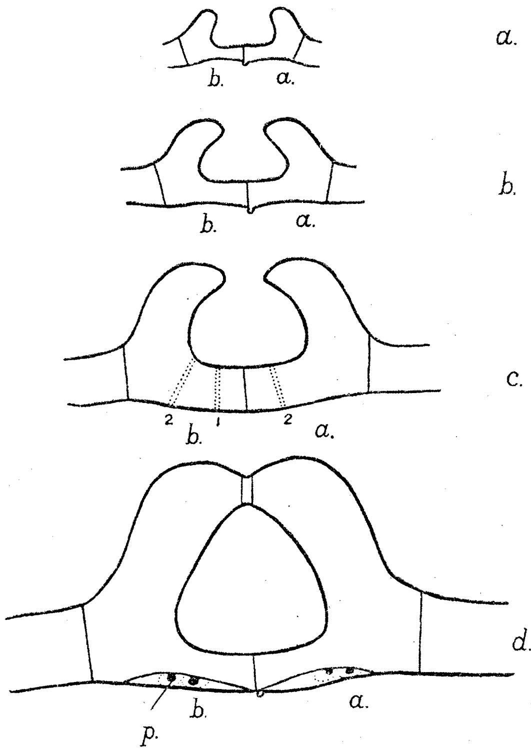
down in contact with plate 4. This condition is represented in fig. 28, *f*. The tubercle on plate 4 has increased enormously relative to those on plates 1, 2 and 3, but is still situated immediately above that on plate 1, while a secondary tubercle has also been formed. As more plates are added alternately to each column plate 4 gradually becomes less conspicuous.

Each plate is laid down in the angle between a genital and an ocular plate. Fig. 28, *a*, shows one of these at a very early stage adhering to the genital plate, when first formed the inter-ambulacral plate is triangular in shape (fig. 28, *b*). Soon it acquires a primary tubercle and alters to the form shown in fig. 28, *c*, which alters, as another plate is being laid down, to that shown in fig. 28, *d*, the primary tubercle being situated adorally. Secondary tubercles now begin to appear, and as the plate recedes from the apical region, it gradually becomes relatively narrower from above downwards and expands laterally (fig. 28, *e*). This alteration, which is very similar to that undergone by a triad, continues while more secondary tubercles and granules are formed.

In the adult urchin the inter-ambulacrum is narrow adapically, broadens out gradually towards the ambitus ("the outline of the test when viewed from the apical pole"), becoming rapidly narrower towards the peristome. Near the apex the plates are similar in shape to those shown in fig. 28, *b–d*, only larger and provided with a number of smaller tubercles and granules. Further down they resemble the plate shown in fig. 28, *e*, in shape, but are much more elongated (from side to side) and furnished with numerous secondary and tertiary tubercles and granules. Below the ambitus the plates become gradually narrower from side to side and bear fewer and fewer tubercles (although some of the secondary ones may be almost as large as the primary ones), until those at the extreme edge of the corona are reduced to the parts which bear the primary tubercles.

Resorption also occurs in the neighbourhood of the peristome in all the inter-ambulacral areas. By the time that the diameter of the corona measures 3·5 mm. the first plate with its tubercle has entirely gone. Gradually the two succeeding plates (2 and 3) are also resorbed, and when the diameter has reached approximately 7 mm. both have disappeared entirely. After this point resorption proceeds very slowly, but eventually the fourth tubercle also goes. In the very largest specimens the fifth tubercle becomes greatly reduced and may also disappear. Thus all the four plates which are laid down in the larva are gradually resorbed, and besides the four primary tubercles a number of smaller ones also disintegrate.

γ. *The Perignathic Girdle.*—Although there is no trace of the auriculæ at metamorphosis they begin to develop very soon afterwards, and when the ambulacrum consists of three plates in each column the primordia of these are present as small internal projections one on either side of each ambulacrum. They are situated a short distance from the oral rim of the corona, near to pore 1, and extend over on to the inter-ambulacra. Even in this early stage these processes incline towards each other and away from the inter-ambulacra. The sutures between the rudimentary processes and the ambulacral plates are very difficult to make out, but can just be distinguished on the inner (aboral) side. These projections gradually increase in size and small inter-ambulacral ridges are formed, so that the girdle recalls the disconnected type of, *e.g.*, *Salenia*. As the processes elongate they bend more and more towards each other (fig. 29, *a–c*), and the inter-



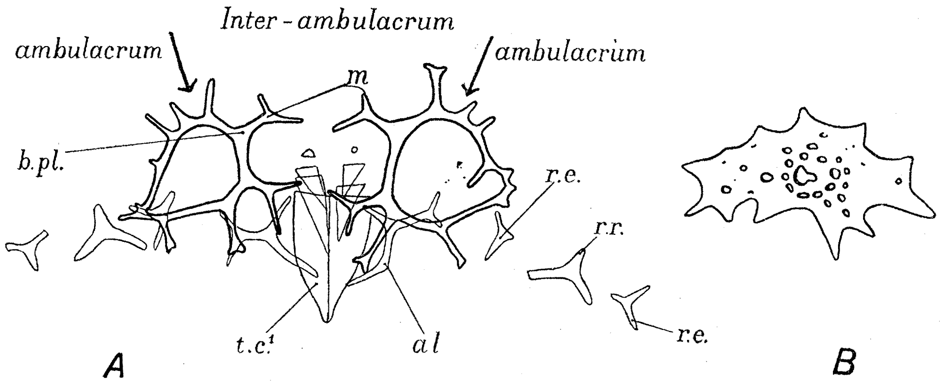
TEXT-FIG. 29.—*a–d*, stages in the development of the perignathic girdle (*d* = 1·3 mm. (*a*); 2·3 mm. (*b*); 5 mm. (*c*); 9·3 mm. (*d*)); *p.*, 1 and 2, podia.

ambulacral ridges become more pronounced. When the test reaches a diameter of 7 mm., the free ends of the projections meet in the centre to form an arch (fig. 29, *d*) over each ambulacral area.

C. *The Plates in the Buccal Membrane.*

In the pluteus ten buccal plates are laid down, a pair in each *inter-ambulacrum* internal to the first inter-ambulacral plate (see p. 265, also fig. 3). When the primordia of these plates are first observed the distance between two adjacent pairs is two to three times that between the members of a pair. Once the triradiate stage is reached two of the rays grow more rapidly than the third, so that the plates grow away from each other (fig. 30, A) and towards those of a neighbouring pair. At metamorphosis these plates (which become the ten large buccal plates of the adult) are openly reticulate, and, owing to the fact that the plates which originally constituted a pair diverge near the corona, are grouped in pairs opposite the ambulacra (figs. 16 and 18). A re-arrangement similar to this occurs in the case of the epiphyses DEVANESEN (1922, pp. 470–1).

At this stage the plates are practically all of equal size. Very soon five buccal tube-feet appear in the plates which are internal to series I*b*, II*b*, III*a*, IV*b*, V*a* of the corona. These plates now increase in size more rapidly than the remaining five, and by the time the test measures 0·67 mm. in diameter the two series can be easily distinguished (fig. 18).



TEXT-FIG. 30.—A., An early stage in the development of a pair of large buccal plates; the elements of the lantern have been inserted to show the position of the buccal plates relative to these. *b.pl.*, large buccal plate; *m.*, the " median " ray of the original triradiate spicule—this ray is less developed than the other two; *t.c*[1]., first cone of the tooth; *al.*, alveolus; *r.e.*, rudiment of epiphysis; *r.r.*, rudiment of rotula. Camera lucida drawing 1 × 525. B. The disc of a primary buccal tube-foot. Camera lucida drawing 1 × 525. (Original 1 × 700.)

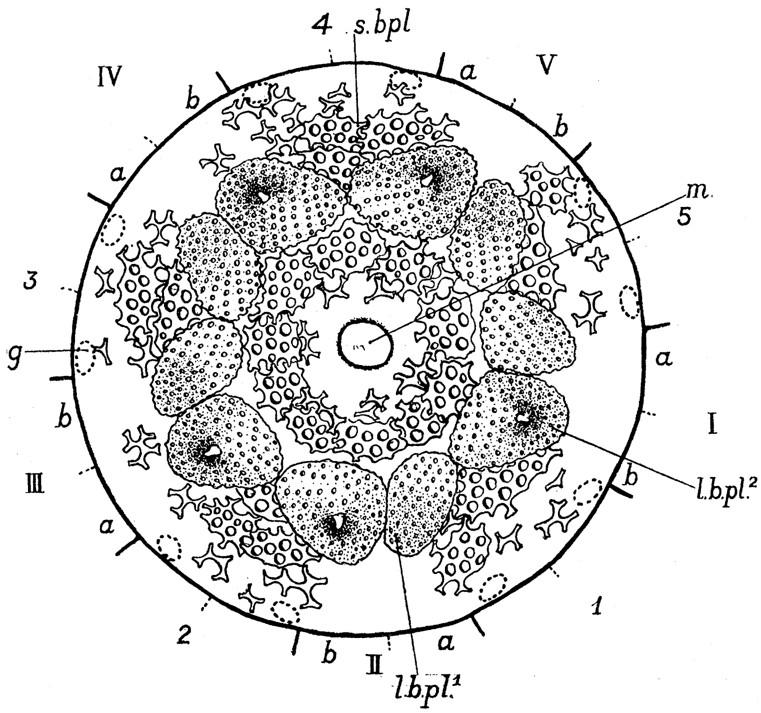
The five buccal tube-feet grow very rapidly so that it has not been possible to trace the development of the calcareous disc. From the very beginning the terminal portion of each tube-foot is oval in outline and the disc is fairly well developed. The disc itself differs from both types, the development of which has been described in Part I. It is simple and appears to have arisen from a single primordium. In shape it is somewhat oval but very irregular in outline (fig. 30, B), and already the calcite is thick and compact* with comparatively few perforations. This type of disc is unique, being confined entirely to these five tube-feet which may be termed the *primary buccal tube-feet.* It obviously differs markedly from the disc formed in the terminal portion of the ordinary ambulatory tube-feet, but may be a modification of that formed in the terminal tube-foot. LOVÉN (1874, Plate 17, fig. 148) gives a figure of the peristome of a young specimen of " *Toxopneustes* " *drœbachensis* showing five primary buccal tube-feet in the same series of plates (I*b*, II*b*, III*a*, IV*b*, V*a*), but the remaining series of plates is, in this species, the larger.

Meanwhile the teeth, which at metamorphosis only project slightly beyond the inner edges of the ten buccal plates, elongate rapidly, growing out to meet each other in the centre (fig. 18, *to.*). The adult mouth is not yet open but, in living specimens, the teeth are seen to move within the buccal membrane. There is no trace of the transient

* All skeletal elements laid down after metamorphosis are, in the early stages, more compact than those formed in the larva.

thorny condition, which occurs in the teeth of the young *Echinocyamus*, Théel (1892). In some cases the adult mouth opens before the test has reached a diameter of 1 mm. As a general rule, however, it does not open till some time later, but nearly always before the diameter has increased to 2 mm.

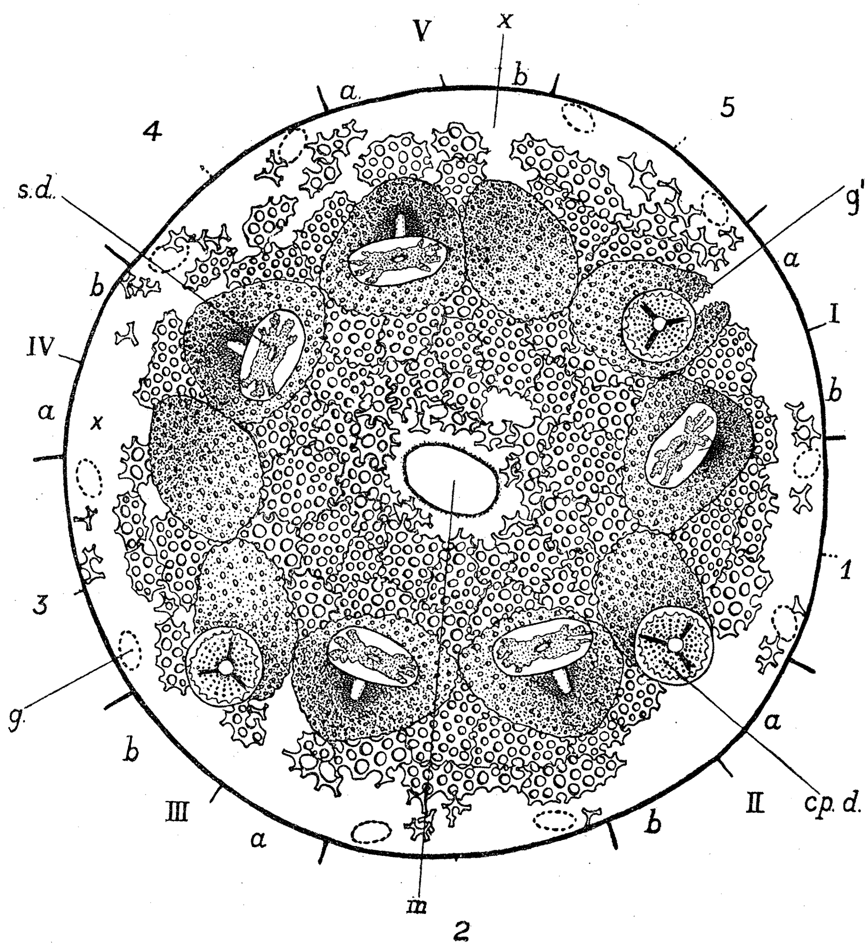
As the ten buccal plates increase in size series I*b*, II*b*, III*a*, IV*b*, V*a* come to differ from the other series in shape as well as in size (fig. 31). The members of a pair incline towards each other and away from those of the two adjacent pairs. When the diameter measures approximately 1·27 mm. small plates are laid down in the buccal membrane in the space between the ten large plates and the corona opposite the *inter-ambulacra*. Soon afterwards additional plates also make their appearance internal to the large plates, and when the diameter of the corona has increased to 2·4 mm. the condition represented in fig. 31 is reached. The second series of buccal tube-feet has not yet



Text-fig. 31.—The plates in the buccal membrane of a young urchin measuring 2·4 mm. in diameter. Only five buccal tube-feet (the primary set) are present, but these have been omitted in the figure. I–V, the ambulacra; 1–5, the inter-ambulacra; *m.*, mouth; *l.b.pl*¹., the first series of large buccal plates; *l.b.pl*²., the second series of large buccal plates, through which the primary buccal tube-feet pass; *s.b.pl.*, small buccal plates; *g.* indicates the position of the skin gills.

appeared and only an occasional small plate has appeared opposite the ambulacra. By this time the external gills are present as simple sac-like outgrowths, and an ophiocephalous pedicellaria has developed on each of the buccal plates which surrounds a primary buccal tube-foot.

Fig. 32 is a diagram of the plates in the peristome of a specimen 3·2 mm. in diameter. The small buccal plates have now increased in size and in number so that an almost continuous meshwork of calcite, in which the sutures are visible, results. Numerous additional plates continue to be added both in the neighbourhood of the mouth and of the corona. Besides the five primary buccal tube-feet three others are now present. These differ from the primary ones in several respects; the terminal portion is circular in outline, the disc is compound and similar to that of an ordinary tube-foot, but is too large and compact to belong to a developing tube-foot.



TEXT-FIG. 32.—The buccal membrane of an urchin 3·2 mm. in diameter showing the buccal tube-feet and the calcareous plates. *s.d.*, simple disc of primary buccal tube-foot. *cp.d.*, compound disc of secondary buccal tube-foot; *g'*., gap formed in plate to accommodate tube-foot. Other lettering as in previous figure.

One of these tube-feet has already entered the buccal plate, which is internal to plate *a* of ambulacrum I, the buccal plate in question having undergone a certain amount of resorption to accommodate the tube-foot. In the case of the other two buccal plates (those internal to the ambulacral plates II*a* and III*b*) little or no resorption has as yet taken place. In other specimens of approximately the same diameter all the five *secondary buccal tube-feet* are present on the peristome, some near to, some at a

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little distance from the buccal plates I*a*, II*a*, III*b*, IV*a*, V*b* before any have entered the plates at all.

The primary buccal tube-feet seem to grow from within through the delicate openly meshed plates for they are never situated external to these. Very little resorption, if any, would be required at this early stage to allow of free passage for a developing tube-foot. By the time the secondary set appears, however, the buccal plates are much more compact. Should the second series of tube-feet develop from within through the buccal membrane as the primary ones appear to do, then they must either be formed external to the plates (the latter undergoing resorption to allow them to enter) or definite pores must be formed in the plates, in the same way as the genital pores are formed, through which the developing tube-feet could pass.

The secondary buccal tube-feet are always, when first observed in the peristome, large and resemble the ordinary tube-feet, the discs being exceedingly well developed. It may be recalled that, when the test has attained a diameter of about 2·6 mm., a single tube-foot is excluded from each ambulacrum. Thus, in all, five tube-feet, those belonging to the first series (I*a*–V*b*), are passed on to the buccal membrane. What happens to these ? The fact that the secondary series of buccal tube-feet are in all respects similar to those found in the corona, and are at first external to the buccal plates, seems to prove that they have in reality come from the ambulacra. Further, small buccal plates are laid down opposite the inter-ambulacra before any appear opposite the ambulacra (fig. 31). Fig. 32 shows that, although plates have now appeared between the large buccal plates and the ambulacra there is a distinct space (X) opposite the plates I*a*, II*a* III*b*, IV*a*, V*b*, which would be sufficient to allow of the passage of a tube-foot. Thus it would appear as if the secondary buccal tube-feet not only come from the corona but are also formed much earlier than the primary series, being laid down in the Echinopluteus and the first set to acquire compound discs (*see* p. 265). The primary set appear so soon after metamorphosis that it is impossible they could have come from the corona resorption at the peristomial margin having as yet scarcely commenced, and the first formed ordinary tube-feet being still a considerable distance from the buccal membrane. Since in fig. 32 only three of the secondary set have passed on to the buccal membrane, resorption must have been more rapid in three of the ambulacra than in the remaining two.

Once all the secondary buccal tube-feet have entered the buccal plates they become completely surrounded by the plates and definite pores are formed. The plates then grow rapidly and gradually assume the size and the shape of the other series (I*b*—V*a*). The two sets of tube-feet can be distinguished for some time because of the difference in shape of the terminal portions.

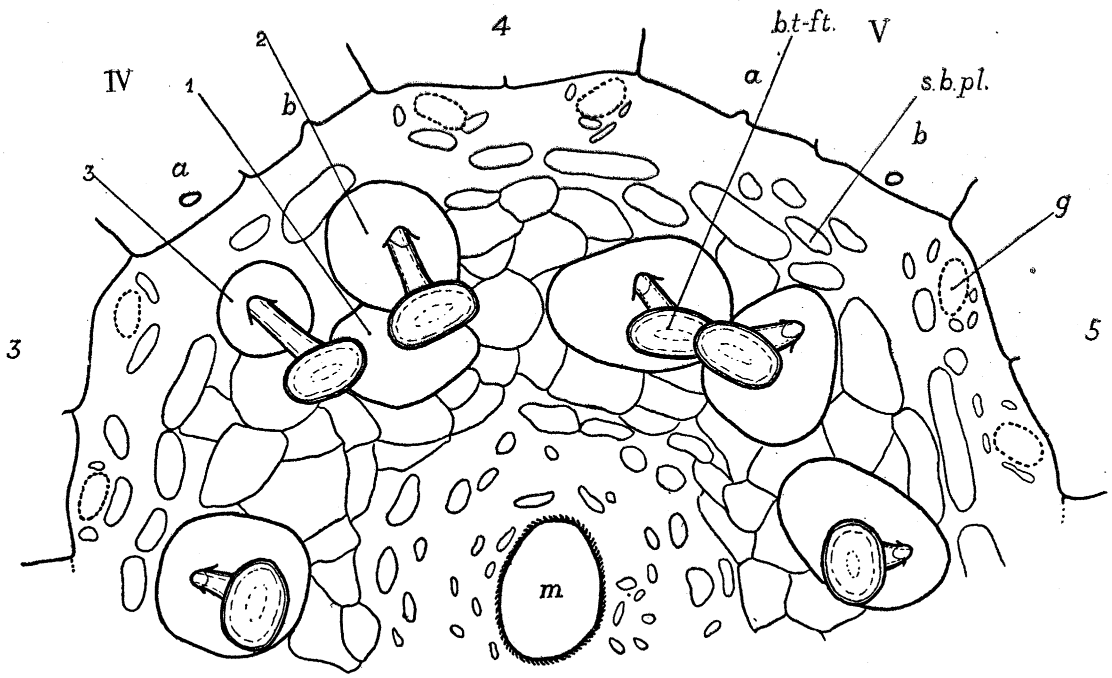
Meanwhile small buccal plates continue to develop and these now appear opposite the ambulacra as well as the inter-ambulacra. The ten large buccal plates, which in the imago are practically in contact with the corona, recede further and further from it and more plates are laid down. While this is taking place more pedicellariæ are formed.

Those on the large buccal plates and the small ones immediately next to them are for the most part large and ophiocephalous, a few are small and trifoliate. In the 'Cambridge Natural History,' Vol. I, "Echinodermata," MacBride writes, "the ophiocephalous pedicellariæ are in *Echinus* the most abundant of all, and they alone extend on to the peristome, where a special small variety of them is found." In the opinion of the writer these small pedicellariæ are trifoliate (triphyllous). A number of the smaller type are also to be found on the small plates which are situated between the corona and the large buccal plates.

First one and later another sphæridium passes from the ambulacrum on to the buccal membrane. These bring with them a small flake of calcite, part of the ambulacral plate to which they had been attached, and persist on the peristome. In the largest specimens a third may be dislodged from at least some of the ambulacra.

Abnormalities.

Although a large number of specimens were examined, very few abnormalities occurred. In several imagos the rim or peristomial margin of the corona is less distinct than usual, the buccal plates having become more or less "fused" to the ambulacral plates and to each other, but the sutures can in most cases be made out.



Text-fig. 33.—Diagram of part of peristome of a young urchin ($d = 4 \cdot 3$ mm.) showing an abnormal set of large buccal plates opposite ambulacrum IV. 1, Original large buccal plate IV*a*; 2, large buccal plate IV*b*; 3, a small buccal plate which has surrounded the tube-foot.

A number of "reversed types" occur in each culture [Ohshima (1921)]. In the peristome of one specimen ($d = 4 \cdot 3$ mm.) one of the secondary buccal tube-feet has become surrounded by a *small buccal plate* (opposite ambulacrum IV*a*). This plate has become quite compact and rounded off to form a miniature "large buccal plate." The original large buccal plate, which is somewhat displaced, still retains its primitive shape, while all the others of the same series have altered considerably after having surrounded the secondary tube-feet. The large buccal plate opposite, IV*b*, also occupies a somewhat abnormal position, being slightly nearer the corona than the others. Both the large buccal plates IV*a* and IV*b* may have become somewhat displaced during their development before the secondary tube-feet passed on to the peristome. On the other hand, the secondary tube-foot in question having entered a small buccal plate "by mistake," so to speak, the subsequent rapid growth of this plate may have contributed largely to the displacement of the two large buccal plates.

In a few specimens one or more of the ten meridians are slightly abnormal in small areas, being otherwise quite normal. For example, in one specimen ($d = 15$ mm.) ambulacra I and II are somewhat distorted from the peristome to the ambitus, becoming quite normal adapically. In only one specimen was the abnormality of the test marked. The formulæ of corresponding series of plates round the peristome were *a, a, a, b, b* and *b, b, b, a, a* instead of the usual *a, a, b, a, b* and *b, b, a, b, a*. Unfortunately, the specimen had been macerated in NaOH and the plates in the apical region had become dislodged before the abnormality was discovered. But an examination of these showed that the genital plates were markedly abnormal. Only two of these had the typical shape (one being the madreporic plate), but the other three were so abnormal that reconstruction, without having previously examined the arrangement *in situ*, could not be undertaken with any degree of certainty.

Discussion.

The primordium of all the skeletal elements in *Echinus* takes the form of a small, almost spherical granule. With the exception of (1) the base of the long typical spines, (2) the base of the sphæridium, and (3) the numerous component parts of a tooth, the triradiate spicule represents an early stage in the development of all skeletal parts. The typical, and probably the most primitive, later development of such a tri-radiate spicule is that in which all three rays are equally developed, each dividing dichotomously at its extremity. This occurs, for example, in the formation of the inter-ambulacral plates (fig. 3) and in the formation of the base of a tetraradiate spine (fig. 8).

It is interesting to note the various ways in which this is modified to form different structures. Two rays develop more rapidly than the third in the formation of: (*a*) the disc of the terminal tube-foot, resulting in the formation of a circle (fig. 12); (*b*) all the nine rudiments of the compound disc of an ordinary tube-foot (fig. 13); (*c*) the base of the pedicellaria blade—here the third ray remains abortive after a certain stage (fig. 11); (*d*) the early stages of the buccal plates (fig. 30, A).

In the development of the plates, for example, growth is more or less confined to a horizontal plane. When vertical growth occurs, it commences typically with a single up-growth from the *centre* of a triradiate spicule, as is the case in (1) the early stage of tubercle formation (fig. 3), and (2) the development of the blade of a pedicellaria (fig. 11). In the formation of the typical spine, also, a single projection arises from the centre of the hexaradiate base (figs. 5 and 6).

One of the most striking features in the early development of the spine is the formation of *three* vertical processes, *one from each ray* of the original triradiate spicule, which is destined to become the base of a tetraradiate spine. Probably in the simplest, most primitive condition each of these processes gave rise to a single prong, the result being a *triradiate spine.* Triradiates are quite common in *E. miliaris.* As has already been described (see p. 272), one of these processes soon divides, each branch forming a prong. This tetraradiate symmetry is indeed curious and quite unique. Elsewhere the symmetry is either tri- or hexaradiate. How, then, has this unusual symmetry arisen? The occurrence of an occasional spine with six prongs suggests that, at some period in the history of these primitive triradiate spines, each of the three vertical processes divided into two to give a hexaradiate form. The tetraradiate spine may have been derived from such a hexaradiate by the elimination (secondarily) of division in the case of two of the projections.

The fact that the primordia of these spines appear in advance of those of the typical spines (see p. 264) lends weight to the view that they are ancestral forms precociously developed. On the other hand, they may be larval modifications.

These tetraradiate spines bear a somewhat superficial resemblance to the spines of an Asteroid, especially as regards the absence of a definite tubercle on the plates to which they are atached. But the development of the spines of *Asterina gibbosa*, LUDWIG (1882), is in close agreement with that of the typical Echinoid spine for, although apparently commencing as a small triradiate, the base becomes hexaradiate and a single vertical process arises from the centre of the base.

The development of the sphæridium shows conclusively that it is really a reduced and modified spine. The foundation of the globular portion consists of six (in some cases five) prongs, similar to those of a typical spine but greatly reduced in length. The irregularity exhibited by the base (fig. 10, *a–e*) is due either to the total loss of a varying number of rays or to the fact that some of the rays remain abortive. The stalk of the sphæridium, which corresponds to the expanded basal portion of a spine, shows the same tendency to reduction. It always remains narrower than the upper portion, and no branches are developed corresponding to γ and γ' (compare figs. 6 and 7, with 10, *f*). THÉEL (1892) found that two sphæridia are sometimes formed in a single ambulacrum in the case of *Echinocyamus*, but that one of these is later subject to a "retroactive developmental process." In *E. miliaris* a second primordium sometimes appears closed to the one which is destined to form a sphæridium. This granule appears to undergo resorption.

SEDGWICK (' Text-book of Zoology,' vol. iii, *Echinodermata*, p. 173, 1909) says of the pedicellariæ of an Asteroid that "they are modified spines, and sometimes small groups of spines are so associated that they can be moved towards one another and act like pedicellariæ." In *Echinus* the relationship of the blade of a pedicellaria to a typical spine is not quite so obvious as that of a sphæridium. The development of the basal portion appears at first sight to be a modification of that of the base of a tetra-radiate spine (compare figs. 8 and 11, *a*–*c*). On the other hand the development of the rest of the blade is more in keeping with that of the typical spine. One vertical process only is developed and that arises from the centre of the original triradiate. The subsequent development is much more modified than is the case in that of a sphæridium, but there is a reduction in the number of prongs to five.

Probably the similarity between the base of the blade and the base of the tetraradiate spine is misleading. In any case it is unlikely that three excentric vertical processes could have been replaced by a central one. The number of rays in the base of a sphæridium is sometimes reduced to three (see fig. 10, *d*). Perhaps the base of a pedicellaria blade may have been evolved from that of a typical spine by the reduction of the rays to three, each alternate one being suppressed. Thus, the blade of a pedicellaria is, in all probability, a modified and reduced typical spine. But how could three such modified spines become associated with each other? It has been mentioned that, in the case of both the long (typical) spines and the sphæridia, there is a tendency to form additional primordial granules. These are transient and do not seem to occur elsewhere in the case of *E. miliaris*. Perhaps this is a relic of the tendency for spines to develop in groups such as are to be found in some Asteroids (SEDGWICK, 'Textbook of Zoology,' vol. iii, *Echinodermata*, p. 173, 1909). Once this grouping of the spines has been acquired the transition to modified blades, working together effectively, is only a matter of time.

In *Echinus* the ophiocephalous type is the first to appear, on the apical region, on the test and on the buccal membrane. Soon afterwards the small trifoliate pedicellariæ appear to be followed later by the gemmiform and the tridactyle types. The blade of the young gemmiform pedicellaria has been figured by SHEARER, DE MORGAN, and FUCHS (1914, p. 338, fig. 19).

The elements of the lantern of Aristotle in Echinoids are generally regarded as homologous with the buccal armature of Asteroidea. Opinions, however, differ as to the homologues of certain elements, notably the teeth. SOLLAS (1899) puts forward the view that (1) the alveoli are transformed first adambulacrals (mouth-angle plates), (2) the tooth represents the odontophore which has acquired a persistent root, (3) the epiphyses correspond to the first ambulacral ossicles, adding, "the radius and the rotula remain problematical."

On the assumption that the first cone is similar to the succeeding ones (*i.e.*, of double origin), DEVANESEN (1922, p. 479) writes, "The homologues of the urchin tooth are to be looked for among the bristles carried by the mouth-angle plates in star-fishes. If two such bristles get flattened, assume a cone-shape and are pushed between the mouth-angle plates, thus becoming partially internal, we have the rudiments of an urchin tooth." Moreover, he puts forward the suggestion that the rotulæ may be modified odontophores, but admits that the great impediment to this view is the fact that, while the latter are interambulacral, the former are ambulacral. It is very unlikely that five single inter-radial ossicles (odontophores) should have, in the course of evolution, assumed a radial position. Therefore SOLLAS' view—that the tooth is an odontophore which has acquired a persistent root—is preferable.

At one stage in the development of the tooth of *Echinocyamus* (THÉEL, 1892) the first cone is furnished with thorny projections. This might suggest that the first cone is distinctly larval. But it must always be borne in mind that it forms, as it were, the foundation of the whole tooth. From the description of the tooth of a young specimen of *Goniocidaris* given by LOVÉN (1892), it seems as if the lamellæ were all simple in this case, neither does SPENCER (1904) mention a double series of lamellæ in the tooth of *Palæodiscus ferox*. Thus the primitive form of the Echinoid tooth consisted apparently of a succession of lamellæ or "cones." In the Echinopluteus of *E. miliaris* one rudiment of a pair originates slightly in advance of the other. This might suggest that the complex tooth has arisen from a linear series, the component parts of which have, owing to crowding, become somewhat displaced, and have arranged themselves in pairs, the first remaining single. Otherwise there seems to be no explanation of this fact.

The very open meshwork exhibited by the developing plates in the pluteus is probably a larval characteristic for, after metamorphosis, the developing plates grow more rapidly and are, from the first, more compact with the exception perhaps of those which are formed in the peristome. The spines, which all develop in the same way as the inter-ambulacral (typical) ones of the pluteus, are also from the first more solid, the prongs and cross bars being more robust.

The young forms of *Goniocidaris canaliculata* and of *Strongylocentrotus* ('*Toxopneustes*') *drœbachensis* figured by LOVÉN (1892), and of *Strongylocentrotus lividus* figured by ÜBISCH (1913, Plate VI, fig. 6), agree with *E. miliaris* in having only ten plates in the peristome at first. Those in the case of *Goniocidaris* (LOVÉN, 1892, Plate II, fig. 9) are markedly "heterotropic" [*i.e.*, one series is considerably larger than the other] and each contains a tube-foot.* LOVÉN terms these plates, which are in all probability equivalent to the ten large buccal plates of *Echinus*, the "five primordial pairs of ambulacral plates."† The development of these plates does not appear to have been worked out for *Goniocidaris*. The ten large buccal plates in *E. miliaris* and *S. lividus* differ from the ambulacral plates in not being from the very start associated with a developing tube-foot. In *E. miliaris*, moreover, the primordia are at first internal to the first inter-ambulacral plate.

* The tube-feet have been omitted in LOVÉN's figure, and no evidence as to the type of calcareous discs which they possess is forthcoming.

† In reality these are not formed until after the first pair of ambulacralplates (LOVÉN's "second ring of ambulacrals") in *Echinus*, *Arbacia*, and *Strongylocentrotus*.

Arbacia pustulosa (ÜBISCH, 1913, Plate VII, fig. 16) differs from *Echinus* and *Strongylocentrotus* in that the ten large buccal plates do not appear until after metamorphosis, and five are, from the very first, associated with developing tube-feet. Were it not for the presence of these tube-feet it would be difficult to say whether the plates were ambulacral or inter-ambulacral in position for they appear to be almost directly below (ventral to) the developing alveoli. Five of these buccal plates are slightly larger than the other five, but the tube feet are not always associated with the former. It is interesting to note also that the primary series of buccal tube-feet is the I*a*, II*a*, III*b*, IV*a*, V*b* series (which, in the case of *Echinus* and *Strongylocentrotus*, is the secondary one).

LOVÉN (1874, Plate XVII, fig. 149) gives a figure of an imago which, in a later paper (1892), he referred to the genus *Echinus*, and which presents several rather puzzling features. Although LOVÉN states that no trace of the larva remains he also says that there are no traces of the alveoli (*mâchoires*). As is the case in the imago of *E. miliaris* there are two ordinary (?)* tube-feet in each ambulacrum in addition to the terminal tube-foot. But the reticulate plates developed in connection with these tube-feet are large and approach much nearer to the future mouth than do the first pair of buccal plates in *E. miliaris*. On account of this LOVÉN (1892, p. 15) clearly regards these plates as the "five pairs of primordial ambulacral plates" (*i.e.*, the ten large buccal plates) for he writes, "This prominent feature in the young animal, the retarded appearance of the other of the two heterotropic series of primary pedicels (*i.e.*, of those which have been termed the 'secondary buccal tube-feet' in *E. miliaris*) the I*a*—V*b*, seems, however, not to be of constant occurrence in the different genera, or perhaps more transient in some than others. It has already been seen that the young *Echinus* (woodcut, p. 11) which has just completed its pluteal stage and has acquired only one ambulacral circle presents a pore and a pedicel in every one of its plates."

From what is known of the imago in the case of *Strongylocentrotus lividus* and *E. miliaris* these pedicels do not belong to the buccal plates but to the first ambulacral plates (*i.e.*, LOVÉN'S second circle of ambulacral plates). But in no other Echinoid imago which has been described up to the present, do the first ambulacral plates extend nearer to the mouth than the first inter-ambulacral plate. Indeed, they, together with the first inter-ambulacral plates, are exactly on a level with each other and form the margin of the corona (see figs. 16 and 18). In the imago figured by LOVÉN no buccal plates may have appeared as yet for they always lag behind the first ambulacral plates, and in *Arbacia* are not laid down till after metamorphosis. If this is so, why should the first ambulacral plates exclude the first inter-ambulacral ones from the peristome? In *E. miliaris* an occasional imago does occur in which the buccal plates partially fuse with the ambulacral plates, or are so near to them that the sutures can only be made out with difficulty. It may be that this has happened in the imago in question, so that the ambulacral and buccal plates have been drawn as one continuous plate.

* The disc is omitted in the figure.

In Cidarids, as the corona increases in size, there is a " gradual streaming of plates " from the apical region to the peristome. A number of plates from the ambulacra, together with a few from the inter-ambulacra, undergo partial resorption and pass on to the buccal membrane. As this is taking place the ten plates present in the peristome of the very young Cidarid are moved inwards and come to be situated immediately round the mouth. In forms like *Asthenosoma* only ambulacral plates are passed on to the membrane. In *Echinus*, on the other hand, although the ten large buccal plates gradually recede from the corona as growth continues, yet at a very early stage small plates are laid down between these plates and the mouth. Small plates are also formed in the gap between the ring of large buccal plates and the corona, and these appear at first only opposite the inter-ambulacra. Moreover, no coronal plates are passed on to the membrane, but a certain amount of resorption takes place. The only traces of actual movement of parts of the corona on to the buccal membrane consist of two (or in some cases three) sphæridia still attached to small flakes of the original ambulacral plates. A single tube-foot is also excluded from each ambulacrum and becomes one of the " secondary buccal-tube feet."

A comparison of the series of figures (figs. 21–27) illustrating the development of the ambulacrum with those given by LOVÉN (1874, Plate XVII, figs. 141–8) for " *Toxopneustes* " *drœbachensis* shows that the amount of resorption which takes place round the peristome is practically the same in both cases. As LOVÉN represents ambulacrum III in his series, column *b* corresponds to column *a* in the figures given for *E. miliaris* (ambulacrum I). It is natural to suppose that in " *Toxopneustes*," which agrees so closely with *E. miliaris* in all other respects, the " secondary buccal tube-feet " would also come from the corona. In fig. 148 there is only one sphæridium in each ambulacrum, the pores are still simple and none have as yet reached the margin. Between this stage and the next (fig. 141) there is a considerable gap, and it is precisely between these two stages that the five tube-feet are excluded from the corona in *E. miliaris*. If, in LOVÉN's series, the pore marked 1 in column *b* be called pore 2, then the arrangement of the podia in the immediate neighbourhood of the peristome agrees exactly with that found in *E. miliaris*. Thus it may reasonably be assumed that pore 1 has gone entirely in the series, I*a*, II*a*, III*b*, IV*a*, V*b* in this species also. Although the first three pores do not, as a general rule, divide in the case of *E. miliaris*, they seem to do so in " *Toxopneustes*." In the latter, also, the compound plates are in the adult more complex than the " Echinoid " triads, but many of the plates which are destined to become demiplates are laid down as primaries and soon undergo reduction. Still, the arrangement of the plates adorally is identical with that found in *Echinus*, the first few compound plates being for the most part triads.

In the early development of the ambulacrum certain primitive features occur. Every tube-foot pore is simple to start with, and all the pores are simple until there are eight to nine plates in each column. Moreover, the podia are arranged uniserially in young forms ; this is a feature of Cidarids and of many fossil forms. All the plates are laid down independently although they are grouped into triads from the beginning. The formation of a triad is in agreement with the suggestion put forward by HAWKINS (1919, p. 405) that the " Echinoid " triad may be formed from the addition (adapically) of an "intercalated " plate to a diad.

It does not appear as if the presence of the primary tubercle were essential to the actual formation of a triad, for the tubercle is only formed after the inception of the third plate (see fig. 20, *d*). The latter, which separates readily from the other two at first, is firmly united to them (especially in older specimens) before the base of the tubercle has expanded on to it at all. But, once formed, the tubercle probably helps to bind the plates more firmly together.

SUMMARY.

PART I.—THE DEVELOPMENT OF THE SKELETON IN THE PLUTEUS.

(1) Apart from the larval spicules calcification commences first in the primordium of the pedicellaria, the rudiments of all three blades appearing practically simultaneously.

(2) Soon afterwards calcification commences in the " echinus-rudiment." Typically the primordia of the various elements are laid down in the following order :—

(1) The ocular plates, two of which are at first associated with larval spicules.

(2) The first inter-ambulacral plate followed soon afterwards by plates 2 and 3 and, considerably later, by plate 4.

(3) The primordia of the tetraradiate spines which in the imago are attached to the ocular plates. Almost immediately afterwards those of the inter-ambulacral spines appear one by one ; sometimes two granules are laid down but only one develops into a spine.

(4) The discs of the terminal tube-feet.

(5) The first pair of ambulacral plates series I*a*, II*a*, III*b*, IV*a*, V*b*, being slightly in advance of the other series.

(6) The ten large buccal plates ; these are at first arranged in pairs opposite the single first inter-ambulacral plate, but later get re-arranged into five ambulacral groups.

(7) The first cone of the tooth (in the earliest stage found, only three of the primordia had appeared—those of the teeth in inter-ambulacra 1, 3, 5). This cone differs from all the succeeding ones in being formed from a single primordium.

(8) The alveoli followed almost immediately by the epiphyses, the rotula and one rudiment of the second tooth cone. All cones subsequent to the first arise from paired rudiments, one rudiment appearing slightly in advance of the other.

(9) The discs of the ordinary tube-feet in series I*a*, II*a*, III*b*, IV*a*, V*b* are laid down at the same time as the elements of the lantern.

(10) Later still the discs of the ordinary tube-feet in the other series of ambulacral plates are laid down ; at the same time the primordia of the five sphæridia appear, these are attached to the second (I*b*, II*b*, III*a*, IV*b*, V*a*) series of ambulacra plates.

(3) Meanwhile, on the right side of the pluteus the genital plates are developing. Genitals 2, 3 and 5 are formed as proliferations of larval spicules, genital 2 at the posterior end of the "dorsalbogen," genitals 3 and 5 in connection with the right post-oral and postero-dorsal rods. Genitals 1 and 4 appear later and are each formed from a single triradiate spicule.

A detailed account has been given of the development of the following :—

(*a*) *Spines*. The typical spines (inter-ambulacral) are formed in the same way as those of *Echinocyamus pusillus*. The development of these, which may be regarded as typical of Echinoid spines, is essentially similar to that of the spines of *Asterina gibbosa*, but more elaborate and represents a more advanced form. The development of the tetraradiate spines, on the other hand, is quite unique. It has been suggested that these may have been derived from a primitive triradiate form which gave rise to a hexaradiate type from which the tetraradiate form may have been secondarily derived. These spines may be either relics of a much more primitive type than those of *Asterina* or larval modifications.

(*b*) *Sphæridium* which is a reduced and modified spine.

(*c*) *Blade of a pedicellaria* which is also in all probability a modified spine.

(*d*) *Discs of the tube-feet*. That of the terminal tube-foot is formed from a single triradiate spicule, that of the ordinary tube-foot from three primary and six secondary triradiates.

(*e*) *Lantern of Aristotle*.—The early stages.

PART II.—THE POST-LARVAL DEVELOPMENT OF THE TEST.

(*a*) *The Apical System of Plates*.

At metamorphosis only the five ocular and the five genital plates are present. Very soon afterwards the sur-anal plate is laid down. At first it occupies the whole of the periproct, but undergoes rapid resorption at one side and separates from the genital ring opposite plates 5, 1, 2. As resorption continues it alters in shape and additional small plates are laid down in the periproct. The sur-anal plate remains for a long time in contact with genital 3, but is ultimately separated from it also. The adult anus opens very early under the sur-anal plate.

The fourth genital plate, which is at first excluded from the periproct, gradually grows towards the centre, undergoes partial resorption when it reaches the periproct and soon assumes the shape common to the others. The madreporic pore, at first simple, divides repeatedly so that numerous pores result and the plate (genital 2) ultimately surpasses the others in size. The genital pores are formed (by resorption of part of the calcite from within) when the diameter measures 4·5–5·5 mm. The outer border of each genital plate (that which is contiguous with the inter-ambulacrum) is at first almost straight but soon becomes slightly convex, and by rapid growth of the central portion the adult form is gradually assumed. The genitals and the oculars are characterised by the presence of numerous deposits of the epistroma in young urchins.

In the imago the ocular plate sends out a ledge of calcite which at first projects over the base of the terminal tube-foot and then gradually surrounds the latter (as it is dwindling) to form the ocular pore. On either side of the pore the portions to which the tetraradiate spines are at first attached grow upward as strong " wings " of solid calcite beneath which the new ambulacral plates are added.

(*b*) *The Corona.*

α. *The Ambulacrum.*—In the imago each ambulacrum consists simply of two plates, one in each column. As new plates are added these are grouped almost from the very beginning into typical " Echinoid " triads, the median plate being laid down as a demiplate. A detailed account of the development of ambulacrum I has been given. Column *a* commences with a pair of primary plates (next the peristome), followed by typical triads, column *b*, with an atypical triad composed of three primaries followed by typical triads. The tube-feet pores are all simple in very young specimens, and uniserially arranged; later they all divide with the exception of pores 1, 2 and generally 3 in each column.

A certain amount of resorption occurs at the peristomial margin, with the result that one tube foot in column *a* is entirely excluded from the corona, while several other tube-foot pores undergo partial resorption. [As all five ambulacra undergo resorption five tube-feet, those belonging to the first plate in series I*a*, II*a*, III*b*, IV*a*, V*b*, are excluded and become the secondary buccal tube-feet.] Two or even three sphæridia are passed on to the peristome, while a few primary tubercles next the peristome also disappear. Resorption proceeds very slowly after the perignathic girdle has become continuous, and the triads, which are at first high, now rapidly decrease in height. As a result of this the podia become crowded in the region of the peristome, and become grouped in almost horizontal rows of three. In older specimens also the sutures tend to disappear.

β. *The Inter-ambulacrum.*—The early stages in the development of the inter-ambulacrum have been described, together with the mode of formation of a single plate and its subsequent alteration in shape. Resorption occurs at the margin, and gradually all the four plates laid down in the pluteus disappear entirely.

γ. *The perignathic Girdle.*—In the early stages it is of the " disconnected " type. When the diameter of the test has increased to 7 mm., the up-growths on either side of the ambulacrum fuse to form a complete arch.

(*c*) *The Plates in the Buccal Membrane.*

At metamorphosis only the ten large buccal plates are present. These are practically equal in size, but when the five primary buccal tube-feet appear soon afterwards in the series I*b*, II*b*, III*a*, IV*b*, V*a* they become markedly " heterotropic." This is due to the fact that the plates through which the primary buccal tube-feet pass increase rapidly in size and assume a different shape from the others. Small buccal plates next make their appearance both external to and internal to the ring of large buccal plates. At first these plates appear (externally) only opposite the inter-ambulacra.

The secondary buccal tube-feet come from the corona and enter the smaller series of large buccal pates (the I*a*, II*a*, III*b*, IV*a*, V*b* series), part of the calcite being resorbed to accommodate them. Then these plates soon assume the size and shape of those in the other series. The two series of buccal tube-feet differ from each other in the following respects :—(1) Those in the primary series do not develop until after metamorphosis, while the secondary ones are laid down in the pluteus, and are, indeed, the first ordinary tube-feet to develop discs ; (2) the terminal portion in the primary set is from the first oval, in the secondary ones it is circular, but becomes oval later on ; (3) the calcareous disc in the case of the primary tube-feet is quite unique, being simple, oval and very irregular in outline ; in the other series it is compound. After the secondary buccal tube-feet have entered the large buccal plates numerous small buccal plates continue to be added, especially external to the ring of large buccal plates (and now opposite both ambulacra and inter-ambulacra), so that the large buccal plates recede further and further from the corona.

LITERATURE.

Bury, H. (1889). "Studies in the Embryology of the Echinoderms," 'Quart. Journ. Micr. Sci.,' vol. 29, pp. 409–450.

Idem (1895). "The Metamorphosis of Echinoderms," 'Quart. Journ. Micr. Sci.,' vol. 38, pp. 45–135.

Devanesen, D. W. (1922). "Development of the Calcareous Parts of the Lantern of Aristotle in *Echinus miliaris*," 'Roy. Soc. Proc.,' B, vol. 93, pp. 468–485.

Fewkes, J. W. (1888–9). "Development of the Calcareous Plates of Asterias," 'Bull. Mus. Comp. Zool. Harvard,' vol. 17, pp. 1–52.

Hawkins, H. L. (1919). "The Morphology and Evolution of the Ambulacrum in the Echinoidea Holectypoida," 'Phil. Trans. Roy. Soc.,' B, vol. 209, pp. 377–480.

Lovén, S. (1874). "Etudes sur les Echinoïdées," 'Kongl. Sven. Veten. Akad. Handl.,' vol. 11, No. 7. Stockholm.

Idem (1892). "Echinologica," 'Bihang Kongl. Sven. Veten. Akad. Handl.,' vol. 18 (4), No. 1, pp. 1–74.

Ludwig, H. (1882). "Entwicklungsgeschichte der *Asterina gibbosa*," 'Zeit. für Wiss. Zool.,' vol. 37, pp. 1–89.

MacBride, E. W. (1899). "Studies in the Development of Echinoidea," 'Quart. Journ. Micr. Sci.,' vol. 42, pp. 335–9.

Idem (1903). "The Development of *E. esculentus* . . . ," 'Phil. Trans. Roy. Soc.,' B, vol. 195, pp. 285–327.

Mortensen, Th. (1913). "Die Echiniden des Mittelmeeres," 'Mitt. Zool. Station zu Neapel,' Berlin, vol. 21, Nr. 1, pp. 1–40.

OHSHIMA, H. (1921). "Reversal of Asymmetry in the Plutei of *Echinus miliaris*," 'Roy. Soc. Proc.,' B, vol. 92, pp. 168–178.

SHEARER, C., DE MORGAN, W., and FUCHS, H. M. (1914). "On the Experimental Hybridisation of Echinoids," 'Phil. Trans. Roy. Soc.,' B, vol. 204, pp. 255–362.

SOLLAS, W. J. (1899). "On Silurian Echinoidea and Ophiuroidea," 'Quart. Journ. Geol. Soc.,' vol. 55, pp. 692–715.

SPENCER, W. K. (1904). "On Structure and Affinities of *Palæodiscus* and *Agelacrinus*," 'Roy. Soc. Proc.,' vol. 74, No. 497, pp. 31–46.

THÉEL, H., 1891–5 (1892). "On the Development of *Echinocyamus pusillus*," 'Nova Acta Reg. Soc. Upsala,' series 3, vol. 15, No. 6, pp. 1–57.

ÜBISCH, L. VON (1913). "Die Anlage und Ausbildung des Skeletsystems einiger Echiniden . . . ," 'Zeit. für Wiss. Zool.,' vol. 104, Heft 1, Leipzig, pp. 119–156.

WOODLAND, W. (1905–6). "Studies in Spicule Formation—3. On the Mode of Formation of the Spicular Skeleton in the Pluteus of *E. esculentis*," 'Quart. Journ. Micr. Sci.,' vol. 49, pp. 305–325.