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LXII.—On the structure of the Echinoidea

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attached to the soft dorsal; three anal spines. Caudal rounded. Pectoral short, rounded. Scales rather large, finely ctenoid.

It is more difficult to come to a final decision as regards the specific affinity of *Psammoperca waigiensis* and *Cnidon chinensis*. The British Museum possesses now six examples:—

1. The typical example, stuffed, from Australia (9 inches).
2. A stuffed example from Victoria (7 inches).
3. An example in spirits from New South Wales (9 inches).
4. A stuffed example from Torres Straits (12 inches).
5. An example in spirits from Manila (10 inches); obtained by Dr. A. B. Meyer, and undoubtedly identical with *Cnidon chinensis*.
6. A dry skin, said to be from China, obtained from a dealer (10 inches long).

In all these specimens the formula of the fins is the same: the first dorsal has only seven spines, not eight*, the eighth spine belonging to the second dorsal fin. In other respects nearly every one of the specimens shows certain peculiarities, so that no two agree perfectly with one another, not even those from South Australia; but I think these differences are so slight as not to allow of specific distinction. Thus the number of scales in the lateral line varies from forty-seven to fifty-five; the vertical fins are sometimes quite naked, sometimes more or less thinly covered with minute scales; the humerus has sometimes two short points behind, sometimes one of the points is slightly denticulated, sometimes the lower is absent altogether. There is only one point by which the Philippine specimen is somewhat more conspicuously distinguished; and that is the distinctly concave profile of the snout; but also in this respect it is approached by that of our Australian example which is preserved in spirits, although the concavity is so slight that it has been entirely effaced in the stuffed specimens.

Under these circumstances I am inclined to regard these fishes as specifically identical.

LXII.—On the Structure of the Echinoidea. By S. LOVÉN.

[Concluded from p. 385.]

THE same arrangement that is expressed by the formula for the two series of the ambulacral peristomial plates, makes itself apparent also in the appearance of the sphæridia. In the Spatangidæ (for example, *Brissopsis lyrifera*) they first show themselves in the one-pored peristomial plate in each ambulacrum, quite close to the suture, and usually incline over towards the

* What I have formerly (in dried specimens) taken for the spine of the second dorsal fin is, in fact, only the hardened first simple ray.

two-pored plate. While the peristome is still pentagonal, and the mouth only a very little removed from the middle of the buccal membrane, a sphæridium has appeared in the two-pored peristomial plate also in *Echinocardium ovatum*; but this is still much smaller than the first. Thus, even here, series I. *a-V. b* comes after series I. *b-V. a*. When the mouth has shifted its position so far backwards that it nearly touches the labrum, each ambulacrum shows a third sphæridium in plate 2 in series I. *b-V. a*; and when the mouth begins to be concealed by the projecting labrum, the fourth is added in plate 2 in series I. *a-V. b*, apparently first in the paired rows of the trivium. A very young *Cassidulus caribæarum*, 4 millims. in length, has already two sphæridia, the unequal size of which shows that of the one-pored peristomial plate to be the older one; when 7 millims. long it has four, all visible, in deep cavities. When it has reached a length of 12 millims., there are six sphæridia, but the overgrowth characteristic of this group has likewise commenced. An outer layer of shell-substance of irregularly reticulate texture, closely resembling a froth, spreads upon the surface of the test; it is seen most distinctly in the sternal region of the unpaired interradium, where it starts from the middle of each plate and extends over its margins in narrow, tortuous, irregular ridges, so as finally, in the adult, to form the uniform surface with small scattered holes which is peculiar to these genera. In the ambulacra this excrescent layer is first seen to raise the margins of the depressions in which the sphæridia are seated, thus forming a projection from them which gradually covers the sphæridia; and just as of each pair the first sphæridium makes its appearance in series I. *b-V. a*, so it is also this which in its order is first concealed, and afterwards that of series I. *a-V. b*, so that they are overgrown in the order of their appearance.

Toxopneustes dröbachensis again may show how the sphæridia appear in the Latistellæ (see Pl. XIV. figs. 1-8). An individual of 3 millims. (fig. 2) has two sphæridia in each ambulacrum:—one, the oldest, on the binary plate of the first primary plate of series I. *b-V. a*, near its margin; another on the ternary plate of series I. *a-V. b*. At the size of 6 millims. (fig. 3) their number is four; 1 stands still nearer the margin of its primary plate 1, and 2 as before, and two new ones have made their appearance—3 on the other primary plate of the binary large plate of series I. *b-V. a*, and 4 on the third primary plate (3) of the ternary of series I. *a-V. b*, which is an entire plate, not on 2, which is intermediate and a half plate. When the animal is a little more grown (fig. 4), it has also four sphæridia, not, however, 1, 2, 3, 4, but 2, 3, 4, 5. The binary large plate

of series I. *b*-V. *a*, both primary plates of which have coalesced, has become depressed to a great extent; and its sphæridium, which was the first to appear and stood on the margin of its primary plate 1, has disappeared. Sphæridium 2 still remains, but, during the progress of the depression, has approached the margin; 3 stands, as before, on the binary large plate of series I. *b*-V. *a*, and 4 on the ternary plate of series I. *a*-V. *b*; and a new sphæridium has made its appearance on the primary plate 1 of large plate 2 of series I. *b*-V. *a*. These sphæridia, 2, 3, 4, 5, are still present after the large plates 1 and 2 of both series have coalesced into secondary large plates, and the animal has become 11 millims. in diameter (fig. 6). But in a somewhat larger animal of 15 millims. diameter (fig. 7), which has five sphæridia, these are not 2, 3, 4, 5, 6, but 3, 4, 5, 6, 7; for the sphæridium 2, gradually approaching the margin, has disappeared, a sphæridium, 6, has been added apparently on the primary plate 1 of large plate 2 in series I. *a*-V. *b*, and yet another, 7, apparently on the primary plate 1 of large plate 2 in series I. *b*-V. *a*. Finally, at the size of 52 millims. (fig. 8), when the ambulacral peristomial plates are large plates of the third order, consisting of 1, 2, and 3 united, their six sphæridia have the ordinal numbers 3, 4, 5, 6, 7, 8, the last of which apparently belongs to primary plate 1 of large plate 3. Thus by the resorption which takes place in the margin of the peristome, two sphæridia have been lost, and one radiole with its tubercle.

Thus the *asymmetry in the Echinoidean skeleton, with relation to its antero-posterior axis*, is expressed within each ambulacrum, in its two subordinate rows of plates, most strikingly in the arrangement, size, form, changes, and movements, during growth, of the peristomial plates and those immediately following them, in the number and position of their pores, in the order of the appearance and disappearance of the sphæridia; and it will probably not fail, upon closer investigation, in the relations of the radioles and pedicellariæ. In effect it abrogates the radiate plan of structure and displays the homologies between the Spatangidæ and Echinidæ, that even under the latter apparently radiate form we find in the bivium, which symmetrically encloses an unpaired interradium, a bilateral arrangement on the two sides of an antero-posterior axis, which is the same in the mature animal in all the different groups in the class.

If in the peristome of *Toxopneustes drübachensis* (fig. 1, Plate XIV.), or of some other Echinid, we unite by straight lines the five plates I. *a*, II. *a*, III. *b*, IV. *a*, V. *b*, and the five, I. *b*, II. *b*, III. *a*, IV. *b*, V. *a*, two pentagons of the same size and form are inscribed in the circle, each of which has three

approximated angles of equal size. These two pentagons are so placed that the side I. *a* V. *b* stands towards the unpaired interradium, and towards the madreporite's interradium the side II. *b* III. *a*, which is homologous with this,—that the four sides which in the two pentagons enclose angles of equal size but not homologous, are parallel two and two, but the sides which are common for the two unequal but homologous angles intersect each other,—and, moreover, so that the two pentagons together form with their outer lines a figure which is symmetrical, not in relation to that diameter of the stoma which coincides with the antero-posterior axis of the animal, but only in relation to a diameter, $a\omega$, which passes through the point where the last-mentioned sides intersect each other, so that all lines which unite the homologous angles of the two pentagons (namely, IV. *a* with IV. *b*, III. *b* with V. *a*, V. *b* with III. *a*, I. *a* with II. *b*, and I. *b* with II. *a*) are reciprocally parallel and perpendicular to the same diameter—and that consequently, if

Buccal area in a young *Brissopsis lyrifera*: *sph.* sphaeridia.

one pentagon is turned round this diameter as upon an axis, it coincides with the other. In the same way we get two similar pentagons in the pentagonal peristome with rounded angles of

the young *Spatangus* (see fig. 3); and it is clear that this is the case also in the typically equally pentagonal peristome of the Clypeastridæ and Cassidulidæ. The diameter $a\omega$ passes, if produced, through ambulacrum IV. and interradium 1.

The interradia are rows of plates of the peristome, different from the ambulacra in growth and movement. If, by boiling in solution of soda, we carefully separate their plates in *Spatangus purpureus*, *Brissopsis lyrifera*, and *Echinocardium ovatum*, we find that many of them are furnished at their adoral angles with a semilunar lamella, which projects within the aboral margin of the preceding plate, which has a corresponding depression on its inner side. *Spatangus* has such a lamella on the third and fourth frontal and the third, fourth, and fifth lateral plates; *Brissopsis* on the third and fourth frontal and third, fourth, fifth, and sixth lateral plates in the hinder row; *Echinocardium* on the third lateral plate in the anterior row. No doubt the same is the case in many Spatangidæ, perhaps also in other irregular Echinoidea. This is an indication that the plates of the interradia are in some degree scales, although they never fulfil the same functions as the scales in the peristome of the Holothuriæ and Crinoidea.

The interradia in the Echinidæ are in a high degree mutually accordant; into the peristome of these they always enter with two plates, a large and a small one. It is generally only in young Echinidæ that the position of these can be observed. *Toxopneustes dröbachensis*, when young, constantly shows that if we mark the animal's right lateral interradium with 1, and consequently the unpaired one with 5, the smaller peristomial plate and the larger new-formed plate close to the vertical plate are found to belong to 1 *a*, 2 *a*, 3 *b*, 4 *a*, 5 *a*, and the larger peristomial and smaller new-formed plates to 1 *b*, 2 *b*, 3 *a*, 4 *b*, 5 *b*. It is the interradium 3, the left frontal of the animal, that changes the position of the plates (see fig. 1, Pl. XIV.). We find that such an arrangement is symmetrical on the two sides of a diameter passing through ambulacrum I. and interradium 3, the same that is the longitudinal axis in *Echinometra*, and in the vertical plane of which it has the curved line of its flexure.

Whilst in *Echinoneus* the interradia greatly resemble those of the Echinidæ in the forms and relative sizes of the plates, so that even the unpaired one, although perforated by the large periproctium, is still in a high degree in accordance with the paired ones, there is nevertheless a remarkable difference with respect to the peristomial plates, which is worth indicating in order that it may be carefully investigated in young individuals, like so many other things in that animal, such as the oblique mouth, &c. Interradia 1, 3, and 5 enter the peristome

with a single plate, 2 and 4 with two plates; and if we reduce the peristome of *Echinoneus* to a circle, this arrangement also is symmetrical to the diameter which passes through ambulacrum I. and interradius 3. All other irregular Echinoidea have in each interradius only a single plate in the peristome. The arrangement of the interradia is symmetrical in relation to the animal's antero-posterior axis, which is also its longitudinal axis, and passes through the unpaired ambulacrum III. and the unpaired interradius 5—with a constant deviation in the Spatangidæ, without deviation in the Clypeastridæ and Cassidulidæ; whilst in these two families all the four paired interradia resemble each other in a high degree, the two frontal above all, and the two lateral are reciprocally perfectly symmetrical, and the unpaired interradius differs little from them, the plates being analogous in proportion and form, but cut out as if eroded for the periproctium, which is surrounded by the same plates during the whole life of the animal. This is the case in a high degree in *Laganum* and *Echinocyamus*, which have one of the youngest plates which pushes into the vertical plate large and pointed. So also in *Clypeaster*, *Stolonoclypus*, *Encope*, *Mellita*, *Echinarachnius*, and *Arachnoides*, in which the younger plates are gradually smaller and smaller, and those which lie close to the vertical plates small and of equal size, diverging and receiving the genital pores between them.

Much of all this is quite different in the Spatangidæ. The frontal interradia are symmetrical in all living genera; and between them and the lateral ones there is a considerable agreement. If the plates 2 in the frontals are very large, and the following ones very short, as in *Breynia*, *Lovenia*, *Eupatagus*, *Plagionotus*, *Maretia*, *Spatangus*, and *Echinocardium*, the same conditions occur in the lateral interradia; if the plates of the frontals approach a nearly equilateral pentagonal or hexagonal form, the same prevails in the laterals. But among themselves the lateral interradia are never alike, always unsymmetrical on both sides of the longitudinal line; and it is always the right lateral interradius, 1, that deviates. Those Spatangidæ, which seem to be most numerous among existing forms, but were very few during the earliest periods of the family, the *Prymnodesmii*, or those which have an infraanal fasciola and the most regular ambulacra, are also those in which this asymmetry is most strictly maintained. All their genera have in the right lateral interradius, in its hinder row, 1 *a*, one plate less than in the same row of the left one, 4 *b*; the first three plates of the right peristomial plate 1 and two following, represent the first four of the left lateral interradius,

namely peristomial plate 1 and the three following 2, 3, 4. One of the three in interradium 1 *a* must therefore be regarded as composed of two plates; and it is clear that it is the second, which consequently should be indicated by 2+3; but both plate 1 and plate 4, and sometimes plate 5, assist in filling up the deficiency which occurs when the right 2+3 is not so large as the left 2 and 3 taken together. In most cases the former is as large as the two latter, as in *Brissopsis*, *Maretia*, *Lovenia*, *Eupatagus*, and *Echinocardium*; and in these, moreover, plate 4 is of equal size on both sides; in *Breynia*, *Plagionotus*, *Spatangus*, *Xanthobrissus*, *Micraster*, *Paleotropus*, and *Meoma* (which last has only a half infraanal fasciola) the plate 2+3 of the right side is somewhat less than the left 2 and 3 taken together; and then it is the right plate 4 in *Micraster*, *Echinocardium*, and *Paleotropus*, and with this also plate 1, and, in *Meoma*, plate 5, that is larger than the corresponding plate on the left side and fills up the deficiency. In *Brissus*, on both sides, plate 2 in 1 *b* and 4 *a*, is so large and so nearly equilaterally pentagonal that it presses away plate 2 in 1 *a* and 4 *b* from all contact with plate 1; and, moreover, plate 2 in 1 *b* is much larger than in 4 *a*, so that it makes up no small part of the measure that must be filled up in order to correspond with 2, 3, 4 in 4 *b*; here, also, 2+3 in 1 *a* is considerably less than 2 and 3 in 4 *b* taken together, and 4 in 1 *a* larger than 4 in 4 *b*.

The second group of Spatangidæ, which is now, so far as we know, less rich in generic forms, the *Prymnadeti*, those which are destitute of an infraanal fasciola, is far less regular as regards what is here in question. Five genera resemble many of the *Prymnodesmii* in this respect—that they have plate 2+3 in interradium 1 *a* of the right side equal in size to the left 2 and 3 taken together, and, moreover, plate 4 of equal size on both sides, as in *Agassizia* and *Schizaster*, or, as in *Maera*, *Abatus*, and *Hemiaster*, plate 2+3 in 1 *a* smaller than 2 and 3 in 4 *b*, and therefore plates 1 and 4 of the right side, and in *Hemiaster* also 5, somewhat larger than on the left. But three other genera are very divergent. *Desoria* has plate 2 of interradium 1 *a* amalgamated, not with plate 3 in the same row, but with plate 2 in 1 *b*; and the same occurs in *Atrapus*; and in the former plate 2 in 4 *b* is besides separated from plate 1. *Paleostoma*, however, is the most divergent. Whilst all other Spatangidæ have, in each interradium, immediately after the peristomial plate 1, a pair of plates 2, this genus has plate 2 simple in both the frontal and lateral interradia; and, moreover, in interradium 1 it is not in 1 *a* that plates 2 and 3 are amalgamated, but in the row 1 *b*.

This is the diversity that the right interradium 1 shows in all known genera of recent Spatangidæ. It is quite clear that it is not the left side that has a plate more, but the right that has a plate less, and that here within a region not far from the peristome, but separated therefrom, the normal structure of the plates is disturbed. It is in the direction of this interradium that the diameter lies in relation to which the ambulacra are symmetrically disposed. Whether this diameter may possibly indicate the heterologous position which the Echinoderm, whilst still residing in its larva, had with regard to the latter, a primordial axis, from which it subsequently passed to another antero-posterior axis, or whether this abnormal coalescence of certain plates on one side of the animal may perhaps have some connexion with what takes place when the Echinoderm took up into itself the stomach and intestine of its larva, are questions which deserve to be borne in mind during further investigations upon the development of the Echinodermata, but which, for the present, we can only treat in a general way.

The unpaired interradium differs far more from the paired in the Spatangidæ than in the other irregular Echinoidea. It has a far more independent structure; and its dissimilar plates, which are essentially symmetrical, are differentiated for various functions. The first, or peristomial plate, which in the young is not very unlike those of the paired interradia, becomes developed into the labrum, with which the animal, during its movement forward in the soft sea-bottom, raises the mass of mud which constantly fills its intestinal canal. Behind the labrum follows the sternum, composed, like all the following segments, of two paired plates, furnished with powerfully movable, more or less oar-shaped radioles, with which the animal rows itself away; and behind the sternum the episternum and the long row of the abdominal plates, which are generally numerous, and which, in most of the existing genera, close at the madreporite, or, in *Hemiaster* and many extinct genera, are separated therefrom by eye-plates or vertical plates, when these close together behind the madreporite.

The labrum, in most, is very short, so that, with its outer margins, it occupies only the first 2-pored radial plate; in others, such as *Marettia*, *Lovenia*, *Breynia*, *Eupatagus*, *Atrapus*, and *Palæostoma*, it is so produced backward that it corresponds to the two or three first radial plates. The sternum presents, most distinctly in the *Prymnodesmii*, a certain correspondence with the plates 2 of the paired interradia, inasmuch as it is usually small when these are very large, as in *Breynia*, *Plagionotus*, *Eupatagus*, and *Lovenia*. Its relation to the bivium has already been mentioned. The plates of the episternum, in

the same group, are narrowed or pointed backward; and their outer margin forms, with the outer margin of the first abdominal pair on each side, the *angulus episternalis*, into which the produced plates of the bivium project. This angle is very deep in *Eupatagus*, *Breynia*, *Plagionotus*, *Maretia*, *Echinocardium*, *Xanthobrissus*, and *Palæotropus*, and shallower in *Lovenia*, *Brissus*, *Meoma*, *Brissopsis*, and *Spatangus*. It is very small in the *Micraster* of the Chalk, in which it makes its earliest appearance, and which has the episternal plates still of nearly the same form as the other abdominal plates; this is also the condition in the Prynadeti, in which all the posterior part of the unpaired interradium (*e. g.* in *Hemiaster*), by its uniformity, has a certain resemblance to the same part in the Cassidulidæ. This group of Spatangidæ also differs from the Prynnodesmii in that the plates of the unpaired interradium belonging to the left side are notably longer than those of the right side. Even the left sternal plate projects beyond the right one in most of them; if not, the episternum and all following segments are elongated. In *Palæostoma* this difference goes very far, inasmuch as the left plate of the episternum lies with nearly the whole of its length behind the right one, and all the following nearly in the same way. A consequence of this is a projection by which the periproctium, which here also is bounded, at least in front, by the same plates during the whole life of the animal, is not always symmetrically enchased—that is to say, that on one side a smaller number of plates attain its margin; and then it is always the left side that is furnished with a plate more than the right side. In general we may observe that in the Spatangidæ the left side is preponderant.

If we compare a very young *Brissopsis lyrifera*, 4.6 millims. in length, with a full-grown one, we find that the paired interradia in the former have already acquired their permanent form, only that the oldest plates (of the peristome) are comparatively broader, and plates 2 a little longer than in the full-grown specimen—and that in the frontals the small individual has eleven or ten plates, and the large one thirteen, two small plates having been added at the ends. In the laterals ten plates may be counted in both. The unpaired interradium has undergone far more change. The labrum and sternum are alike in both; the episternum in the small individual very short, its posterior margin very narrow; and the præanal plate, that which does not enter into the periproctium, and which changes most of all the plates of the test, is still three times as long as broad, while in the adult its length and breadth are nearly equal. In the latter there are 5–8 anal plates, in the young 5–9; the whole number of plates in the young is fourteen, in the adult fifteen.

It appears from this that the interradia in the Spatangidæ are enlarged principally by the growth of the individual plates, very little by the addition of new plates near the vertical plates. Every plate has a nucleus, which may often be recognized as its umbo, and is surrounded internally by the curves of growth.

If we examine a *Mellita hexapora* 6·5 millims. in length side by side with an adult of 85 millims., we find (besides the changes in the interradia of the ventral side, which are a consequence of the outgrowth of the ambulacra at their expense) that all the interradia in the small individual have from 9 to 10 plates, and in the large one 13 or perhaps 12; for it is scarcely possible to ascertain how far the plate through which the periphery passes is or is not divided into two by a suture. Here, also, the unpaired interradium is differentiated from the rest, although not so much as in *Brissopsis*. The hiatus ("lunula"), which occurs early in this interradium (all the others are situated in the ambulacra and have not yet made their appearance), is in the young nearly circular, in the adult long and narrow; and it shifts its position during growth, so that in the former it is bounded by the ventral plates 2 and 3, and by the dorsals 5, 6, and 7, but in the adult by the same ventrals (2 and 3) but by the dorsals 6, 7, and 8; the dorsals approach the margin, and there even, in some degree, become ventrals. The periproctium, which, like the stoma, is much larger in proportion in the young than in the adult, is round in the former and surrounded in front by a narrow margin of plate 2, which gradually disappears, so that finally plate 1 constitutes the anterior boundary of the aperture, which is oval in the adult. The circumstance that the number of pairs of plates in the interradia in the adult only in a slight degree exceeds that in the youngest, is not difficult to observe also in the Cassidulidæ and regular Echinidæ; whilst in all the augmentation within the ambulacra is far more considerable, and extraordinarily great in the petala of the Irregulares, in which it is greatly multiplied. We soon ascertain that in all Echinoidea the interradia and ambulacra grow and move independently, the former as the plated perisome, the latter as fixed arms.

In *Brissopsis* it is easy to see that the peripetalous fasciola strikes over the same interrarial plate in the adult as in the young, over plates 4 and 5 in the frontals, 6 and 7 in the laterals, and over the tenth plate of the unpaired interradium; and it keeps in both to the same ambulacral plate in the bivium, namely the 14th or 15th, in the paired radii of the trivium to the ninth or tenth, but shifts, apparently, in the unpaired ambulacrum from plates 4 and 5 to plates 5 and 6. So also the infraanal fasciola passes in young and old over plate 3 of the

unpaired interradium (the episternum) and its plates 4 and 5, and over plates 6, 7, 8, and 9 of the inner rows of the bivium. The fasciola consequently grows nearly equally with the plates of the test—but not perfectly; for it shifts a little on the plate within the limits of which it remains. On the inside of the test no indication of it is seen; it does not occupy an interspace between the plates of the test, but is entirely external, and belongs to a stratum of the test which lies without the radioli. For we see sometimes, *e. g.* in *Agassizia*, how, perfectly unaffected and entire, it covers groups of radiolar tubercles which are perfectly recognizable, as to form and arrangement, as through a piece of gauze, and in size are but little inferior to those of the same group which bear radioles immediately beyond its margin. Or we see, for example in *Plagionotus*, a crack in it; and through this the subjacent layer with its radiolar tubercles sticks forth. It has fractures which run transversely; during growth joints arise, when its close rows of tubercles change their direction; and sometimes such a joint coincides with the suture between subjacent plates, sometimes not, when the fasciola passes over it unaltered. Both the peripetalous and infraanal fascioles contain special forms of tentacles which do not overstep their boundaries. In *Brissopsis* the peripetalous fasciola contains, in the unpaired ambulacrum, the powerful tentacles with annular calcareous disks, and in the paired ones branchiæ; the infraanal constitutes the limit between the large tentacles wreathed with cirri, belonging to the inner rows of the bivium, which are produced so that their pores fall within its circle, and the simple, finger-shaped ones, which issue from the ambulacral plates of the sides. When we observe the entirely external position of the fasciola, how it glides over ready developed radiolar tubercles, how the most powerful external organs stand forth only within its circle, how in certain genera (such as *Plagionotus*, *Eupatagus*, and *Breynia*) the tubercles of the test, which on one side of the boundary indicated by it are small and but slightly developed, suddenly make their appearance of large size and strongly marked on the other side, and if we, moreover, note the opposition between the dissimilarity of the regions thus distinguished in the Spatangidæ, and the thorough uniformity in the Cidaridæ, Cassidulidæ, and *Echinoneus*, which have no fasciola, we are induced to ask whether a membrane, perhaps following the largest circumference of the test, may not cover the sides of the dorsal surface, and then, in some forms, check the development of the radioli, but beyond its border, which is the fasciola, leave two free fields for the outer organs and the hard structures of the test, one around the vertex and one infraanal. But this is of little con-

sequence; the fasciola is still an unexplained organ. It has a border-line ("Saumlinie"), says Johannes Müller, comparable with the ciliary border of the larva in these respects, that it forms closed loops and produces an extremely brisk ciliary movement. Its satin-like close clavulæ of equal height, the shafts of which, and not the rounded and soft heads, are the vibratory organs, as was already observed by Johannes Müller, are in a high degree sensitive; and if a few of them are touched, many pass instantly into a common waving movement. With respect to the important question whether the Echinoderm has taken this over from its larva, and the membrane bounds it, it is worth remembering that the infraanal fasciola and the lateral (Desor) exclude each other.

On the dorsal surface, in all recent Echinoidea, the five ambulacra and the five interrada meet at a circle of five ocellar plates and, typically, five vertical plates. The latter have been called genital plates, because, in most cases, the efferent ducts of the genital glands have their external apertures, the genital pores, in them, and they have been regarded as belonging to the organs of reproduction. But they are no more a part of these than the plates of the unpaired interradium are a part of the nutritive organs because in the irregular Echinoidea the anus perforates them. It is easy to ascertain that the plates which have here hitherto been named vertical plates are present and ready formed in young individuals which are not yet fertile, and to observe how it is only at a later period, when the genital glands are matured, that their efferent ducts, oviducts, or *vasa deferentia*, perforate the plates from within. The madreporite, on the other hand, is commenced early during the larval state, and is undistinguishable from the vertical plates, while the genital pores in certain cases are distant from them. The greater the part occupied in the vertical plates by the aquiferous system, the smaller is that of the genital organs; and, *vice versâ*, when the former is small the latter is large. In the Spatangidæ the genital pore is wanting in the plate towards which the percolating apparatus spreads from its central region—so far, that of the normal five never more than four remain, in some not more than two. When, as in *Laganum*, the madreporite, which in some species of that genus opens into a ramified fissure, occupies the middle of the stellate ring, or, as in *Echinocyamus*, it consists only of a single pore, and when, besides, as in both these genera, the interrada close with one plate of the last pair very large and wedge-shaped, the genital pores in the vertical plates are situated near their margins; but when the madreporite is more widely expanded, so that it occupies the whole star of

the vertex, they are placed between the vertical plates and the interrada, as in *Mellita*, or, as in *Clypeaster*, entirely in the latter and separated from the vertex by their last two or three plates. Cotteau long ago made the important observation that an Echinid also, namely *Goniopygus*, has the genital pores outside the vertical plates, near their apices*. But in all the Echinidæ every one of the five vertical plates bears its genital pore, and the madreporite is confined to one of them only, namely 2, the right anterior one. It cannot be doubted that the madreporite and sand-canal are carried to this position in this way—that the intestinal canal, which, in the irregular Echinoidea, has its anal orifice surrounded by the periproctium in the unpaired interradium and only in that, but there terminates at any point from the neighbourhood of the mouth till it cuts through the circle of the vertical and ocellar plates, opens in the Echinidæ in the middle of that circle, which closes round it. While the mouth, which opens earlier, has in all Echinoidea the same position with relation to the ambulacra and interrada, and its peristome independently formed regularly by the same plates fitted for the purpose and in a definite order, the anal aperture has a highly variable position, surrounded by eroded plates, in which it occupies during growth a gradually increased space.

In a young *Toxopneustes dröbachensis* of 5 millims. the vertical plates form a closed circuit, each over its interradium, and in their reentrant angles the five plates which bear the eyes are placed equally regularly. This is also the case in adult individuals of *Echinus*, *Sphærechinus*, and *Psammechinus*, and also in the Salenidæ. But in *Toxopneustes* and most others this primordial and normal arrangement is soon disturbed. The eye-plates of the bivium are gradually pushed into the circle on both sides of the vertical plate of the unpaired interradium 5, between this and 1 on the right side and 4 on the left. It is eye-plate I. that first reaches the inner circumference, and next eye-plate V., as in most genera, such as *Loxechinus*, *Lyttechinus*, *Helicoidaris*, *Tripneustes*, *Boletia*, *Salmacis*, *Echinoidaris*, *Acrocladia*, and *Echinometra*; in *Amblypneustes* and *Mespilia* they come quite near it. Of the eye-plates of the trivium, IV. approaches the inner circumference, which it reaches in many; II. also approaches it, but in a less degree; and III., the eye-plate of the unpaired ambulacrum, is always distant from it. In *Diadema*, on the other hand, all the eye-plates are seen more or less completely to touch the anal

* "Echinides fossiles du Département de la Sarthe," pp. 152, 154, pl. 26. fig. 2, and pl. 27. fig. 25; "Echinides fossiles du Département de l'Yonne," ii. p. 50, pl. 52. fig. 14: Bull. Soc. Géol. Fr. 2^e sér. xvi. p. 162.

membrane. This change of position depends, no doubt, upon the circumstance that the periproctium, by the resorption, especially, of the vertical plates 1 and 5 and by stretching, is enlarged more rapidly and strongly than the breadth of the vertical plates increases, and that the eye-plates, on which the growth of the ambulacra reacts as a *vis à tergo*, are driven into its median space. Vertical plate 2, which contains the madreporite, is enlarged more than the others, and keeps back eye-plates II. and III.

The anal aperture is produced in the same way in the Spatangidæ and Echinidæ. Quite young individuals of the former have the periproctium much more dorsal than older ones, as is the case in a high degree in a *Spatangus purpureus*, 2·025 millims. in length; this species is destitute of the peripetalous fasciola. So early as this the periproctium is nearly round, with the anus about in the middle. The anal membrane is closely covered with thin imbricated scales, which form circles:—the innermost one of long, narrow, pointed lamellæ, connivent around the anus; and around this one or more, consisting of larger triangular scales; the outermost a circle of still larger plates. Of these last, in many genera, the adoral grow preponderantly, so that the periproctium is gradually elongated, and the anus comes to be situated more excentrically in an aboral direction. It is otherwise in the Echinidæ.

In his memoir on the Echinoidea collected by Pourtales in the great depths between Florida and Cuba, Alexander Agassiz states that in a very early stage, when, however, the mouth with its jaws is already developed, "the anal system of the Echinidæ is limited to a single subanal plate, which makes its appearance before the genital and ocellar plates, and long remains more prominent than the other plates, which are added to complete the enlarged anal system"*. The pentagonal or somewhat rounded space which is enclosed by the five vertical plates is embraced at this stage by a single unpaired disk. Soon afterwards, in a young *Toxopneustes dröbachiensis*, place begins to be prepared for the anus; but this occurs not in the middle of the disk, but excentrically and outside of it. The margins of vertical plates 1 and 5 are absorbed, and between them and the central disk an interspace is produced which is occupied by the soft general integument. In this is formed a pair of free, rounded, oblong, calcareous pieces, which do not coalesce with the disk. Whilst the periproctium enlarges so that it becomes oval in an oblique direction, and the disk is raised a little at its free margin, although

* 'Contributions to the Fauna of the Gulf-stream' &c. pp. 281, 284, 285. From 'Memoirs of the American Academy,' ix. p. 12.

it constantly remains attached by that opposite to vertical plate 3, another pair of rounded pieces appears in the enlarged interspace, and another near vertical plates 2 and 4; and, as many such are added, gradually becoming smaller and smaller, their number is greatly increased; while the original central disk, which itself does not grow much, is still long recognizable by its position and size. Finally the periproctium is eroded into a large oval aperture; the calcareous pieces which closely fill its covering membrane become very numerous, and the surrounding plates strongly eroded. The anal aperture, which is not completed until this augmentation of the calcareous pieces in the skin is considerably advanced, is always situated more or less excentrically in the apex of the membrane, which gradually rises conically, and normally in the direction of ambulacrum I.; and the oval periproctium generally has its longest diameter in the same direction from interradius 3 to ambulacrum I., the same that is the longitudinal axis of the test in *Echinometra*, and in relation to which the peristomial plates of the interradia are symmetrically arranged in the Latistellæ.

This formation of hard pieces of calcareous network occurring in the central space, within the circle of the vertical plates, and which, in the earliest stage, gives origin to a single disk, but afterwards, during growth, divides itself regularly into different centres for the production of numerous, free, smaller and smaller pieces, agreeing in their texture with the first disk—the whole of this structure, although in close connexion with the appearance of the anus, belongs nevertheless not to its development but to that of the dermal skeleton; and the complex of hard parts which originates therefrom is an independent part of the latter. It recurs in the Salenidæ, not early broken up into different small parts, but constant, coherent, and solid, in the pentagonal disk which here regularly occupies the central space. At the appearance of the anal tube it is partly eroded by absorption in its posterior margin, but still more the vertical plates lying behind, in *Heterosalenia* and *Salenia*, 1 and 5, in the normal direction towards ambulacrum I.,—in *Acrosalenia*, *Goniophorus*, and *Peltastes* only plate 5, as has been explained by Cotteau, who was the first that correctly oriented both these and all other forms of Echinidæ, in the manner here confirmed. In these genera it is not an added supernumerary plate, but a normal part of the skeleton, which in them retains during the whole life of the animal its original form but little altered by the intrusion of the anal tube; whilst in other Echinidæ it is very early changed into a flexible covering, or, as in *Diadema*, entirely disappears. It seems

probable that careful investigations will show that this independent central disk may recur in the irregular Echinidæ in the median area of the vertex, which is penetrated by the madreporite, and in many of them (*Pygurus*, *Clypeus*, and others) is very large.

If we get rid of the notion that the vertical plates are an appendage of the generative organs and the central disk of the alimentary canal, if we see the latter in young Echinidæ in its original state, and consider, moreover, the vertex of the Salenidæ as being entire and not eroded from the periproctium, we obtain an arrangement of these parts of the skeleton the nearest homologue of which is to be sought in an Echinoderm of a class which is regarded as very distinct from the Echinoidea. The *Marsupites*, only known as fossil, a Crinoid without a peduncle, has in the pole opposite to the mouth a single pentagonal disk closely embraced by the five basalia. It is the same arrangement as that of the vertex in the young of *Echinus* and in the Salenidæ. The central disk and the basalia, with the rest of the plates in *Marsupites*, have striæ or grooves which are perpendicular to the suture, and may be traced up to the middle of the plate, and make their appearance most distinctly when its outermost calcareous layer is eaten away. But this character is no peculiarity of *Marsupites* or of the numerous Crinoidea in which it occurs. If we carefully examine the central disk and vertical plates in small Echinidæ, we find exactly the same structure. It may be discerned even on the surface by direct light, but is exceedingly distinct by transmitted light and suitable treatment. We see the pentagonal plate divided into five triangular areas, which have its five sides for their bases, their apices united in its middle; the reticulated texture is arranged, in each area, so that straight parallel rods perpendicular to the base have narrow interspaces between them. In the middle of the plate the rods and interspaces of the different areas meet together and unite, crossing each other in a closed and apparently irregular network; but in the sutures those of one plate are seen to meet those of another in the same direction. This structure recurs in all plates in the Echinoidea, whether regular or irregular, and is the same that has long been known in the Cystidea. In the fossil Salenidæ these striæ are seen very generally; and the structure of parallel rods in the interior is very distinct in a living *Salenia* from the great depths near the Antilles, for which, as for a *Pygaster* from the same depths, and numerous other valuable objects, our Royal Museum is indebted to Dr. Axel Goës's conscientious and indefatigable researches.

Another trait which expresses the homology between the

base of *Marsupites* and the vertex of the Salenidæ is to be found in the elevated ridges which in both unite the middle points of the plates; and the strongly developed vertical plates of the Salenidæ scarcely present any "sculpture" which does not recur in a similar form in the Crinoidea.

Now, since the central disk in the young Echinidæ and in the Salenidæ is to be regarded as homologous with that of *Marsupites*, the five plates which embrace it, and which here are called vertical plates, but have hitherto borne the name of genital plates, are *ipso facto* to be interpreted as basal pieces (basalia), and the "eye-plates" in their reentrant angles as radial pieces (radialia). A calyx is present in its essential parts, homologous, by its position at the pole opposite to the mouth, its constitution, and its structure, with that of the Crinoidea. But since the Echinoidea are free animals which turn their mouth towards the surface whence it takes its food, the calyx comes to be the vertex of the dermal skeleton instead of its base. It receives the newly formed plates of the corona, the basalia meeting the growing ends of the interradia, and the radialia those of the ambulacra. In the Echinidæ which have their anal aperture where the peduncle of the Crinoidea is attached, the calyx is normal and recognizable in its form; in the Clypeastridæ it is most frequently entirely penetrated by the madreporite, which effaces the sutures of the pieces; and in the irregular forms with an elongated antero-posterior axis and a developed bivium (*Echinoneus*, Cassidulidæ, and Spatangidæ) it becomes entirely abnormal, and, in the Collyritidæ, during the Jurassic and Cretaceous periods, was broken up, so that the two radialia which meet the bivium were separated from it by the perisome. But it is not absent from any form of Echinoidea.

The investigations which are here communicated will, it is hoped, speedily appear in a more detailed form, illustrated by a selection from numerous figures carefully prepared by M. A. M. Westergren.

EXPLANATION OF PLATE XIV.

Fig. 1. A young *Toxopneustes dröbachensis* of 4 millims., spread out from the peristome. I., II., III., IV., V., ambulacra; 1, 2, 3, 4, 5, interradia. In the middle the mouth with the teeth; around this, in the buccal membrane, ten free pore-plates, two for each ambulacrum, of which the five which lie before I. *a*, II. *a*, III. *b*, IV. *a*, V. *b* are perceptibly larger than the others. Peristomial plates I. *a*–V. *b* and I. *b*–V. *a* are united by straight lines; and by this means two pentagons are inscribed in the circular stoma, symmetrical only in relation to the diameter *a* ω . The plates of the vertex kept together, upon interradium 2 (where the madreporite has its place), with the central disk, *d*, *c*. The inner circle,

already enlarged and elongated in the direction of ambulacrum I. by the absorption of the vertical plates 1 and 5 at their inner margins; in the interspace small pieces of calcareous network show themselves. The verticals are not yet perforated by the genital pores. Of the eye-plates, I. has already pressed in between 1 and 5, and II. approaches the inner circle.

Figs. 2-8. *Toxopneustes dröbachensis*. Ambulacrum III., to show its changes during growth. 1, 2, 3, &c., primary plates and tentacular pores; 1, 2, 3, &c., large plates; 1, 2, 3, &c., sphaeridia; 1, 2, 3, radiolar tubercles.

Fig. 2. Young of 3 millims. The tentacular pores still in nearly unaltered primordial curves. Two sphaeridia.

Fig. 3. Young of 6 millims. The tentacular pores already distinctly arranged in secondary curves. Four sphaeridia, 1, 2, 3, 4. The peristomial plates depressed. The radiolar tubercle 1 in *a* 1 much diminished.

Fig. 4. Young, somewhat larger. The peristomial plates more depressed; in *a* 1 the two primary plates have coalesced. Sphaeridium 1 has disappeared, and 5 has been added. Radiolar tubercle 1 in *a* very small, that in *b* 1 diminished.

Fig. 5. Young, somewhat larger still. In *a*, large plates 1 and 2 have coalesced to form a binary peristomial plate; in *b* the sutures of the primary plates have disappeared. Radiolar tubercle 1 in *a* 1 lost, in *b* 1 diminished.

Fig. 6. Young of 11 millims. diameter. In this, as in the following, large plate 3 in *a* has only three primary plates. Large plates 1 and 2 coalesced into a binary plate, also in *b*. Radiolar tubercle 1 has disappeared both in *a* and *b*.

Fig. 7. Young individual of 15 millims. The binary large plates 1+2 in both rows depressed. Sphaeridium 2 has disappeared, and 6 and 7 have been added. Radiolar tubercle 2 diminished.

Fig. 8. Adult individual, of 52 millims. diameter. Large plates 1, 2, and 3 in both rows have coalesced to form ternary peristomial plates. One sphaeridium, 8, added. In *b* there is still, apparently, a residue of radiolar tubercle 1.

Fig. 9. Stoma of a very young *Toxopneustes dröbachensis* of 2 millims. diameter. Of the free plates in the buccal membrane those which belong to I. *a*, II. *a*, III. *b*, IV. *a*, V. *b*, have not yet acquired pores. One sphaeridium in each ambulacrum in I. *b*-V. *a*.

Fig. 10. Young of some northern Echinide, 0.6 millim. in diameter, from the ventral side. The pigment-spots are omitted, and the radioli only partially represented. No remains of the larva; no trace of jaws; no mouth or anus. Five large primordial tentacles, which, according to Krohn, soon disappear. Within these five pairs of smaller permanent tentacles, each of which stands over a disk of calcareous network, the first primary plates in the ambulacra. Outside of and between the pairs of these there are other disks, probably the foundations of the interradia. From an individual preserved in spirit.

Fig. 11. One of the large primordial tentacles with its disk, and in the latter a ring of calcareous net. In the wall of the tube longitudinal and transverse muscular fibres.

Fig. 12. One of the smaller permanent tentacles in the young animal, fig. 10, with its disk and a portion of the calcareous net which lies beneath its base.

Fig. 13. The oblong, externally pointed opening in the calcareous network, the pore, over which the tentacle stands.