Studies On The Pseudofasciole Of The Scutellids (Echinoidea, Scutellidae)

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https://doi.org/10.5109/22589

出版情報：九州大学大学院農学研究院紀要. 6 (2), pp.41-93, 1939-05. Kyushu Imperial University
バージョン：
権利関係：

Journal of the Department of Agriculture, Kyūsyū Imperial University, Vol. 6, No. 2,
May 20, 1939

STUDIES ON THE PSEUDOFASCIOLE OF THE SCUTELLIDS (ECHINOIDEA, SCUTELLIDAE)[1]

Hayato IKEDA

Plates 2—13

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[1] Contributions from the Zoological Laboratory, Kyūsyū Imperial University, No. 106.

PREFACE

The chapters in this treatise are arranged for the most part in the order in which the present investigation was pursued. They were written originally not as parts intended to make up a compact whole, but each rather in the form of an interim report at the close of a period of inquiry. For this reason they contain some repetitions, which I have not attempted to remove when putting these papers together.

The field of the present investigation has extended over all the members of the Scutellidae, with an exception of only one form, *Echinodiscus bisperforatus* var. *truncatus*, and even in this case, I think, I have made a guess not very wide of the mark. Concerning the three forms, namely, *tenuissimus* and *bisperforatus* in the genus *Echinodiscus* and *deciesdigitata* in the genus *Rotula*, I have had to put up with an indirect method of examining figures instead of specimens. All the rest I was fortunate enough to study at first hand without going abroad. Naturally I am under an immense obligation to many colleagues who assisted me in one respect or another, especially to those who furnished me with the requisite material. I would fain offer my heartiest thanks to all of them,—no less to those kept in the privacy of my remembrance than to those mentioned in the text or the foot-notes. Very particular thanks are due to Professor HIROSHI OHSHIMA, of Kyūsyū Imperial University, Dr. THEODOR MORTENSEN, of Copenhagen, Dr. HENDRICK ENGEL and the authorities of the Zoological Museum in Amsterdam, and Dr. HUBERT LYMAN CLARK and the authorities of the Museum of Comparative Zoology at Harvard College, Cambridge, Mass., for an exceptional encouragement with which they favoured me, as specified below.

In Chapter 1, the specimens observed include no more than 2 genera and 3 species. To relieve poverty of material, reference was favourably made to the figures of 5 other species belonging to 3 genera, found in the works of several echinologists.

In Chapter 2 and Chapter 4, I am indebted to Dr. MORTENSEN and Prof. OHSHIMA. During his recent tour in Europe, Professor OHSHIMA was so kind as to comply with my request and examine some scutellids in the collection of the British Museum, and to his generosity I owe the evidence cited. Moreover, on his visit to Dr. ALBERT PANNING at the Zoological Museum in Hamburg, he wrote to me about a really interesting line which he had observed there in a specimen of *Echinodiscus auritus* LESKE. On the other hand, if it had not been for the kind permission of Dr. MORTENSEN to utilize some of his specimens, I could not have set forth an important part of my observation and opinion with so decisive a tone.

Chapter 3 treats of the specimens in the collection of the Zoological Museum in Amsterdam, the loan of which was procured through the good offices of Dr. ENGEL. It gave me great pleasure to observe these specimens, especially as they included some forms belonging to the two genera, *Encope* and *Mellita,* which had been perplexing me.

In Chapter 5, all those forms of the Scutellidae, which I had to leave untouched before, were brought under my observation through the kindness of Dr. H. L. CLARK, who offered me an opportunity to study on loan these valuable specimens.

It must be repeated that the generosity of the authorities of the museums both at Amsterdam and at Cambridge in lending me their rare specimens and especially the kindness of those who, on their own responsibility, have procured loans for me are indeed beyond all estimation, considering, among other difficulties, that these brittle things had to be transported half way round the globe to me and back again at the risk of sustaining damage.

Last, but not least, apart from the supply of material and facilities of study accorded by him, I must mention Professor OHSHIMA's excellent advice and constructive criticism in particular, which have been of the greatest aid throughout the course of the preparation of the present treatise.

CHAPTER 1

The "pseudofasciole", or zigzag line, found on the surface of the body in some scutellids

While I was observing, during April 1935, a small but important collection of echinoids sent by Mr. HIDEYA NAKAMURA of the Kominato Marine Biological Station of the Imperial Fisheries Institute, my attention was drawn to certain indented shadings on some specimens of *Astriclypeus manni* VERRILL with unimpaired spines. Since then, by re-examination of some dry specimens of the same species in the collection of our laboratory from several localities, I found, in those of them which had well-retained spines, a dark shading with an indented edge falling longitudinally on both the dorsal and oral surfaces of the posterior interambulacral zone. But, so far as I know, no statement on such a shading was published until the one by myself (IKEDA, 1935b).

In proceeding further to inquire into the question before us, it was necessary first to examine different forms of the scutellids with respect to the indented shading. In some specimens of *Echinarachnius mirabilis* (A. AGASSIZ) from Hukuoka Bay, where this form is common, I succeeded in making out the same indentation as had already been found in *A. manni*. In this case the posterior interambulacral zone was longitudinally divided by the indentation into two almost equal parts, the lighter and darker half-zones[2], so that, with a fine effect of chiaroscuro produced thereby, this posterior zone was distinctly marked out from all the other zones. At the same time, I was struck by the peculiarity of the zigzag line dividing these two parts. In addition to the examination of these specimens which I collected myself, I could best observe the same kind of indentation in some specimens of *Echinarachnius brevis* **IKEDA** from Muroran (IKEDA, 1936)[3].

More instances can be cited very easily from literature. In Figure 4 of AGASSIZ's Plate XIII^{d} (1873) showing the dorsal view of *A. manni*[4], one can easily trace a part of the zigzag line in the posterior interambulacral mid-zone, although the author does not at all refer to it.

Furthermore, the genus *Echinodiscus*, several members of which were figured excellently by DÖDERLEIN in his photographs (1902, Pl. LXV), called my attention to the indented shadings in particular. It seems fairly reasonable to consider that the shadings are of no

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[2] The term half-zone denotes either the lighter or the darker half of the interambulacral 5, as distinguished from a 'column'.

[3] In obtaining these specimens I am much obliged to Professor TOHRU UCHIDA of the Hokkaido Imperial University.

[4] Judging from what AGASSIZ (1872, p. 93; 1873, p. 539) said, the example may have been one of the specimens from "Linguin, China Sea", whereas, CLARK (1925, p. 171) described this form as a species indigenous to Japan, and therefore we may have doubts about its distribution. The matter must not be decided hastily in favour of CLARK whose judgment has so far been supported by subsequent collectors (cf. RATHBUN, 1886, p. 285).

casual character, as they invariably occur in these photographs. The shadings, for instance, can be found on the dorsal views (Figs. 4a, 5) of two specimens of *E. tenuissimus* (AGASSIZ et DESOR) from Thursday Island. The same kind of shading is also recognizable, though somewhat obscurely, on both the dorsal and oral views (Figs. 3, 3a) of an example of *E. auritus* LESKE from Ceylon. And again, the dorsal view (Fig. 6) of a partly denuded test of *E. bisperforatus* LESKE from Singapore shows a similar shading. All these shadings appear to have a fairly close resemblance to that of *A. manni*, and it is interesting to see that these photographs show the shady parts always on the right-hand side. But DÖDERLEIN passed over the shadings without remark.

Again, the figures in the plates of both CLARK (1904, Pl. 10, Fig. 58) and COE (1912, Pl. XXVII) show somewhat obscurely a part of the indentation in the dorsal view of *Echinarachnius parma* (LAMARCK); CLARK's specimen came from Woods Hole and COE's from somewhere in Connecticut. Also in the photograph by MORTENSEN (1927b), in which the dorsal view of *E. griseus* MORTENSEN is shown, a part of the indented shading is traceable, though not clearly. I found these indentations[5] much like those of *E. mirabilis*. None of the echinologists seems to have shown any concern about these facts, although it has already been noticed that all the forms in this genus resemble one another very closely in certain other features.

I am now going to consider the indentations mainly from what I have observed on the dorsal surface of *E. mirabilis* as a type of the whole genus, and both the dorsal and oral surfaces of *A. manni*, by which the most nearly related and similarly-shaped *Echinodiscus* may reasonably be represented at the same time, and especially to dwell on the zigzag line or the indented border between the lighter and the darker parts in the posterior zone. Reference will be made occasionally, among other data, to what I have seen in the above-mentioned figures by AGASSIZ, DÖDERLEIN, CLARK, COE and MORTENSEN.

The spines of a sea-urchin are, as a rule, arranged radially,

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[5] I could subsequently ascertain by observations of some specimens of the same species from Sakhalin, collected for me by Mr. TOMOE UKITA, that the indentation in this form was quite similar to that in the young individuals of *E. mirabilis*, appearing on the abactinal surface only.

as may naturally be expected from the shape of the test. Nevertheless, in the genera *Echinarachnius* and *Astriclypeus* the spines of the posterior interambulacrum are inclined in a peculiar way; *i.e.* the spines in each half-zone diverge from those in the other half-zone at a larger angle than ordinary spines do from one another. Therefore, according to the angle of the light that falls on them, these half-zones may be illuminated in a different way from each other. This convinces me that the chiaroscuro depends directly upon the inclination of the spines. Evidently it does not follow that one half-zone is constantly shady and the other constantly bright; indeed one and the same side may be made bright or shady according to the angle of illumination.

At first sight, I took it for granted that the zigzag line formed by the meeting of the lighter and darker parts must agree exactly with the longitudinal suture of the plates. So, for the purpose of assuring myself, I took a specimen and put a mark on the test with a needle along one section after another of the zigzag, and then removed all the spines for examination. The result did not answer my expectation, the needle-marks left upon the plates ran regularly intercrossing every element of the longitudinal suture. In the light of this fact it is very interesting to turn to the photographs in DÖDERLEIN's Plate LXV mentioned before, which show both the dorsal and oral views (Figs. 3, 3a) of *E. auritus* LESKE. For on these photographs is impressed a very striking pattern showing just how the zigzag intercrosses the suture, and that, in spite of the fact that the original examples seem to be fully coated with spines.

A turn in the zigzag line which occurs on a plate of one column of the zone is repeated by another turn on the corresponding plate of the other column, so that every two turns make a pair. When one of the pair is made to come at the end of a tooth of the indented shading, the other is at the bottom of a cutting. Therefore, by disregarding the turns at the re-entrant corners, the number of turns in the zigzag line will conveniently be represented by the number of the salient angles or the teeth of the indented shading. Every species seems to have its own number of teeth. In *E. mirabilis*, so far as I can see, the number of the teeth on the dorsal surface varies from nine to twelve, and in *A. manni* seven to ten; while on the oral surface of *Echinarachnius* the line cannot be detected. On the other hand, in *Echinodiscus* and *Astriclypeus* the line extends on both the dorsal and oral surfaces. On the oral surface it develops between the periproctal opening and the distal margin of the test; the line in this portion, which is not so clearly visible as on the back, has only one tooth or two. The relation between the line and the suture of the plates is identically the same on the oral side as on the dorsal.

That the line results from a peculiar inclination of the spines has already been said; but it is a question whether this inclination is ascribable to a highly specialized differentiation of the muscles with which the spine is closely attached to the tubercle (HAMANN, 1887). The spines of the posterior interambulacral zone do not seem to have any particular form, neither is there any special arrangement of tubercles along the zigzag, and one cannot find any trace of the zigzag line on a denuded test. In other words, tubercles do not indicate the existense of the zigzag line, while the existence of spines is fundamentally necessary for the display of the indentation.

In forming the horizontal suture in the interambulacral 5, the plates of the right column slip back slightly behind the corresponding ones of the left column in the dorsal view. This usually occurs not only in clypeastroids (to which the Scutellidae belongs) but also in spatangoids; and in the Scutellidae, it may be regarded as one of the main causes that form the indentation in question.

In such genera of the clypeastroids as *Clypeaster*, *Arachnoides*, *Laganum* and *Peronella* (though they are closely allied to the Scutellidae which comprises the genera *Echinarachnius*, *Echinodiscus*, *Astriclypeus*, *Dendraster*, *Encope*, *Mellita* and *Rotula*), I could not find any similar line; and moreover, judging from the above-observed data, it is certain that the line is quite distinct from all forms of the fasciole peculiar to the spatangoids. Hence it is presumably a new character of the said members of the Scutellidae and its existence may even be expected in the hitherto untouched members of this family, such as *Dendraster*, *Encope*, *Mellita* and *Rotula*. The inquiry however into these forms with reference to the line will be left for the future, as at present they are not within my reach. Whether this remarkable character is constant in the present family, as yet I have not sufficient evidence to determine.

It is exceedingly remarkable that the line exists only in the space between the periproctal opening and the apical system, or in other words, that the line is not permitted to extend any farther, but is restricted within a definite space of the posterior zone, so that the line may have different lengths according to the distance from the apex to the periproct, the position of which sometimes varies. In the young *Echinarachnius*, for example, the periproctal opening is situated on the supramargin, and after maturity, on the margin of the test⁽⁶⁾ in most of its members (CLARK, 1904; IKEDA, 1935a). This opening in most species of this genus therefore takes various positions on the abactinal side in the course of the growth of the animal. To make this clear, it is of course necessary to compare with one another as many individual varieties as possible. And the shifting of the periproct in the scutellids during the growth of the animal seems to take a backward direction, as is also the case with certain spatangoids. In *Dendraster* and *Echinodiscus* the periproct seems to have shifted so far as to cross over the margin and open on the oral side, as in *Astriclypeus*. In *Encope* and *Mellita*, besides this feature⁷⁾, there is a hole in the posterior interambulacral mid-line, piercing the test. Hence it may be assumed that here the line is made as much shorter as the hole interferes with the line. After all, on the basis of many observed facts, it does not seem unreasonable to look upon the zigzag line, thus representing the track of the backward migration of the periproct with age, as something like a record of the history of an individual in its development.

The line takes a course distinct from that taken by any form

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⁶⁾ In most members of *Echinarachnius* the periproctal opening is generally on the margin, or, more strictly speaking, on the longitudinal suture of the 3rd pair of plates in the interambulacral 5.

⁷⁾ It has since been confirmed by the examination of many materials at my disposal that, in the full-grown animals, the plates lying between the peristome and the periproct as well as those between the periproct and the margin of the test, vary in number according to the genus, except in some forms of *Echinarachnius*, in which the periproct opens on the margin. In *Dendraster*, for instance, the periproctal opening is usually situated on the line of the longitudinal suture of the 3rd pair of plates in the interambulacral 5; in *Echinodiscus*, *Astriclypeus*, *Encope*, *Mellita* and *Rotula*, on the 2nd pair.

of fascioles[8] which invariably enclose a certain area of the body (LOVÉN, 1874), but on the other hand the line seems to be related to the fasciole in the fact at least that it has an indisputable tendency to extend, as the fasciole does, from a protuberance of one plate to that of another (IKEDA, 1935c, d); so that if this structural detail is taken into consideration, the zigzag line may be regarded as a most primitive kind of fasciole. After all, we shall perhaps be unable to find out any structure quite similar to the zigzag line in other families of the Echinoidea. I have proposed for the line of the above-mentioned members of the Scutellidae a name "pseudofasciole", with the idea of distinguishing it from all forms of the fasciole.

The pseudofasciole was ascertained to occur in the following 3 genera including 8 species in the Scutellidae[9]. 1. **Echinarachnius parma* (LAMARCK), 2. *E. mirabilis* (A. AGASSIZ), 3. *E. brevis* IKEDA, 4. *E. griseus* MORTENSEN, 5. **Echinodiscus auritus* LESKE, 6. **E. bisperforatus* LESKE, 7. **E. tenuissimus* (AGASSIZ et DESOR), 8. *Astriclypeus manni* VERRILL.

CHAPTER 2

The pseudofasciole of the genera Dendraster, Encope and Mellita

In illustrating the zigzag line in the previous chapter, a large extent of investigation was left for the future. At that time I had to deal with very few specimens, those which served my purpose being extremely limited in variety of forms; and more materials had to be acquired before the line could be regarded as an unquestionably valid feature. The data shown in the present chapter are particularly concerned with the question of the zigzag line of some other forms which were not dealt with before.

The line in question is found in the following species, as was substantially confirmed by Professor OHSHIMA on his visit to the

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[8] The varieties of the fasciole found in the spatangoids by VAN PHELSUM in 1774 and afterwards by others (MÜLLER, 1854; GRAY, 1855; LUDWIG u. HAMANN, 1902; IKEDA, 1935c) are the main characters distinguishing families as well as genera, as shown by CLARK (1917) and MORTENSEN (1927a).

[9] Those marked with an asterisk were studied indirectly by means of photographs.

British Museum; 1. *Dendraster excentricus* (ESCHSCHOLTZ), one dry specimen from Anheim Bay; 2. *Encope emarginata* (LESKE), two specimens from Brazil, both of them being 11 cm in length; 3. *Mellita sexiesperforata* (LESKE), one specimen from St. Thomas, 7 cm in length. Referring to these specimens he said: They have each, on the dorsal surface only, a zigzag line different in form from each other; and in two genera, *Encope* and *Mellita*, the line is not extended to the oral surface on account of the formation of a hole. (Such holes are known as lunules).

Besides these examples, Professor OHSHIMA found that anything like the zigzag in question had not been discernible in the genus *Rotula*.

Afterwards, thanks to the kindness of Dr. MORTENSEN, I was fortunate enough to examine the following two dry specimens: 1. *Dendraster excentricus* (ESCHSCHOLTZ); a specimen from Nanaimo, Vancouver; 5.7 cm in length; collected in 1913: 2. *Mellita sexiesperforata* (LESKE); a specimen from Tobago, British West Indies; 4.3 cm in length; collected in 1916. From them it was proved conclusively that these species had each a different zigzag on the dorsal surface, a fact as to which until then I had not been quite satisfied.

In addition to the instances above adduced, in a specimen of *Echinarachnius parma* var. *obesus* H. L. CLARK from Paramusiruzima in the Kuril Islands, (which was presented through the kindness of Mr. YOSINE HADA), a zigzag line was distinctly visible on its dorsal surface only, as had been expected to be the case.

The line was called by the name of pseudofasciole, because of its close resemblance to the fasciole. Indeed they are very much alike in some points, but they seem to have many significant differences in structure. Accordingly, in dealing with the pseudofasciole, the importance of these dissimilarities rather than of the similarities must be emphasized, especially with regard to its course as well as to its relation to the tuberculation. The pseudofasciole in every variety of it takes a course quite different from that of the fasciole, running always from the apex of the test to the anal opening; and it is in every respect rather more primitive than the fasciole, being not so highly specialized and variable as the latter. Such small spines as clavulae, with which the fasciole is coated, are never seen in the pseudofasciole at all.

This line is to be regarded as the most remarkable one among so many features in the majority of the members of the Scutellidae, for nothing quite equivalent to this line seems to have been known in all the echinoids. This fact suggests the existence of an interesting point which may turn out to be of considerable value in the comparative study of different forms of sea-urchins. In the Echinoidea there are now two cases known in which the test is partly spined in a peculiar way; namely, the spatangoids with their fascioles and the scutellids which have the pseudofascioles under discussion.

In most cases, the zigzag line is plainly visible to the naked eye even on the animals alive in the water, though it requires some practice to find them, while it is almost entirely hopeless to search for indented shadings without the proper lighting.

So long as the specimens are fully coated with spines in a good state of preservation, the pseudofasciole will be found only on the surface of the interambulacral 5, though it is not always easy to find it. In order to make a successful search for the zigzag line, first, the light must not be too strong, and secondly, the animal must be held in such a position that the light falling upon it brightens the spines on one side only, leaving the other half dark. This particular device for discovering the line has been applied to all cases alike, and proved to be the right method. By this method, we can see the zigzag line dividing the surface longitudinally into two parts, the right- and left-hand sides, one of which shines by reflection of light and the other remains comparatively dark. This chiaroscuro is due to a peculiar inclination of the spines, which, on each side, turn their tips away from the other side; so that the brilliance or the obscurity of one side or half-zone is not its inherent and unchangeable property, but depends solely upon the position in which the specimen is exposed to light.

Naturally, the inclination of the spines determines the boundary which runs between the two sides in the form of a zigzag ridge. Now, the ridge may well be said to have the semblance of a longitudinal suture in that mid-zone; but if it is traced cautiously with a needle, the marks left upon the denuded plates will show a course running over both columns of that zone alternately—*i.e.* say from column a to b and then back to a and so on—forming a zigzag line of which every other turn comes in one column. It is indeed a simple fact that the ridge runs in zigzags, but the making of the zigzag course is not so simple as it may seem. In fact, the elements of the line run as if they were sewing together both columns a and b in the interambulacral 5, and thus each section of the whole line intersects the corresponding part of the longitudinal suture of the plates beneath. Therefore, if one sees the two series of zigzag lines lying one upon the other, one will have an impression that a number of X-shaped crosses gradually increasing in size towards the distal end are linked into one tapering longitudinal chain. As may be inferred from this, it was utterly impossible to make the needle-marks coincide with the line of the suture over any length.

It must be emphasized that this is an entirely different thing from the suture of the plates. The angles of the zigzag, however, vary, as the angles of the suture line do, both in number and size according to the genus.

The number of the turns[10] in the zigzag generally ranges from 6 to 12 on the dorsal side, while only 1 or 2 can be observed on the oral side. Specific differences are small. Still smaller, and very slight indeed, is the individual variation. Generally speaking, on the dorsal side each genus seems to have its own range in the number of the turns in either column of the zone, as follows: *Echinarachnius* 9–12, *[11] *Dendraster* 7–8, *Echinodiscus* 6–7, *Astriclypeus* 7–10, * *Encope* 3?, * *Mellita* 3–4, *Rotula*?. And as a rule, these numbers are in accordance with the number of the plates in the corresponding column.

With reference to the horizontal suture of the plates, all the plates of the right side (5b) slip back slightly behind the corresponding plates of the left side (5a) in the dorsal view. This arrangement of the plates causes that bending in the horizontal suture which determines the size of the angle in the zigzag, and the angle is always in direct proportion to the degree of bending, except for the case that the occurrence of the turn of the zigzag in an unexpected proximity of the line of the longitudinal suture makes the angle larger.

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[10] Cf. Chapter 1.

[11] The examples of those marked with an asterisk were observed by Professor OHSHIMA, two of which—*Dendraster* and *Mellita*,—were examined by myself also.

Again, every angle, in each species, regularly increases in size together with the plates, which, apart from the individual variation, become somewhat larger as the animal grows; a methodical observation discloses how each individual takes different forms in different stages of its development. Besides, in whatever stage of development an individual may be, the relative size of its plates counts for much in determining the angles; those on the dorsal side of a full-grown creature generally range from 30 to 50 degrees, while on the oral side the usual size is 50 degrees or thereabouts.

The origin of the line is not known for certain, but it is almost certain that it appears first at the apex and extends gradually on the dorsal surface. After its first appearance at the top, the line increases in the amount of zigzagging—that is, every angle, as well as the length and the extent of deviation of every section, becomes greater—as it proceeds distally on the dorsal surface, until it comes to an end reaching the anal opening. But when the anal opening is situated on the oral side, the scope of the zigzagging on that side diminishes as the line is extended from the distal end towards the periproct. Thus in most cases the line begins at the top and, extending downwards, reaches its full length on the supramargin or on the margin or in the adoral region, according to the final position of the anal opening. We can find the examples of the three kinds of termination in the genera *Echinarachnius* and *Astriclypeus*, the former representing the first two cases while the latter typifies the last-mentioned.

In the forms with the interambulacral lunule, such as *Encope* and *Mellita*, the zigzag extends from the apex to near the anterior edge of the hole, and no zigzag is found on the plates situated beyond the lunule. This disappearance of the line beyond the lunule cannot be explained satisfactorily until more materials are obtained. In view of the formation of ambulacral lunules, it might be assumed that the last pair of plates on which the line is clearly visible had suddenly ceased to extend the line any farther and just begun to form the lunule when this procedure was passed on to the next pair of plates, which in course of their development took part in extending the incipient hole. Then in the same way the pairs that grew after them contributed to the procedure till the lunule was completed, but the pair of plates that came together to complete the circumference of the lunule somehow failed to resume the zigzag line after their meeting, and their example was followed by all the plates that developed behind them. This assumption excludes all possibilities of the presence of the zigzag on the plates of the distal region of the zone. However, from the nature of the pseudofasciole which, in other forms of the family, runs all the way between the apex of the test and the anal opening, I think that the plates beyond the interambulacral lunule may have vestiges of the line, and thus probably the interambulacral lunule is different from the ambulacral lunule in the process of formation.

In any case, the line, which is continuous from apex to anus in simpler individuals, in *Encope* and *Mellita*, the most advanced forms, takes an irregular or a more complicated course, its continuity being broken by the lunule, even if it does not come to a full stop there. The existence of a lunule in the zone, in effect, determines whether the line is continuous or discontinuous. It must be noticed at the same time that the fact which I have mentioned above points to the coincidence existing between the specialization of the test as a whole and the complexity of the pseudofasciole in particular. It may well be expected that the place a certain form takes in the scale of evolution among the members of the Scutellidae will be suggested by the form of its pseudofasciole, when the comparative study of various shapes of the line has been properly pursued.

In the following comment, which, it is feared, does not deserve much attention, I have tried to dwell on the mechanism of the ridge at some length. The mechanical construction may be largely due to the part played by the muscles that bind the bases of the spines to the test around the tubercles, while partly it may depend upon the inclined planes of the plates. The presence of the tubercles alone does not indicate the extension of the ridge[12], while it is essential for the existence of the ridge that the spines, or at least their bases, remain intact; the ridge disappears when the animal is stripped of its spines. In fine, the muscles around the bases of the spines probably play a double principal role; taking advantage of the sloped surfaces of the plates, they shape themselves into the ridge, which in turn supports

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[12] Cf. The relation of the zigzag line to the tubercles and spines. Chapter 1.

the muscles in the other role of theirs, *i.e.* in giving the spines the peculiar inclination which is the immediate cause of the presence of the zigzag line.

What does the pseudofasciole mean to the animal? I do not know enough of the line to describe its exact function, and its full significance is still beyond my comprehension. However, it may be taken for granted that it strengthens that portion which is regarded to be weak, being loosely knit in order to make room for the digestive canal within the test. Now that it is clear that the whole problem cannot be solved so simply, a more accurate description of these points is left for future researches.

One should almost wonder why such a remarkable character has so long escaped the notice of many a preceding echinologist; it may be surmised that not a few overlooked the line, taking it simply for that of the suture.

According to the descriptions by KLEIN (1754), LESKE (1778), AGASSIZ (1841), VERRILL (1867), MORTENSEN (1927 b), CLARK (1935), IKEDA (1936) and some other echinologists, 7 genera, comprising 22 species and 3 varieties, are known in the Scutellidae. Of these, 6 genera, including 11 species and 1 variety, have now been proved to possess the non-sutural zigzag line. Thus, it has been effectively evidenced that in all probability the pseudofasciole holds constant in the present family. Only, as was pointed out above, inquiries into the genus *Rotula* failed to gain the expected result, and it remains a doubtful case still. If further examination should happen to prove it to be a specialized form, the most interesting and fruitful course might be sought in phylogenetic researches. This is a mere speculation, which is not yet supported by any direct observation. Unfortunately, no specimen of this genus has been available in our laboratory.

New material used in this chapter is as follows. Reported data: 1. *Encope emarginata* (LESKE), 2. *Rotula* sp. Both report and specimens: 3. *Dendraster excentricus* (ESCHSCHOLTZ), 4. *Mellita sexiesperforata* (LESKE). Specimen: 5. *Echinarachnius parma* var. *obesus* H. L. CLARK.

CHAPTER 3

Observations of the pseudofascioles of some scutellids in the collection of the Zoological Museum in Amsterdam

The pseudofasciole was first found on the surface of the body of certain scutellids from Japan, such as *Echinarachnius mirabilis* (A. AGASSIZ) and *Astriclypeus manni* VERRILL; and then its presence was proved to some extent in some forms of the genera *Dendraster*, *Encope* and *Mellita*. But this did not quite satisfy me, especially so far as the last two were concerned. The fact that the line was visible only between the apex and lunule did not dispel my suspicion that it might still be found at least on some of the plates in the distal part of the interambulacral 5. On the other hand I presumed that the existence of the interambulacral lunule determined whether the pseudofasciole was continuous or discontinuous, the former type being represented by *Echinarachnius*, *Dendraster*, *Echinodiscus* and *Astriclypeus*, and the latter by *Encope* and *Mellita*.

In the present chapter I shall dwell on the pseudofasciole in some species of those genera which have perplexed me hitherto.

The examples observed were 23 individuals belonging to 3 genera, which included 5 species and 1 variety, as follows: 1. *Dendraster excentricus* var. *elongatus* H. L. CLARK, 2. *Encope emarginata* (LESKE), 3. *E. micropora* AGASSIZ, 4. *Mellita longifissa* MICHELIN, 5. *M. quinquiesperforata* (LESKE), 6. *M. sexiesperforata* (LESKE).

Dendraster. This genus, including a species and a variety, has the anal opening on the oral side, and the pseudofasciole appears on the oral surface as well as on the dorsal; but the position of the anal opening is so near the margin that little room is allowed for the development of the line on the oral surface.

1. *Dendraster excentricus* var. *elongatus* H. L. CLARK. Three specimens from San Diego, California, were observed; they were donations by the Museum of Comparative Zoology, Cambridge. In the following table are given the features of these specimens:

Specimen	Length (cm) (Antero-posterior axis)	Number of turns of pseudofasciole	
		Dorsal surface	Oral surface
No. 1	5.2	8	trace
No. 2	3.8	7	?
No. 3	3.4	7	?

The number[13] of turns of the line varied from 7 to 8 on the dorsal surface, and on the oral surface there was a mere scratch of a line. The angle at each turn on the dorsal surface generally ranged from 30 to 40 degrees; whereas, there was no angle to be found on the oral surface.

The variation which was observed in the number of turns and the size of angles corresponds to the number and size of the coronal plates in each column; and the turns on the dorsal surface alone increase in number and size with the age or the growth of the test. It was quite reasonable that no turn was visible on the oral surface, considering the number of the plates between the margin and the anal opening. The pseudofasciole of the largest specimen is shown in the plate.

Encope. The test is stout, with a posterior interambulacral lunule and 2 or more marginal lunules in the ambulacral zones. In this form the pseudofasciole is distinctly discernible on the dorsal surface only, being discontinuous owing to the presence of a lunule in the posterior interambulacral mid-zone. In other words, the line is divided into two sections by the hole, the one between the apex and the anterior edge of the hole, and the other between the posterior edge of the hole and the distal end of the test. For the sake of convenience, I propose here to call the former the prelunular part and the latter the post-lunular part of the abactinal pseudofasciole. The angles in the specimens will be counted below both individually and specifically.

2. *Encope emarginata* (LESKE). Five specimens were observed. Of these, 4 specimens were from Santa Marta, Columbia, and one (No. 5), donated by the late Professor R. KOEHLER, was from the coast of Brazil (Rio de Janeiro). The features of these specimens were as follows:

Specimen	Length (cm) (Antero-posterior axis)	Number of turns of pseudofasciole	
		Prelunular part	Post-lunular part
No. 1	6.5	4	2
No. 2	5.7	4	2
No. 3	6.5	3 ?	2
No. 4	5.3	3 ?	2
No. 5	10.0	4 ?	2

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[13] Cf. Chapter 1.

3. *Encope micropora* AGASSIZ. One specimen from California was observed, and its length and the number of turns of its pseudofasciole were as follows: Length 10.1 cm; turns in prelunular part 4?, in post-lunular 2?.

The abactinal pseudofasciole in these forms is apparently composed of the prelunular and post-lunular parts, as may be seen in the figures. The prelunular part has 3 or 4 turns, while the post-lunular part has always only 2. The size of the angles ranges from 30 to 50 degrees on an average in the prelunular part, and between 60 and 80 degrees in the post-lunular part. This variation in the size of the angles corresponds to that of the coronal plates, while the variation of the number of turns in the prelunular part appears to depend upon the difference in the size of the tests.

Mellita. The test is usually flat and comparatively thin, with an interambulacral lunule and 4 or 5 ambulacral lunules. The pseudofasciole is quite distinct on the dorsal surface only and is discontinuous on account of the intervention of a lunule in the posterior interambulacral mid-zone, as is the case in *Encope.* The number of turns in the specimens will be given below both individually and specifically.

4. *Mellita longifissa* MICHELIN. Two specimens were observed. One of them was from Acapulco, Mexico; length 2.4 cm; the pseudofasciole had 1? turn in the prelunular part and 2? turns in the post-lunular part. The other was a specimen which was collected by AGASSIZ and donated by the Museum of Comparative Zoology, Cambridge; 5.5 cm in length; the pseudofasciole was indistinct in the prelunular part, while 1? turn was visible in the post-lunular part.

5. *Mellita quinquiesperforata* (LESKE). One specimen from Mexico was observed. The features of this specimen were as follows: Length 4.8 cm; the prelunular part of the pseudofasciole imperceptible; the post-lunular had 2? turns.

6. *Mellita sexiesperforata* (LESKE). Twelve specimens were observed. One of them was collected by Mr. BOEK at St. Martin, West Indies, and its length and the number of turns of its pseudofasciole were as follows: Length 8.8 cm; the number of turns in the prelunular part 4?; in the post-lunular part 2. The

other 11 specimens were collected by Mr. BOEK also, at Saba, West Indies. They were all small, being no longer than 1.4 cm or so, and the respective features of the specimens were as follows:

Specimen	Length (cm) (Antero-posterior axis)	Number of turns of pseudofasciole	
		Prelunular part	Post-lunular part
No. 1	1.4	2 ?	partly denuded
No. 2	—	3	partly broken
No. 3	—	3	„
No. 4	—	1 ?	„
No. 5	—	3	1 ?
No. 6	1.4	1 ?	partly denuded
No. 7	—	?	„
No. 8	—	2 ?	„
No. 9	—	2 ?	„
No. 10	—	2 ?	„
No. 11	—	2 ?	„

As was shown above, the larger specimens of *Mellita* had 2 turns in the post-lunular part, and generally 4 in the prelunular; in the smaller ones the turns were usually 2 or 3 in the prelunular part, while no turn was recognizable in the post-lunular part, for those specimens were found impaired on their arrival. The size of the angle at each turn, observed in a specimen of *M. sexiesperforata*, ranged from 80 to 90 degrees in the prelunular part, and 90 to 100 degrees in the post-lunular part.

I said in an earlier chapter that the genera *Encope* and *Mellita* had, contrary to my expectation, no visible line on the plates between the hole and the distal end of the test. Subsequently I noticed that the figure showing the abactinal view of *Mellita quinquiesperforata* given by CLARK (1904, Pl. 10, Fig. 63) had, in the above-mentioned region of the test, what appeared to be a part of the indented shading indicating the presence of a pseudofasciole. But this was not an adequate basis for the withdrawal of my former statement. Accordingly the question(14) remained whether the formation of the hole, going on simultaneously with the growth of the plates around it, took place prior to the growth of the plates in the distal part or, on the contrary, the hole began to be formed in the plates after they and those following them had made some considerable development. In the first case

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(14) Cf. Chapter 2.

the zigzag line might not have been continued beyond the hole, while in the latter case the part of the zigzag line which should have been already extended over the distal region would not have been obliterated without some other cause. In the mean time I could not abandon my opinion that the latter process was more consistent with the nature of the pseudofasciole, and that the hole must have developed secondarily by resorption through the test, and not simultaneously with the successive growth of the mutually corresponding plates in both columns.

The discovery of the line on the coronal plates of the distal part, which I related above, made me almost certain that the plates of the zone first developed in the usual way, accompanied both by the backward migration of the anal opening and the prolongation of the zigzag line, and then the hole began to be formed secondarily in its final position.

I happened to find that the same problem, which I intended to solve in my own way, *i.e.* through the study of the pseudofasciole, had already been taken up by several students, who had reached the same conclusion as I had aimed at, by observing especially individual variations in the shape of the hole itself. AGASSIZ (1872), CLARK (1904), JACKSON (1917) and CROZIER (1919) pointed out that in *Encope* and most of *Mellita*, the ambulacral lunules are developed by the inclusion of reëntrant marginal notches as a result of the prolongation of the plates, whereas the interambulacral lunule is formed by the deepening of a dorsal and an oral depression that continues until the test is pierced through. Among those echinologists, JACKSON (p. 491) describes *Encope annectans* JACKSON as the most primitive form of the genus, and calls attention to the fact " that the lunule in the interambulacral 5 (of this fossil form) is still imperforate ", being peculiarly represented by mere dorsal and oral grooves.

From these observations it appears that there is essentially no difference between a continuous and a discontinuous pseudofasciole. But, apart from the question whether the hole developed secondarily or otherwise, the actual presence of a gap in the middle of the line is so remarkable a feature, that it convinces me of its significance. Thus it does not seem altogether meaningless to distinguish the lines by the presence or the absence of a lunule, especially so far as concerns abactinal pseudofascioles. In this regard, it may also be pointed out—in addition to the fact that the term "discontinuous" has a twofold meaning in this case, as will be explained later on—that, in spite of the different process of formation, the interambulacral lunule occurs only in those forms that possess the ambulacral lunules, so that the presence of a discontinuous pseudofasciole always implies the presence of ambulacral lunules, though the reverse does not apply to all cases in the scutellids (cf. *Astriclypeus*).

The spines of the oral side, which are longer and slenderer in appearance, though in reality rather thicker than those of the dorsal, seem to serve the animal principally as instruments of locomotion. For, in *Astriclypeus* and most of *Echinarachnius*, the primary spines on the oral side are fairly highly specialized, so that a minute examination of them alone suffices to make one conclude that they evidently serve the animals mainly as instruments of locomotion. Besides, PARKER (1927) and PARKER and VAN ALSTYNE (1932) regarded the spines on the oral side as the main part of the locomotive organs from the observations of some living examples of *Echinarachnius parma* in motion. According to my observations of the spines alone, the same is presumably the case in *Encope* and *Mellita*(15). Here, indeed, the oral side of the test is not so thickly coated with primary tubercles as the dorsal, especially in the shallow furrows formed longitudinally along the mid-line of the interambulacral 5 at both ends of the lunule. It seems rather likely than otherwise in these genera that this fact, together with the specialization of the actinal spines, has made the zigzag line disappear from the oral surface. The discontinuous pseudofasciole, which characterizes these two genera, therefore is distinct from the continuous one in that, besides being divided by the lunule in the posterior zone, it is not continued by an actinal pseudofasciole, but cut short on the margin before it reaches the periproct. Hence the twofold meaning of the term "discontinuous" I have alluded to above. Thus it is apparent that

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(15) In most members of the Scutellidae the spines on the actinal side are distributed and inclined symmetrically with regard to the antero-posterior axis (cf. figures). *Echinodiscus* and *Astriclypeus*, which have actinal pseudofascioles, are excepted (cf. figures); so also is *Rotula*, which I have had no opportunity to examine myself.

the two genera resemble each other as closely in the features of the pseudofasciole as they do in the other characters.

The following 4 genera, including 9 species and 2 varieties, have a continuous pseudofasciole; 1. *Echinarachnius parma* (LAMARCK), 2. *E. parma* var. *obesus* H. L. CLARK, 3. *E. mirabilis* (A. AGASSIZ), 4. *E. brevis* IKEDA, 5. *E. griseus* MORTENSEN, 6. *Dendraster excentricus* (ESCHSCHOLTZ), 7. *D. excentricus* var. *elongatus* H. L. CLARK, 8. *Echinodiscus auritus* LESKE, 9. *E. bisperforatus* LESKE, 10. *E. tenuissimus* (AGASSIZ et DESOR), 11. *Astriclypeus manni* VERRILL. And so far as my observations go, the following 2 genera, including 5 species, have a discontinuous pseudofasciole: 1. *Encope emarginata* (LESKE), 2. *E. micropora* AGASSIZ, 3. *Mellita longifissa* MICHELIN, 4. *M. quinquiesperforata* (LESKE), 5. *M. sexiesperforata* (LESKE).

Thus the pseudofasciole was observed in 6 genera, comprising 14 species and 2 varieties. In the following table are given the numbers of turns and the sizes of angles in those genera in which the line was hitherto observed. The abactinal pseudofasciole given in the table designates either the continuous or the discontinuous one found on the dorsal surface. The actinal, appearing on the oral surface, belongs to the category of the continuous, no discontinuous one having been found among them. It will be noticed that the actinal pseudofasciole never occurs by itself but goes always together with the abactinal continuous, of which it is an extension.

Genus	Abactinal pseudofasciole		Actinal pseudofasciole	
	Number of turns	Size of angles (Degree)	Number of turns	Size of angles (Degree)
Echinarachnius	9–12	30– 40	—	—
Dendraster	7– 8	,,	(a scratch of a line)	—
Echinodiscus	6– 7	30– 50	2	30–50
Astriclypeus	7–10	,,	,,	,,
Encope in prelunular part	3– 4	,,	—	—
Encope in post-lunular part	2	60– 80	—	—
Mellita in prelunular part	4	80– 90	—	—
Mellita in post-lunular part	2	90–100	—	—

One may entertain an idea that the number of turns and the size of angles in the zigzag line are useful as indices to the size or the age of the test, for these features of the line vary in accordance with the number and the size of the coronal plates, which, apart from specific variation, increase to some extent as the animals grow.

The data, which have not only been observed personally but also incidentally recorded in the figures by AGASSIZ (1841) and LOVÉN (1874), lead me to conclude that, in more advanced adult forms having discontinuous pseudofascioles like *Encope* and *Mellita*, the part between the hole and the distal end of the posterior zone has, on the abactinal side, usually two or three plates in each column, which agrees with the number of turns in the post-lunular part of the pseudofasciole.

As was suggested in the preceding chapter, from observations of the varieties of the shape that the pseudofasciole takes in various forms of the Scutellidae, attention may be called to the relationship among the members of the family, which was correctly determined by CLARK (1914).

Of the forms studied in this chapter, the following 5 were brought under my observation for the first time:—*Dendraster excentricus* var. *elongatus* H. L. CLARK, *Encope emarginata* (LESKE), *E. micropora* AGASSIZ, *Mellita longifissa* MICHELIN, *M. quinquiesperforata* (LESKE).

CHAPTER 4

The pseudofasciole: its absence in Rotula and its significance from evolutionary point of view

In the Scutellidae are known 22 species and 3 varieties, belonging to 7 genera, of which 14 species and 2 varieties, belonging to 6 genera, have already been examined for the pseudofasciole. The result was that lines representing the actinal or abactinal, the continuous or discontinuous pseudofascioles, were confirmed in all of these forms.

From this fact it may be presumed that the line is also present in all the other members of the family hitherto untouched. Only in the genus *Rotula* the line was not recognizable and it has been put aside as a doubtful case. In the present chapter I will first give an account of my renewed observations of this exceptional genus, and then discuss at some length the importance of the pseudofasciole in the present family.

The genus *Rotula* comprises two species, *deciesdigitata* (LESKE) and *orbiculus* (LINNÉ). When, as was stated before, Professor OHSHIMA examined for me some specimens of the Scutellidae in the British Museum, these two forms were among those observed, and in them he could not find the pseudofasciole. Not long afterwards a specimen[16] of *orbiculus* from the Congo was presented to me by Dr. MORTENSEN, and after my own careful search, I was assured beyond all doubt of the entire absence of any such line from the surface of the body[17].

Now I was confronted with the problem of how it happened to be absent in this particular genus. It seems to me that this is possible mainly in consequence of an extremely remarkable differentiation that has operated on the primary spines of this genus. Various forms of the Scutellidae that have come under my observation, all but one genus, *Rotula*, had more or less specialized primary spines on their oral surface only. This specialization, which apparently makes those spines serve as instruments of locomotion, is lowest in *Echinarachnius*, while in *Encope* and *Mellita* there is the most conspicuous contrast between the primary spines on the dorsal surface and those on the oral, owing to a very high degree of differentiation to which their actinal primaries have attained. And, as the actinal pseudofasciole is lacking in these two genera, it may be assumed as a general rule that the disappearance of the zigzag line occurs when the spines have attained to a certain stage of specialization. When applied to *Rotula*, the hypothesis can, in my opinion, be shown as valid and competent. For, in *Rotula*, the primary spines on the oral surface, notwithstanding their being the most highly specialized in the family, do not contrast very strikingly with the primaries on the dorsal surface, because in *Rotula*, it seems, the specialization was not restricted to the primaries on the oral surface, but those on the dorsal surface were also greatly affected. Therefore, though it does not follow that, in *Rotula*, the abactinal spines serve as

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[16] The line of the longitudinal suture in the ambulacra as well as the interambulacra is distinctly visible in this specimen in spite of its spines, perhaps because the spines are sparsely distributed.

[17] Photographs of a specimen of *R. deciesdigitata* from Porta Praqa, which is in the collection of the Swedish State Museum, Stockholm, and which appears to have well-retained spines, were recently presented to me through the kindness of Dr. TORSTEN GISLÉN. On the photographs taken by him showing the dorsal and oral aspects I could not make out the line.

instruments of locomotion, it may naturally be expected that what has disappeared from the oral surface of *Encope* and *Mellita* will not remain on the dorsal as well as the oral surface of *Rotula*.

I have found that CLARK's observation (1914, p. 65) strongly supports this opinion of mine: "Judging from the characters of the test alone", he says, "*Rotula* may well be considered the most highly specialized form of clypeastroid known either living or fossil. On the other hand, all the characters of *Echinarachnius* point to it as one of the least specialized members of the family (the Scutellidae) and it is very possibly quite near the ancestral stock from which the scutellids arose".

In terms of this classification of the scutellids, the simpler the form, the more obviously the pseudofasciole is displayed. In *Echinarachnius*, which is ranked among "the least specialized members of the family", the pseudofasciole takes the plainest and the most fundamental form, for it covers the whole length between the apex and the periproct in one unbroken line, which, moreover, is completed on the dorsal side, without any possibility of crossing over to the oral surface. *Dendraster* is not very far removed from *Echinarachnius*, but its pseudofasciole, which is very pronounced too, had to extend for a distance, however short, over the oral side, in order that it might reach a full length with its termination at the periproct. In more advanced forms like *Echinodiscus* and *Astriclypeus*, the line has some complexity; the actinal pseudofasciole in these two genera is much longer than in *Dendraster* of the same size and makes two pairs of turns, while it is much less distinct than the abactinal line. In still more advanced genera, *Encope* and *Mellita*, the line has disappeared from the oral surface on account of the specialized primary spines, while the abactinal pseudofasciole is discontinuous owing to the intervention of the hole. Here the disappearance of the line from the oral surface is due to a factor quite different from what makes in *Echinarachnius* the actinal line impossible by the nature of the pseudofasciole. Finally, the tendency to lose the pseudofasciole, which has appeared on the oral surface in *Encope* and *Mellita*, asserts itself in the extreme in *Rotula*, the most highly specialized form. Thus the total absence of the zigzag line in this particular genus should be regarded as an instance of retrogression which progress entails, and does not, in my opinion, diminish the force of the conclusion that the pseudofasciole holds constant in the present family.

When CLARK referred to "the characters of the test" for his classification of the scutellids, it goes without saying that he little dreamt of the zigzag line. It is very interesting that his judgment upon the relationship of the members of the scutellids has been corroborated by the comparative study of various forms of the pseudofasciole. Indeed, it is not too much to say that observation of the zigzag line alone would have led to the same conclusion. This feature, it seems to me, is so significant.

It was mentioned by LOVÉN (1892) that "in the Echinoidea the growth of the corona is effected by new plates being successively added to the dorsal terminations of the interambulacra as well as the ambulacra, and by their increasing in size and solidity" (p. 17). The case of the scutellids of course is not an exception from that rule, but in the scutellids the process must necessarily be accompanied by an extension of the pseudofasciole[18]. At the same time the observations by FEWKS (1886), GORDON (1926) and IKEDA (1935a) have made the fact clear that the periproctal opening in certain forms of *Echinarachnius* moves backwards as the test grows

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[18] The instances of *Echinarachnius* adduced below, though not quite satisfactory, will give some suggestions at least about the relation between the development of the test and the elongation of the pseudofasciole in an individual.

Species	Length of specimen (cm)	Number of turns of pseudofasciole	Locality
parma	4.5	9	Buzzards Bay
	6.1	10	East Port
mirabilis	1.4	5	Kominato
	1.5	5	Amakusa
	1.7	7	”
	2.8	9	Mutu Bay
	6.6	12	Hukuoka Bay
brevis	2.0	6	Kominato
	2.6	7	”
	5.6	10	Hukusima
griseus	1.9	5	Hokkaido
	2.5	7	”
	2.6	6	”
	3.5	8	”
	3.7	9	”
	3.9	7	”

and increases in size, and that movement, in my opinion, gives rise to a prolongation of the pseudofasciole. Hence the inference I have already ventured that the pseudofasciole, arising at the apex, perhaps at a certain stage of the development of the test, and extending within the interambulacral 5 towards the anal opening with the growth of the test, may well be regarded as a memento not only of the backward migration of the periproct but also of the development of the whole test.

I have, so far, little applied myself to inquiries into the function of the pseudofasciole, and in this regard I have only to repeat what I suggested before—that the line sometimes seems to protect the plates facing each other over the longitudinal suture from breaking apart along the interambulacral mid-line.

To conclude by saying the least of it, it has now been made quite certain that the pseudofasciole is the most remarkable of the numerous features in the members of the Scutellidae, and no structure similar to it probably will be found in other families of the Echinoidea. To the features of the Echinoidea a new distinctive one has been added: the pseudofasciole, which is peculiar to the Scutellidae, and in which the test is as characteristically spined as it is in the fasciole of the Spatangina (MÜLLER, 1854; GRAY, 1855; LUDWIG u. HAMANN, 1902).

New material: *Rotula orbiculus*, one specimen sent by Dr. MORTENSEN. The following specimens, although not new material, were of considerable use for the present researches. As most of them are of the forms that do not occur in Japan, I wish to thank those gentlemen who were so kind as to spare me precious specimens from their collections: *Echinarachnius parma*, several specimens with well-retained spines sent by Mr. A. H. CLARK of Washington and Dr. H. L. CLARK of Cambridge, Mass.; *Echinodiscus auritus*, a large specimen from the Philippines (much larger than a specimen of the same species from Japan in my possession) sent by Mr. J. S. DOMANTAY of Manila; *Dendraster excentricus*, many fresh specimens from Nanaimo, British Columbia, sent by Dr. W. A. CLEMENS of Nanaimo; and those of *D. excentricus* var. *elongatus* from Pacific Grove, Cal., sent by Dr. E. DEICHMANN and Mr. R. L. BOLIN of Pacific Grove; *Mellita*, some forms sent by Mr. A. H. CLARK.

CHAPTER 5

The pseudofascioles of some scutellids in the collection of the Museum of Comparative Zoology at Harvard College

The deficiency in material felt in the present investigation was at last filled up almost completely[19] by acquiring the loan of some specimens in the collection of the Museum of Comparative Zoology at Harvard College. They represented 4 genera and 7 species, of which 2 genera and 5 species have not been mentioned in the previous chapters, as I had not been able even to examine figures of them.

All of the specimens answered to what I had expected of them with reference to the zigzag line, except the specimen of *E. bisperforatus* which was deprived of most of its spines, and only retained some scanty remnant on the actinal side and in the anterior region of the abactinal side. The specimen of *Rotula orbiculus* assured me of the absence of the line in this species (cf. Chapter 4) and the rest revealed the line on the back, though some of them were partly denuded on either the actinal or the abactinal side.

The pseudofasciole usually extends on the surface of the body from the apical field to the periproctal opening, and takes a peculiar shape according to the characters of the forms.

Echinarachnius. The anus of *Echinarachnius* opens on the margin or the supramargin of the test, so that the line is developed on the abactinal side only. Such a line as this was called an abactinal continuous pseudofasciole in an earlier chapter.

1. *Echinarachnius asiaticus* MICHELIN. A specimen (No. 4215) taken by the "Albatross" off Cape Nalacheff, Kamchatka, was observed. Its features are as follows: it is 6.2 cm in length and possesses a typical zigzag line making more than 6 turns, with angles ranging from 30 to 40 degrees, in each column of the interambulacral 5; and this line has a fairly close resemblance to that of *E. parma.*

Encope. Like *Mellita, Encope* has a lunule in the mid-line of the posterior interambulacral zone. The zigzag line in these

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[19] The typical specimen of *E. bisperforatus* var. *truncatus* (AGASSIZ) has not come under my observation, but inference may safely be drawn from the specimen of *E. bisperforatus* (No. 4144), which is labelled as "approaching to *truncatus*" (cf. note 23).

genera is an abactinal discontinuous pseudofasciole, that is to say, it extends on the back only and is divided by the hole into two parts, the prelunular and post-lunular parts.

2. *Encope perspectiva* AGASSIZ. The specimen observed (No. 2419) is from Nazatlass, Mexico, and is 10 cm in length. The line is partly perceptible on the back. It has 1? turn in the prelunular part, but no turn is visible in the post-lunular part. In this example the peculiar inclination of primary spines seems to be invisible on either side of the line on the abactinal surface, owing to the fact[20] that the primaries, having a characteristically thick end in the shape of a club, are arranged so close together that, in superficial appearance at least, there are left little intervals among them.

3. *Encope michelini* AGASSIZ. The specimen observed (No. 2401) is from Sorasota Bay on the west coast of Florida, measuring 12.1 cm in length. The line is perceptible on the back. There are 4? turns in the prelunular part (this part is not to be seen in its whole length, as the dorsal side of the specimen is partly denuded near the anterior end of the lunule), and the angles at these turns vary from 40 to 70 degrees. In the post-lunular part the number of turns is 2, the angles being more than 60 degrees.

4. *Encope californica* VERRILL. The specimen observed (No. 2317) is from Los Animas Bay, Mexico. The specimen is 12.8 cm in length, with the left posterior quarter of its margin imperfectly developed. The line is visible on the back; the prelunular part has 5 turns, with angles measuring about 50 or 60 degrees, and the post-lunular part has 1? turn.

5. *Encope grandis* AGASSIZ. The specimen observed (No. 3821) is from San Lucas, Lower California. It is 12.1 cm in length and possesses the line. The number of its turns is 1? in the prelunular part, and 2 in the post-lunular part, the angles of the former being about 40 degrees and those of the latter more than 50 degrees.

All these examples of *Encope* have been ascertained to have the pseudofasciole on the dorsal side, but none on the oral side. And the line answers in every detail to the descriptions given in

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[20] All forms of the Scutellidae have primary spines with more or less thick ends, but *E. perspectiva* is an extreme case.

the preceding chapters. The absence of the line on the oral side depends, as I said, upon the specialization of the primary spines on that side. Moreover, the actinal ambulacral furrows, bifurcating so as to encircle the lunule, and further sending branches out into the mid-zone, leave a comparatively narrow space between; and this may be another cause of the absence. I had taken some notice of this fact in the other forms of *Encope* and also in *Mellita* but I had not been quite satisfied, until I was convinced of it by these examples.

Rotula. As has been reported previously, *Rotula* is the most specialized group in the Scutellidae, and comprises 2 species, *deciesdigitata* and *orbiculus.* I have expected to find no zigzag line in these forms, both from the observation of Professor OHSHIMA executed on my behalf at the British Museum of Natural History[21], and from my own subsequent examination of the specimen of *orbiculus* from the Congo and the study of the figures of *deciesdigitata* from Porta Praqa[22]. Here another example of *orbiculus* is described as it was examined regarding the zigzag line.

6. *Rotula orbiculus* (LINNÉ). The specimen (No. 4751) is from the Cape Verde Islands, being 36 cm in length. The primary spines on both the actinal and abactinal sides are not only very slender but also very sparse, and it seems to be on account of this character that the zigzag line is absent. Besides this, the fact that the longitudinal suture of plates in every zone on both the dorsal and the oral sides is in the present form exceedingly conspicuous, and that the primaries do not appear near the suture of the plates, may perhaps be one of the causes of the absence of the line.

All the forms of the genus *Echinarachnius* have now been ascertained to have on the back a pseudofasciole, which is called the abactinal continuous pseudofasciole. The pseudofasciole on the specimen of *Echinarachnius* before me is more conspicuous than any I have ever observed, and it is interesting to see that the line first occurs, and most conspicuously, in a genus which is regarded as one of the least specialized members of the Scutellidae, and, becoming more complex and less distinct in proportion to the evolutionary progress, disappears in the most advanced

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[21] Cf. Chapter 2.

[22] Cf. Chapter 4.

genus *Rotula*. In other words, the line is peculiar to this family, and, among the members of the family, its visibility is inversely proportionate to the degree of the specialization not only of the line itself but also of the test as a whole.

As for *Echinodiscus*, an exception must be made of *E. bisperforatus* var. *truncatus* (AGASSIZ), the only form, as I have alluded elsewhere, that I have had no opportunity to study either in specimen or in figure. However, judging from the characters of the denuded specimen (No. 4144)[23] of *E. bisperforatus* from Java, especially from the shape of the test, it seems to me highly probable that the line of var. *truncatus* closely resembles that of the species (cf. Chapter 1), provided that the variety also has the line in question. In that case, on the basis of the facts already reported, it may naturally be assumed that all the forms of the genus *Echinodiscus* are much like one another in the features of the pseudofasciole.

All the members of the genus *Encope* have now been examined, and their lines positively ascertained to occur on their back, excepting the line of *E. perspectiva*, which was not quite distinct, so far as the example[24] was concerned.

According to CLARK's description (1914), the genus *Mellita* comprises 4 species, of which, however, he said in his letter to me that the species *Mellita pacifica* VERRILL was "probably invalid"[25]. Therefore, what was stated before (cf. Chapter 3) will suffice to show that the line is distinctly perceptible on all the members of this genus.

In those scutellids which have the pseudofasciole, the inclination of the primary spines is symmetrical with regard to the antero-posterior axis both on the actinal and the abactinal sides, except in that region of the posterior interambulacral mid-zone in which the zigzag line runs (cf. Chapter 2). This peculiar arrangement in the inclination of the spines does not occur in allied forms in the Clypeastrina.

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[23] This specimen is labelled as "approaching to *truncatus* but not typical" (cf. note 19).

[24] I am not at all disappointed at a single example failing to satisfy me; for I have not always succeeded in finding the typical pseudofasciole even in *E. mirabilis*, which species has normally the most conspicuous pseudofasciole in all the scutellids.

[25] His letter dated the 6th of May, 1937.

As for *Rotula*, which lacks the line, it is interesting to see that, in spite of the difference in the shape of the test, it somewhat resembles the genus *Peronella* of the Clypeastrina in the general appearance of the primaries.

Considering the structure, it is assumed that the line is formed, in contrast with the symmetrical inclination of the spines in the other parts of the test, from the causes mentioned before (cf. Chapter 2), namely, the backward slip of the right column in the interambulacral 5, the peculiar sloping of the plates in the zone, and the specialization of the muscles with which the spine and the tubercle are bound together.

List of material on loan. Studied for the first time: *Echinarachnius asiaticus* MICHELIN, *Encope perspectiva* AGASSIZ, *E. michelini* AGASSIZ, *E. californica* VERRILL, *E. grandis* AGASSIZ; previously studied in figure: *Echinodiscus bisperforatus* LESKE (this particular specimen was useful for its approaching to var. *truncatus*); previously observed: *Rotula orbiculus* (LINNÉ).

Appended hereunder is a list of the members of the Scutellidae with their pseudofacioles specified.

SCUTELLIDAE

Genus	Species	Pseudofasciole
Echinarachnius		simple; abactinal continuous
	parma (LAMARCK)	
	parma var. *obesus* H. L. CLARK	
	asiaticus MICHELIN	
	mirabilis (A. AGASSIZ)	
	griseus MORTENSEN	
	brevis IKEDA	
Dendraster		complex; abactinal continuous and actinal continuous
	excentricus (ESCHSCHOLTZ)	
	excentricus var. *elongatus* H. L. CLARK	
Echinodiscus		complex; abactinal continuous and actinal continuous
	auritus LESKE	
	tenuissimus (AGASSIZ et DESOR)	
	bisperforatus LESKE	
	bisperforatus var. *truncatus* (AGASSIZ)	

Genus	Species	Pseudofasciole
Astriclypeus		complex; abactinal continuous and actinal continuous
	manni VERRILL	
Encope		complex; abactinal discontinuous
	emarginata (LESKE)	
	micropora AGASSIZ	
	perspectiva AGASSIZ	
	michelini AGASSIZ	
	californica VERRILL	
	grandis AGASSIZ	
Mellita		complex; abactinal discontinuous
	quinquiesperforata (LESKE)	
	longifissa MICHELIN	
	sexiesperforata (LESKE)	
	(*pacifica* VERRILL)	
Rotula		wanting
	deciesdigitata (LESKE)	
	orbiculus (LINNÉ)	

CHAPTER 6

The function of the pseudofascioles as observed in the behaviour of some scutellids, with a brief note on regenerated pseudofascioles

In an earlier chapter I have suggested that the pseudofasciole seems to protect the plates of the test bordering one another along the longitudinal suture in the interambulacral 5 from breaking apart along the mid-line. This represents a statical function of the line. I shall now proceed to dwell on the biodynamical significance of the line to some scutellids living in the sand, and to jot down in passing a few lines about regenerated pseudofascioles.

Echinarachnius mirabilis (A. AGASSIZ) and *Astriclypeus manni* VERRILL, which occur abundantly in shallow waters along the coast of Hukuoka Bay, were observed with regard to the function of the pseudofasciole. Most of the observations were carried out on the sandy beach during three successive summers commencing in 1935. As soon as these living scutellids are placed, oral side down, on submerged sand, they begin to creep about. *E. mirabilis*, like *E. parma* (LAMARCK) (cf. PARKER, 1927), leaves a characteristic trail on the sand behind it as it moves on. The trail is attributable to the spines under the anus, for such a trail does not appear when these spines are shorn off (Pl. 4, Fig. 7). The speed is not very great. In *Echinarachnius*, the fastest that I have observed crept at the rate of 7 mm per minute, and in a considerable number of trails made by 30 individuals the average rate proved to be 6 mm per minute. In *Astriclypeus*, the highest rate was 13 mm per minute, and the average of 20 individuals was 10.5 mm per minute. But they cease to move on or in the sand when the temperature is below 7°C, while their activity is conspicuous when it is above 15°C. Once under the surface of the sand, these animals do not tend to come up again; they move less rapidly but rarely altogether stop moving after they have completely concealed themselves. At any rate, they are to be found moving or, as it happens very rarely, resting, buried in the sand in a characteristic horizontal position indicative of a diageotaxis. The sand which covers their dorsal side is of a thickness of less than 5 mm[26], and *Astriclypeus* sometimes remains only half-buried.

Gandolfi-Hornyold (1910, 1914) stated that in some spatangoids the spines of the fascioles cause a movement of water on the body of the animal which is very important for the respiration. According to Gislén (1924), the ciliary movement found on the epithelium of the plates of the test in *Echinocyamus minutus* (Pallas) of the clypeastroids and in some of the spatangoids also brings about a respiratory current. The ciliation on the spines in *E. parma* was mentioned by MacBride (1909)[27] and by Parker and Van Alstyne (1932), and I think it probably serves the animal living in the sand with a respiratory current. The two last-mentioned reports are all that I have ever seen as to the ciliation of the spines in the scutellids.

While observing the behaviour of the animals, I found that the movement of sand-grains along the zigzag line was different from that in the other parts of the surface of the body. I saw, moreover, water-movement occurring along the line simultane-

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[26] According to Clark (1904), *E. parma* in natural surroundings lives more or less in the sand; Roxas (1928) mentions that *Echinodiscus auritus* Leske is half-buried under the sand at low water; and it is known through Clark's description (1935) that *Dendraster excentricus* var. *elongatus* Clark is oriented in a vertical position with the periproct uppermost and the anterior portion, one-third to one-half of the test, buried in the sand or the sandy mud.

[27] MacBride (1909) gave figures of some sand-dollars (Figs. 243, A and B), calling them by the name of *Echinarachnius parma*, but the name does not seem to be correct; probably they belong to a member of the genus *Dendraster*.

ously with the sand-movement on the surface. Of these, the water-movement may supply the respiratory tube-feet of the petals on the dorsal side with a respiratory current. Naturally it must be distinguished from the ciliary current on the spines, though it may tend to make the latter more effective. In any case, it seems quite reasonable to attribute these movements to the presence of the pseudofasciole, and to try to find in them a clue to its function. In fact, it is also noticed that, when some scutellids move, the spines of the whole surface, excluding those of the pseudofasciole, successively make vigorous swings[28], while those of the zigzag line seem to beat in a characteristic manner, independently of the rest. The peculiar inclination of the spines of the line must, in part at least, account for their remarkable movement, and therefore seems to be of no little significance in the function of the line. In short, the pseudofasciole, with its sand and water movements, may be considered to control the direction of the animal's locomotion and bear its share, however small, in respiration, and on the other hand to sweep the excrements away from the anus.

The behaviour in natural surroundings described above, seems to be almost the same as that of *E. parma* observed by PARKER (1927), and also that of *Mellita sexiesperforata* (LESKE) observed by CROZIER (1920). As for the concealment, our species may be said to possess a slight positive geotropotaxis[29], as noticed in *E. parma* by PARKER, and a negative phototropotaxis, for our species are highly sensitive to light, and tend to retire into a darker part of their environment, as a regular echinid *Arbacia punctulata* (LAMARCK) does (cf. HOLMES, 1912). Accordingly it is sometimes rather difficult to obtain exact knowledge of the behaviour in natural surroundings by means of experimentation with those forms. This, however, I do not think a serious handicap so far as my study is concerned with the function of the pseudofasciole; and even as to the behaviour itself, it may safely be assumed that any reaction observed in the course of experimentation is apt to occur under similar conditions in the natural environment. The

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[28] The ordinary locomotion appears to be effected by the rhythmical strokes of the spines on the oral side.

[29] In a regular echinid *Diadema* (= *Centrechinus*) *antillarum* (PHILIPPI) studied by PARKER (1922), the reverse is the case.

observations described in the following paragraghs, it must be mentioned, have resulted from very simple experiments, each animal being placed in a basin of submerged sand taken from its habitat.

The two forms *E. mirabilis* and *A. manni* exhibited, as *E. parma* (cf. PARKER, 1925, 1927), three types of locomotions, namely, rectilinear, rotating[30] and righting movement. In the first type our specimens were able to creep forward and backward in the direction of the antero-posterior axis when placed normally, or oral side down. The forward movement, in which they move always with the anterior edge foremost, is quite usual, while the backward one, in which the posterior edge comes first, is fairly rare[31]. So far as I can see, the other two types of locomotions are auxiliary to the first type, whether the animals be placed normally or upside down. And it is especially in the forward movement of the animal placed normally on the sand that the zigzag line is found performing a fairly important part. I shall therefore describe here some fundamental facts about the function, leaving particulars to the study of each form.

As the normally-placed animal moves forward on the sand, the sand-grains gradually spread over its dorsal surface from the anterior edge to the posterior; but they usually leave the line uncovered for a while after the complete disappearance of the other parts of the body. If it moves backward, the grains diverge from the pseudofasciole to right and left and spread over the posterior region[32]. In rotation in the normal posture, the spread of the grains is more marked on either the left or the right side of the body in the dorsal aspect, according to the direction of the movement which may be clockwise or counter-clockwise; but the grains that have first covered most of one side stop short of the zigzag line, which remains uncovered for a tolerably long time. In this case, as in the forward movement, the sand reaches the line at last but it is hindered from running across the line. Now, if some grains are put just upon the line of an individual in for-

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[30] In rotation, like *E. parma* observed by PARKER (1927), our forms may turn with their mouths as the centre.

[31] PARKER (1927) stated that *E. parma* cannot move backward in process of burrowing itself.

[32] In *Astriclypeus*, the inverted individual moves backward in the same manner.

ward movement, they will be conveyed partly forward, and partly backward, along the line. When those which are conveyed forward arrive at the apical field, they gradually spread all over the petals and their neighbourhood, while those which fail to reach the apical field are usually cast away from the posterior edge of the body by help of the spines of the line. This latter way of transportation is also seen both in rotation and in backward movement. On the whole the transportation of the grains is slower than the locomotion of the creature, and this fact is of importance especially with regard to the righting movement.

The method of locomotion differs in detail between *E. mirabilis* and *A. manni* according to the body-shape, but in the function of the pseudofasciole there seems to be an accordance on the whole.

Echinarachnius mirabilis (A. AGASSIZ): This species, rather small in shape, has the abactinal continuous pseudofasciole, and the relation between the behaviour of the animal and the function of the line is observable on the dorsal surface only.

When the sand-dollar placed normally on sand moves forward, the spread of sand-grains takes place in a bilateral symmetry with regard to the antero-posterior axis, as is the distribution of the spines over the body. In the locomotion of the animal, those spines successively swing to and fro from their roots with vigorous strokes, carrying the grains. The spines of the scutellids are terminated with a characteristical expansion, which makes them fit for carrying the grains; this specialization is most pronounced in the spines of the dorsal side, and the swing takes place in such a manner that the spines transfer grains in the direction opposite to that of the animal's locomotion. The movement of the spines thus plays an essential part in locomotion, though it is not clear whether in our species the locomotive tube-feet seen scattered for the most part on the dorsal side (cf. MÜLLER, 1854) work supplementarily, as in *E. parma* (cf. PARKER and VAN ALSTYNE, 1932) and *M. sexiesperforata* (cf. CROZIER, 1920).

Astriclypeus manni VERRILL[33]: The species, large in size, has 5 ambulacral lunules and the pseudofascioles both abactinal continuous and actinal.

In the types of locomotion it agrees generally with *E. mira-*

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[33] The sample identified by VERRILL (1867) is a spineless test.

bilis, in spite of the fact that lunules and the actinal pseudofasciole are wanting in the latter. The abactinal pseudofasciole of *Astriclypeus* seems to serve, like that of *Echinarachnius*, as a rudder and an instrument for driving sand-grains. Being much longer, it is more active than the actinal; the latter seems merely to swing away the excretion out of the anus. The sand is transported quite easily to the dorsal or the oral side in case of necessity by the large primary spines growing inside the lunule. This manœuvre is very important on the sand, for instance, in the righting movement and the concealment of the body.

It may be assumed from the foregoing observation that in the forward movement of *Echinarachnius* and *Astriclypeus*, a part of the sand-grains which are spread over the petals through the agency of the spines of the abactinal pseudofasciole may make a circuit, being carried back by the spines on the dorsal side from the anterior region towards the line which carries them to the apical field again. Probably a circulation of the grains occurs on the dorsal surface of the animal in its natural life in the sand, and as it goes on, it produces a movement of water so as to supply the animal with fresh water. If this assumption be valid, the movement may be of no little service to the respiratory tube-feet; it may intensify the effect of the ciliary current in case of the presence of cilia in our forms. Furthermore, the sand carried backward along the line and thrown away from the posterior edge of the test seems, in *Echinarachnius*, to accomplish the clearing of the excretion from the marginal anus.

While our forms creep forward in the normal posture, the sand, as was stated above, does not easily cross over the line from one side to the other, but stops at some distance before it reaches the line. This appears to be in order to keep the animal under an even pressure and prevent it deflecting from its course. In the forward movement the spread of sand on the dorsal side is in a bilateral symmetry, but in rotation both the extension and the quantity of distributed sand are more or less asymmetrical with regard to the zigzag line. This lack of symmetry may in some degree stimulate the locomotive organs, or, strictly speaking, the spines on the oral side, tending to bring about a change of direction, somewhat like a vertical rudder of a boat. When an inverted individual of *Astriclypeus* moves forward, the sand transported by the spines of the actinal pseudofasciole moves always in the direction opposite to the movement of the animal. It is interesting to note that this mode of transportation makes an inverted image of that of the dorsal side of an animal placed normally.

Encope and *Mellita,* having the abactinal discontinuous pseudofasciole, possess an interambulacral lunule. If this lunule corresponds in function to the ambulacral lunules of *Astriclypeus,* the sand-grains that cover the dorsal surface in forward motion must partly be carried up there from the oral side through this hole. These grains, together with the majority that are carried from the anterior edge by the spines on the dorsal side, must make the spines of the prelunular part of the zigzag line much busier than those of the post-lunular, because the prelunular part is directly connected to the apical field. As for the absence of the line on the oral side of these forms some tentative explanations were given in an earlier chapter. The explanations refer to the specialization of the spines on the oral side and the close approach of the ambulacral furrows on that side to the mid-zone of the interambulacral 5. Besides those, the proximity of the hole to the anus and to the posterior edge of the test may be mentioned here. The reason is this. There are remarkably large primary spines inside the hole, which presumably work with such vigorous strokes that they can cause not only sand-movement but also a water-current through the hole. In that case, these primary spines take the place of the spines of the actinal line, the hole being conveniently situated to clear excrements away. This speculation has a very interesting bearing upon the fact that the presence of an interambulacral hole implies the absence of the line on the oral side. I pointed it out only from what was observed in the external appearance, but now an ample reason for the absence seems to be found in the function of the hole. It may also be asserted that between *Echinarachnius* and *Dendraster* or between *Astriclypeus* and *Echinodiscus* there is a resemblance in the function as well as in the superficial form of the zigzag line.

The scutellids have the shape of a flat disk as the result of a high specialization(34), but the ambulacral and interambulacral

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(34) The flat shape may protect the scutellids from overturning by the force of waves on the sandy bottom, as can be judged from the description of MACBRIDE (1909) who observed the stability of *E. parma.*

zones are each continuous from the dorsal side down to the oral, as in other regular echinoids. Indeed it is evident, from the locomotion of our forms, that the spines on the dorsal side cooperate with those on the oral side, though, as stated above, the former are less active than the latter.

The following experiments show the effects of mutilation upon the forward movement of animals placed normally: (1) The deprivation of spines[35] on the right side in the oral aspect (the ambulacral V and its neighbourhood) caused the diversion of the course to the right, while that on the left side (the ambulacral I and its neighbourhood) to the left. (2) On the contrary, by the stripping of spines on the right side in the dorsal aspect (the ambulacral I and its neighbourhood) the rectilinear movement was forced to curve fairly to the left, and that on the left side (the ambulacral V and its neighbourhood) to the right. This is perhaps because the operation upon a certain region of the dorsal surface stimulates, in some way, the nerves inside the corresponding part of the oral surface, so that they may excite the activity of the locomotive spines of that side[36]. Lapse of time, therefore, nullifying the stimulus of the mutilation, apparently brings the animals back to their ordinary course of progress[37]. In the first instance, however, the spines taken away are themselves part of the main organs of locomotion, so that the power of movement is diminished on the injured side of the body, and the stronger side pushes the body round. In this case, the recovery of a straight course cannot be expected before the regeneration of the spines. In either case, the curvature of the circular course was proportional to the dimension of the denuded section. In all these experiments the deviation from the original course began with a rather sudden turning of the body in a new direction. This motion is indeed for a very short distance, but it appears to be sufficiently different from either a rectilinear or a circus movement to be regarded as a part of a rotating movement. The direction of rotation is chiefly determined, in much the same way as in the circus movement, by the region from which spines are removed.

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[35] The deprivation of spines involves the desquamation of the epithelial membrane.

[36] Cf. HERRICK, 1924.

[37] In *Astriclypeus*, the time required for recovery was about 15 hours.

Echinarachnius and *Astriclypeus* were subjected to another trial. When specimens 8–8.5 cm long of *Astriclypeus* from Ōmura Bay were burdened with from 5 to 20 grams of sand on the right side in the dorsal aspect, they made a curve apparently towards the left with an introductory rotation. Thus the direction the animal took was contrary to the side which was loaded with sand. This reaction is evidently due to the weight of sand. It naturally breaks the balance of activity of the spines between the sides of the oral surface. The path taken in the forced movement has exactly the same character as in the aforesaid denudation in the corresponding region. Under more than 30 grams of sand, however, most of the animals curved somewhat towards the burdened side. It is because the weight was too much for them to counteract. A single exception was an individual 9.5 cm long, which could endure the weight of no less than 50 grams without turning to the burdened side. In case of the specimens 5.5–6 cm long of *Echinarachnius* from Hukuoka Bay, the threshold of stimulation and the maximal stimulus were 15 and 50 grams of sand respectively (cf. VERWORN, 1913, 1914). This fact may appear rather curious, for it shows that the maximal weight of the sand in these two forms was not proportional to the size of the animals. But *Echinarachnius* conceals itself in the sand by burrowing rather deeper than *Astriclypeus*, so that when the animals are of about the same size the former must bear the greater weight of sand in concealment. This habit may naturally be assumed to account for the higher threshold of stimulation or comparative smallness of irritability in *Echinarachnius* in spite of its smaller size.

The reaction to weight thus manifests itself in the spines of the oral side. It may be admitted that the epithelial membrane of the oral side serves as a stereoreceptor (cf. WARDEN, JENKINS and WARNER, 1934), and the inner nerves of the oral side react accordingly (cf. UEXKÜLL, 1896, 1900). As a result of this, a tonic statoreflex may be found in the oral spines, which is produced by means of the muscles that bind those spines to the tubercles. Then these processes combined must make the actinal spines of certain zones more active than the rest. The reaction to weight thus brings about a circus movement. It also occurs, on the other hand, that an obstacle in the way turns the course into a circuit; and in this case also the introductory rotation is accompanied with an asymmetrical spread of sand over the dorsal surface. Now, the ordinary progression appears to be accomplished by the dynamical equilibrium which chiefly depends upon the bilateral symmetry of the body-shape and of the distribution of the spines (cf. KÜHN, 1919). In forced movements, however, the co-ordinate movement of the spines on the oral side was disturbed, and it modified the geometrical character of the path, without affecting the diageotaxis. Thus forced movements, as shown in my experiments, simply assumed the nature of circus movements (cf. LOEB, 1918). So far as my species are concerned, this modification of the path may perhaps depend not so much upon the frequency as upon the amplitude of the swings of the irritated spines on the oral side, for these swings seem to be hardly distinguishable from those of the unirritated spines. After all, the immediate cause of the circus movement is in an obstacle or some stimulus, though the asymmetrical spread of sand over the dorsal surface, if it happens to take place at the commencement of the altered course, must in turn increase the tendency of circulation.

From the facts mentioned elsewhere is drawn an inference that in *Astriclypeus* the lines of the dorsal and oral sides originally formed one continuous whole, but there is an essential difference of function between these two parts. The actinal pseudofasciole of this form is inactive compared with the abactinal one, only removing the matter ejected from the anus. On the other hand, the abactinal pseudofasciole has a less complicated function in this form than in *Echinarachnius* in which a simple line, almost half as long as the diameter of the test, fulfils a twofold function.

Sufficient instances, I think, have now been given to make it clear that the spines of the zigzag line are very important for those animals in regulating the direction of their forward movement and in cleansing the excretion from the anus. Those spines are distinguished from the rest by their peculiar inclination, and as they are essential to the appearance of the zigzag line, so also are they to its function. It may be safe to conclude therefore that the more conspicuous the zigzag is in its structure, the more effective in its function.

Like *Echinarachnius* and *Astriclypeus*, the allied forms *Clypeaster japonicus* DÖDERLEIN and *Peronella lesueuri* (AGASSIZ) live on the sandy bottom in the shallow coastal water, and in their ordinary progression and rotation the spines on the oral side work like those of the scutellids. In *P. lesueuri* the movement of the abactinal spines is altogether radial, not being bilaterally symmetrical as in the scutellids. Nevertheless when experimented on its locomotion, an individual was found half-buried in sand, as *Astriclypeus* also very rarely is. *P. lesueuri* has rather remarkable locomotive tube-feet. This species and *C. japonicus* lack the pseudofasciole on either side of the test, as I have stated in a preceding chapter. It is perhaps because they do not live in sand but on it. The line seems to be necessary to the scutellids only because they live in the sand which is very porous[38]. This fact reminds us of spatangoids burrowing in sand (cf. HOFFMANN, 1871; GANDOLFI-HORNYOLD, 1910; SCHWARZ, 1930; GISLÉN, 1924), in mud (cf. EICHELBAUM, 1909) or in gravel (cf. OHSHIMA, 1931). Those animals have some kinds of fasciole consisting of clavulae[39]. Of those the peripetalous and the anal fascioles correspond to the zigzag line in their functions. The former, surrounding the petals as the name implies, serves the respiratory tube-feet in the petals with current of fresh water, while the latter clears away the material discharged from the anus (cf. MACBRIDE, 1909; GANDOLFI-HORNYOLD, 1910, 1914). On the other hand, a certain function which is performed by the pseudofasciole in the scutellids is excluded from the fasciole in the spatangoids. The fasciole, in all its forms, is used exclusively as the organ of water-movement. This division of function may be regarded as due to the differentiation of the body-shape in these animals. The part of a rudder, for instance, is apparently performed by the interambulacral 5, which is more or less elongated in the posterior part like a tail[40]. In the pseudofasciole of the scutellids only a slight sign of differentiation is found, as in the complex pseudofasciole of *Astriclypeus*. Apropos of differentiation, the spatangoids are more advanced in the general shape, too, being globulous on the whole, while the scutellids are all flat.

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[38] The porosities of the sand measured by the pycnometer are as follows: The sand from Ōmura Bay, Nagasaki-ken, where *Astriclypeus* occurs is 2.37: that from Hukuoka Bay where *Echinarachnius* occurs is 2.53.

[39] The clavulae are characteristically small spines and very strongly ciliated (cf. MORTENSEN, 1927 a).

[40] In the spatangoid *Moira atropos* (LAMARCK) PARKER (1927) saw a straight-away locomotion. The movement may partly be effected by such a tail as this, with which the body-axis agrees, though partly by the primary spines on the sternum.

Regeneration of the pseudofasciole

It is well known through the description of KORSCHELT (1927) that in the echinoids there are many cases of regeneration. And CROZIER (1919) mentions in his study of *Mellita sexiesperforata* that he saw regeneration and re-formation of the lunules in this form. Recently I saw some specimens of *E. mirabilis* and *A. manni* which have evidently regenerated the spines of their tests and re-formed their pseudofascioles. A damaged section seems to regenerate from its periphery in more than two months. If the section contains a zigzag line, it seems to be re-formed there, subsequent to the appearance of the peculiar inclination of the spines.

In one case, the re-formed line appears to connect both ends of the broken line, though the re-formed section does not seem to have exactly reproduced the original line, and its zigzagging is very irregular. In another case, an irregular zigzag line is formed in the regenerated part, without being perfectly connected with the undamaged section at either end, but approximately running over the region which may have been covered by the lost portion of the line. In either case, a part which is spined similarly to one or the other side of the zigzag line is found forming a detached patch in the opposite half-zone. Therefore the inclination of spines in the regenerated section is probably under the same influence as the spines at the undamaged end immediately adjacent to the damaged section are subject to; so that, there seems to be two sources of influence affecting the re-formation of the line, one at the anterior end of the re-formed line and another at the posterior. If the inclination of the spines of the re-formed line agrees completely with the original inclination both at the anterior and the posterior ends, the line will be perfectly connected to the undamaged parts; while if it disagrees at either the posterior or the anterior end, the line is not quite continuous.

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EXPLANATION OF THE PLATES

Plate 2

Echinarachnius mirabilis (A. AGASSIZ); Figs. 1, 2:
Echinarachnius griseus MORTENSEN; Figs. 3–5:
Mellita sexiesperforata (LESKE); Figs. 6, 7:
Astriclypeus manni VERRILL; Figs. 8–11.

Fig. 1. Dorsal view of a specimen from Hukuoka Bay; × 1.
Fig. 2. Part of a denuded test from Mutu Bay showing how the pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.
Fig. 3. Dorsal view of a specimen from Hokkaido; × 1.
Fig. 4. Oral view of another specimen from the same locality; × 1.
Fig. 5. Dorsal view of a specimen from Sakhalin; somewhat enlarged.
Fig. 6. Dorsal view of a specimen from Tobago; × 1.
Fig. 7. Oral view of the same specimen; × 1.
Fig. 8. Part of a specimen from Tuyazaki showing the abactinal pseudofasciole; somewhat enlarged.
Fig. 9. Same specimen showing the actinal pseudofasciole; somewhat enlarged.
Fig. 10. Part of a denuded test from Ōmura Bay showing how the abactinal pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.
Fig. 11. Part of a denuded test from Kominato showing how the actinal pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.

Plate 3

Echinarachnius brevis IKEDA; Figs. 1, 8:
Dendraster excentricus (ESCHSCHOLTZ); Figs. 2, 3:
Dendraster excentricus var. *elongatus* H. L. CLARK; Figs. 4, 5:
Astriclypeus manni VERRILL; Figs. 6, 7.

Fig. 1. Oral view of a smaller specimen from Hukusima; × 1.
Fig. 2. Dorsal view of a specimen from Nanaimo; × 1.
Fig. 3. Same specimen showing the abactinal pseudofasciole; somewhat enlarged.
Fig. 4. Dorsal view of a specimen from San Diego; × 1.
Fig. 5. Same specimen showing the abactinal continuous pseudofasciole; somewhat enlarged.
Fig. 6. Dorsal view of a specimen from Tuyazaki; × 1.
Fig. 7. Oral view of the same specimen; × 1.
Fig. 8. Dorsal view of a specimen from Hukusima; × 1.

Plate 4

Echinarachnius asiaticus MICHELIN; Figs. 1–3:
Dendraster excentricus (ESCHSCHOLTZ); Figs. 4–6, 8:
Echinarachnius mirabilis (A. AGASSIZ); Fig. 7:
Echinarachnius parma (LAMARCK); Fig. 9.

Fig. 1. Dorsal view of a specimen from Kamchatka; × 1.

Fig. 2. Same specimen showing the abactinal continuous pseudofasciole; × 2.

Fig. 3. Oral view of the same specimen; × 1.

Fig. 4. Specimen from Nanaimo showing the abactinal continuous pseudofasciole; × 1.

Fig. 5. Part of another denuded test from the same locality showing how the pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.

Fig. 6. Part of the oral view of the same specimen; × 1.

Fig. 7. Animal from Hukuoka Bay, from which the spines under the anus were removed, moving forward on the sand, without leaving central trail; slightly reduced.

Fig. 8. Specimen from Nanaimo showing the actinal side; × 1.

Fig. 9. Denuded test from Quebec showing how the abactinal continuous pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.

Plate 5

Encope californica VERRILL; Figs. 1–3:
Rotula orbiculus (LINNÉ); Figs. 4, 5.

Fig. 1. Dorsal view of a specimen from Mexico; slightly reduced.

Fig. 2. Part of the same specimen showing the abactinal discontinuous pseudofasciole; × 1.5.

Fig. 3. Oral view of the same specimen; slightly reduced.

Fig. 4. Dorsal view of a specimen from Cape Verde Islands; × 1.

Fig. 5. Oral view of the same specimen; × 1.

Plate 6

Encope michelini AGASSIZ; Figs. 1–3:
Echinarachnius parma (LAMARCK); Figs. 4, 5.

Fig. 1. Dorsal view of a specimen from the west coast of Florida; slightly reduced.

Fig. 2. Part of the same specimen showing the abactinal discontinuous pseudofasciole; × 1.5.
Fig. 3. Oral view of the same specimen; slightly reduced.
Fig. 4. Dorsal view of a specimen from Buzzards Bay; × 1.
Fig. 5. Same specimen showing the abactinal continuous pseudofasciole; somewhat enlarged.

Plate 7

Encope perspectiva AGASSIZ; Figs. 1–3:
Echinodiscus auritus LESKE; Figs. 4, 5.

Fig. 1. Dorsal view of a specimen from Mexico; slightly reduced.
Fig. 2. Part of the same specimen showing the dorsal posterior interambulacral zone and its neighbourhood; × 1.5.
Fig. 3. Oral view of the same specimen; slightly reduced.
Fig. 4. Part of an imperfect specimen from Philippine Islands showing the abactinal continuous pseudofasciole; × 1.
Fig. 5. Same specimen showing a part of the actinal pseudofasciole; × 1.

Plate 8

Encope grandis AGASSIZ; Figs. 1–3:
Echinarachnius mirabilis (A. AGASSIZ); Fig. 4.

Fig. 1. Dorsal view of a specimen from Lower California; slightly reduced.
Fig. 2. Part of the same specimen showing the abactinal discontinuous pseudofasciole; × 1.5.
Fig. 3. Oral view of the same specimen; slightly reduced.
Fig. 4. Animal from Hukuoka Bay in the forced movement; showing the trail left on the sand; most of the spines on the right side in the neighbourhood of the pseudofasciole were removed from the animal; slightly reduced.

Plate 9

Mellita sexiesperforata (LESKE); Figs. 1–3:
Mellita quinquiesperforata (LESKE); Figs. 4, 5.

Fig. 1. Dorsal view of a specimen from Saint Martin, West Indies; × 1.

Fig. 2. Part of the same specimen showing the abactinal discontinuous pseudofasciole; somewhat enlarged.
Fig. 3. Oral view of the same specimen; × 1.
Fig. 4. Dorsal view of a specimen from Mexico; × 1.
Fig. 5. Oral view of the same specimen; × 1.

Plate 10

Encope micropora AGASSIZ; Figs. 1-3:
Mellita quinquiesperforata (LESKE); Fig. 4:
Rotula orbiculus (LINNÉ); Fig. 5.

Fig. 1. Dorsal view of a specimen from California; × 1.
Fig. 2. Same specimen showing the abactinal discontinuous pseudofasciole; somewhat enlarged.
Fig. 3. Oral view of the same specimen; × 1.
Fig. 4. Part of a specimen from Mexico showing the abactinal discontinuous pseudofasciole; somewhat enlarged.
Fig. 5. Dorsal view of a specimen from the Congo; × 1.

Plate 11

Encope emarginata (LESKE); Figs. 1-3:
Mellita longifissa MICHELIN; Figs. 4, 5.

Fig. 1. Dorsal view of a specimen from Rio de Janeiro; × 1.
Fig. 2. Same specimen showing the abactinal discontinuous pseudofasciole; somewhat enlarged.
Fig. 3. Oral view of the same specimen; × 1.
Fig. 4. Dorsal view of a specimen from Mexico; × 1.
Fig. 5. Oral view of the same specimen; × 1.

Plate 12

Encope emarginata (LESKE); Figs. 1-4:
Dendraster excentricus var. *elongatus* H. L. CLARK; Figs. 5-8:
Astriclypeus manni VERRILL; Fig. 9:
Echinarachnius mirabilis (A. AGASSIZ); Fig. 10.

Fig. 1. Dorsal view of a smaller specimen from Santa Marta; × 1.
Fig. 2. Same specimen showing the abactinal discontinuous pseudofasciole; somewhat enlarged.

Fig. 3. Another specimen from the same locality showing a part of the abactinal side; somewhat enlarged.

Fig. 4. Oral view of the largest one from the same locality; × 1.

Fig. 5. Specimen from Pacific Grove showing the abactinal continuous pseudofasciole; × 1.

Fig. 6. Oral view of the same specimen; × 1.

Fig. 7. Part of a larger denuded test from the same locality showing how the abactinal pseudofasciole intercrosses the longitudinal suture of the plates in the interambulacral 5; × 1.

Fig. 8. Part of the same test showing the actinal side; × 1.

Fig. 9. Regenerated abactinal pseudofasciole of a specimen from Tuyazaki; × 1.5.

Fig. 10. Same of a specimen from Hukuoka Bay; × 1.5.

Plate 13

Echinarachnius mirabilis (A. AGASSIZ); Figs. 1-3:
Astriclypeus manni VERRILL; Figs. 4-6.

Fig. 1. Animal from Hukuoka Bay in course of forward movement: sand-grains placed on abactinal pseudofasciole being carried forward from near the margin; × 2/3.

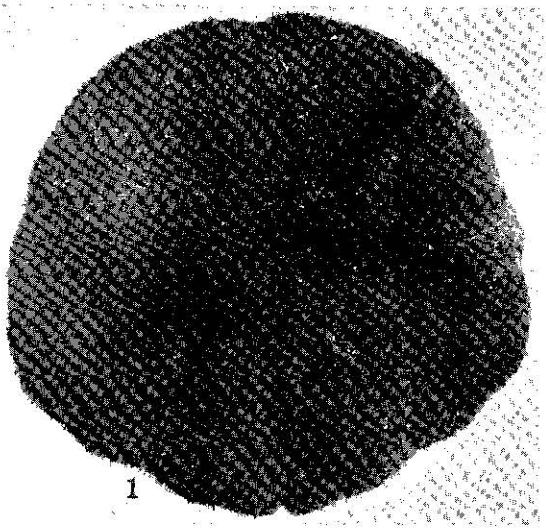
Fig. 2. Same individual in course of backward movement; grains placed on pseudofasciole being carried backward from near the apical field; × 2/3.

Fig. 3. Same individual buried under the sand, leaving the pseudofasciole last to be covered; × 2/3.

Fig. 4. Animal from Ōmura Bay moving forward, the sand-grains being transported from the oral side to the dorsal through the two posterior ambulacral lunules; 2/3.

Fig. 5. Same individual as seen some minutes afterward; 2/3.

Fig. 6. Another individual from the same locality moving forward: grains placed on abactinal pseudofasciole being carried forward from near the margin; 2/3.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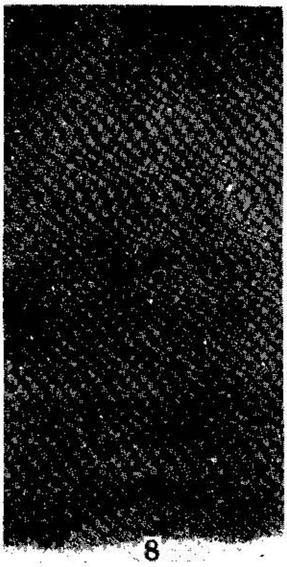
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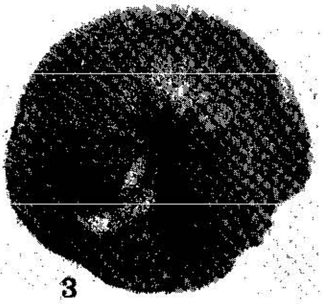
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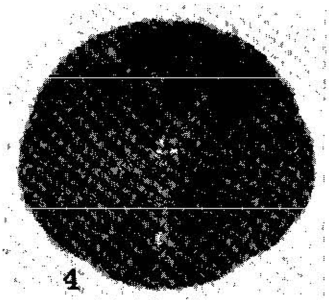
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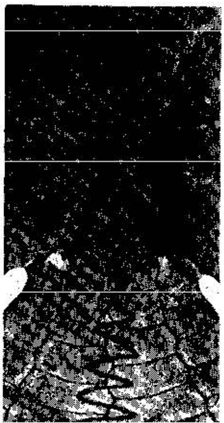
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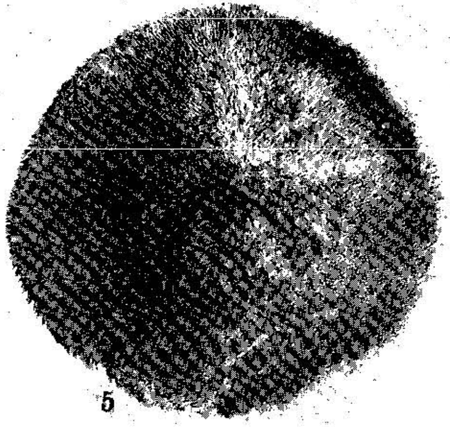
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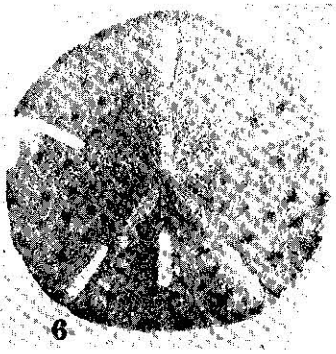
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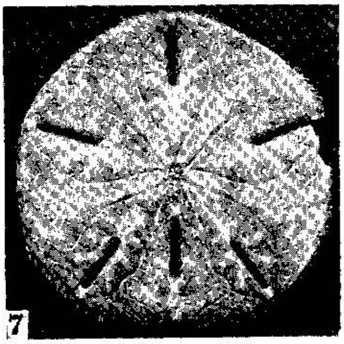
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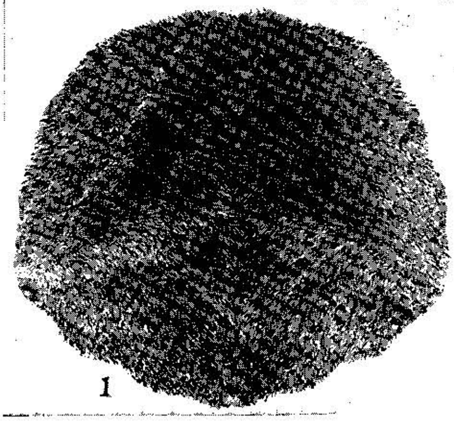
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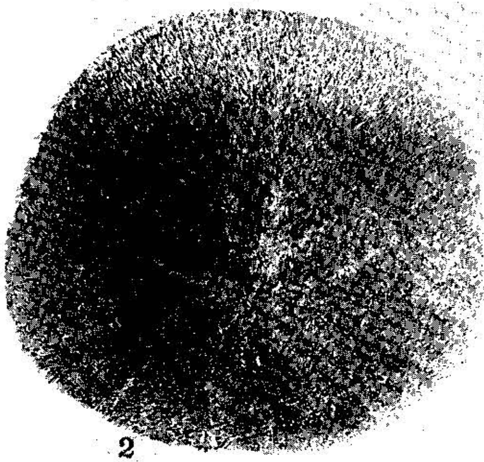
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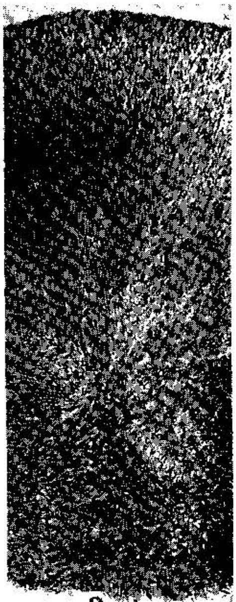
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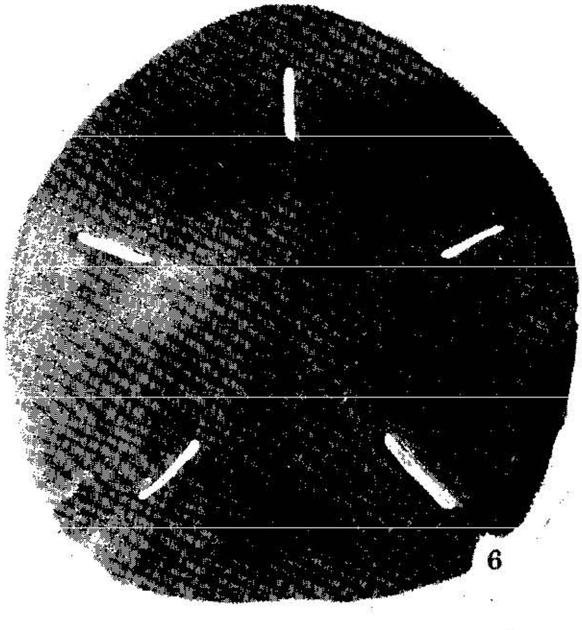
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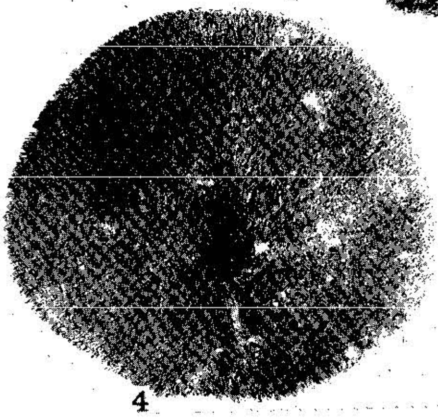
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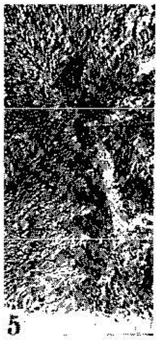
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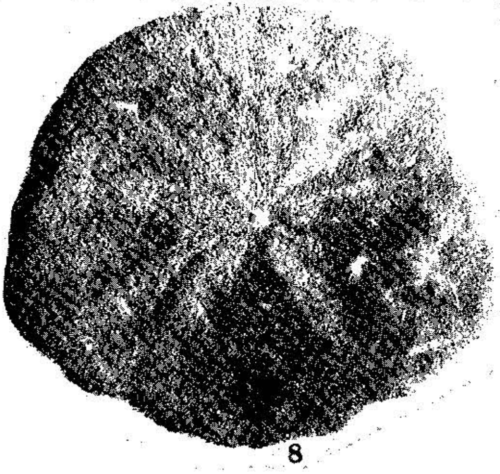
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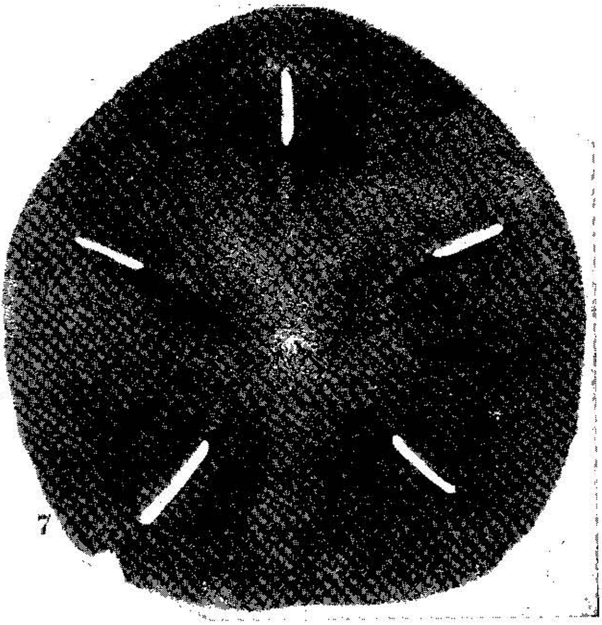
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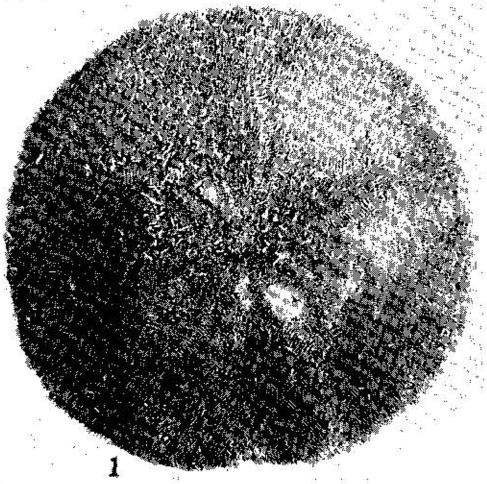
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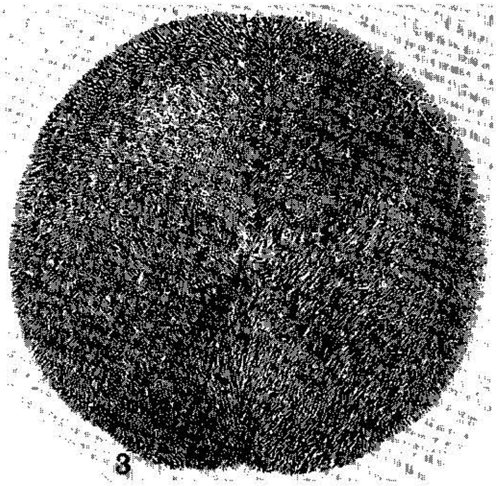
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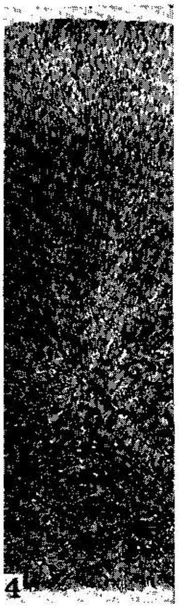
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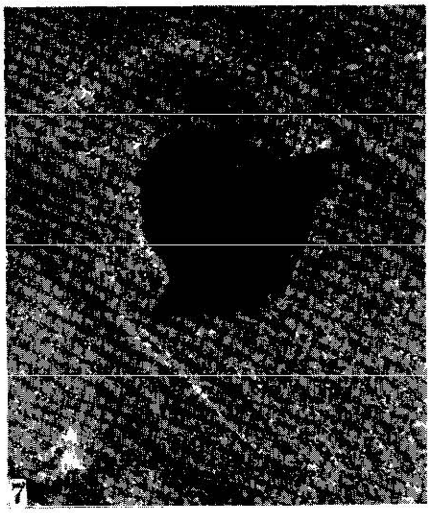
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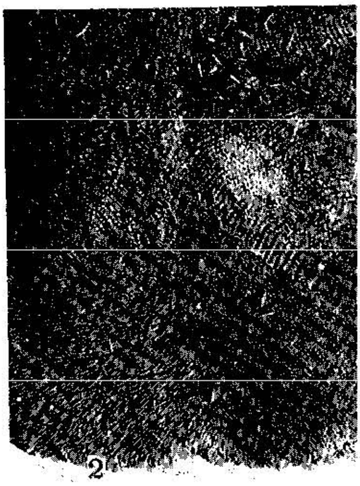
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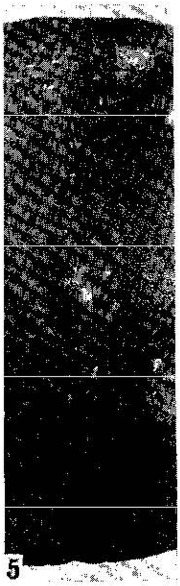
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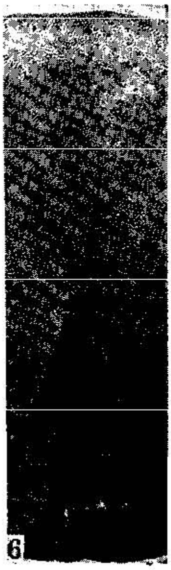
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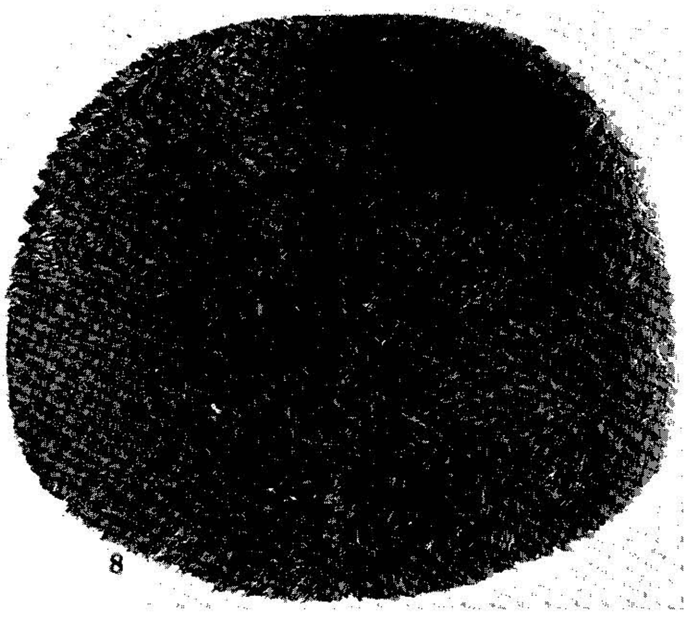
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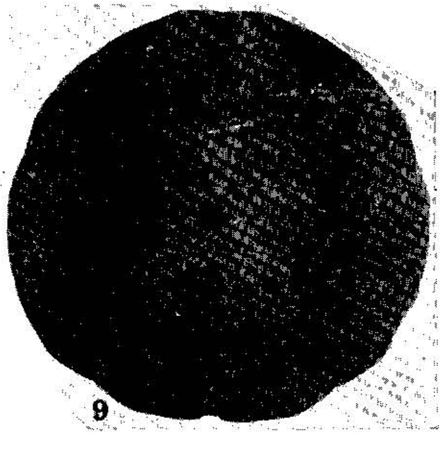
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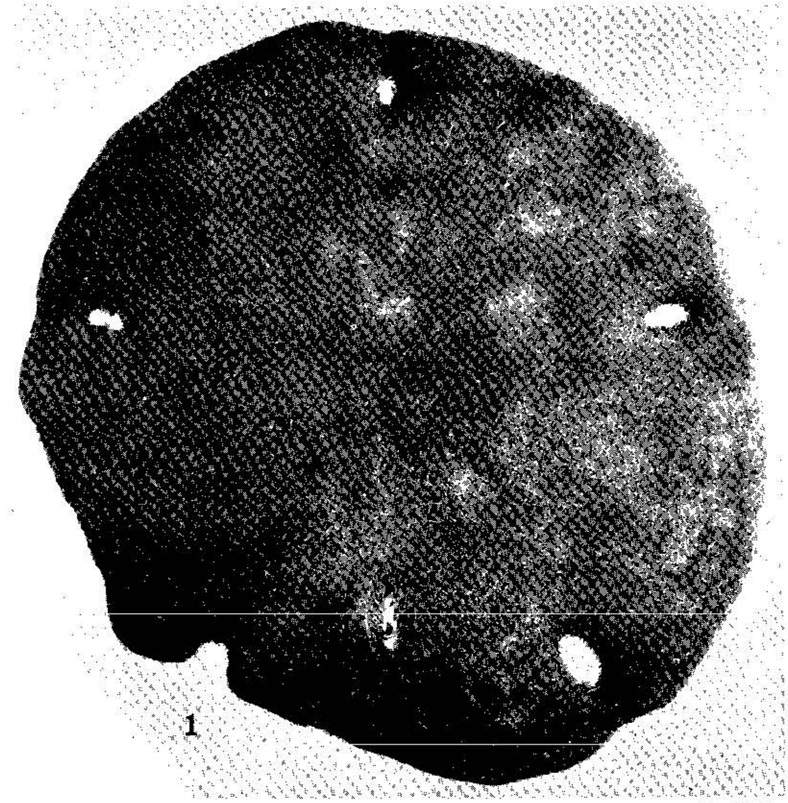
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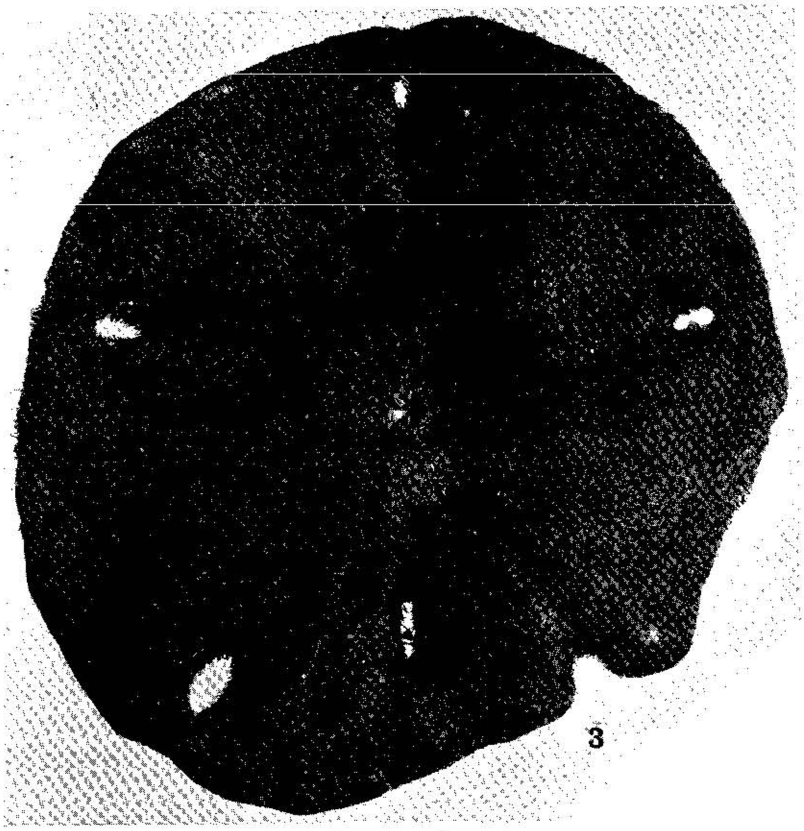
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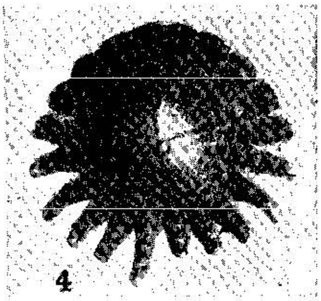
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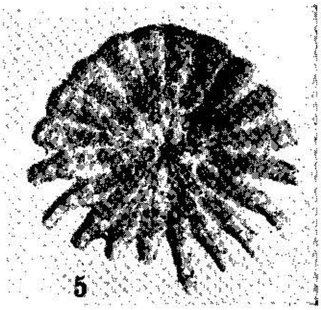
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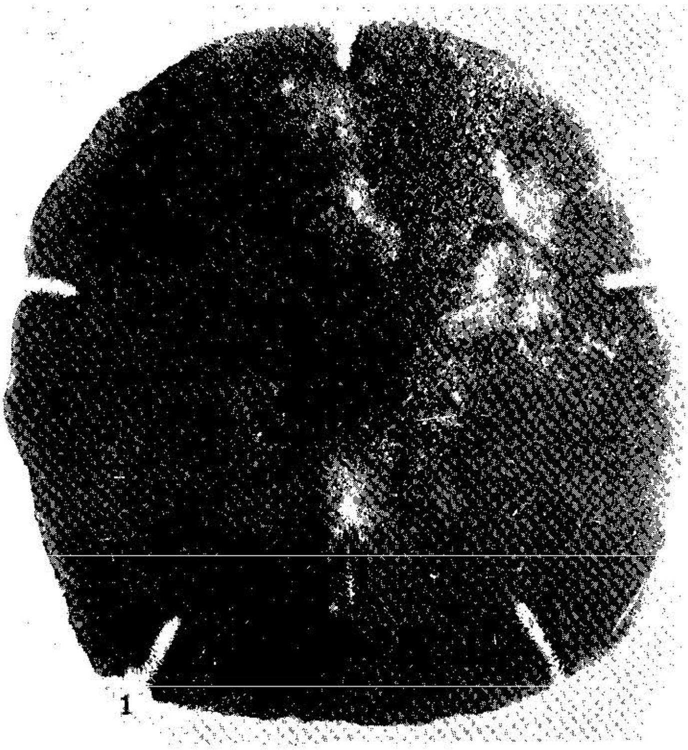
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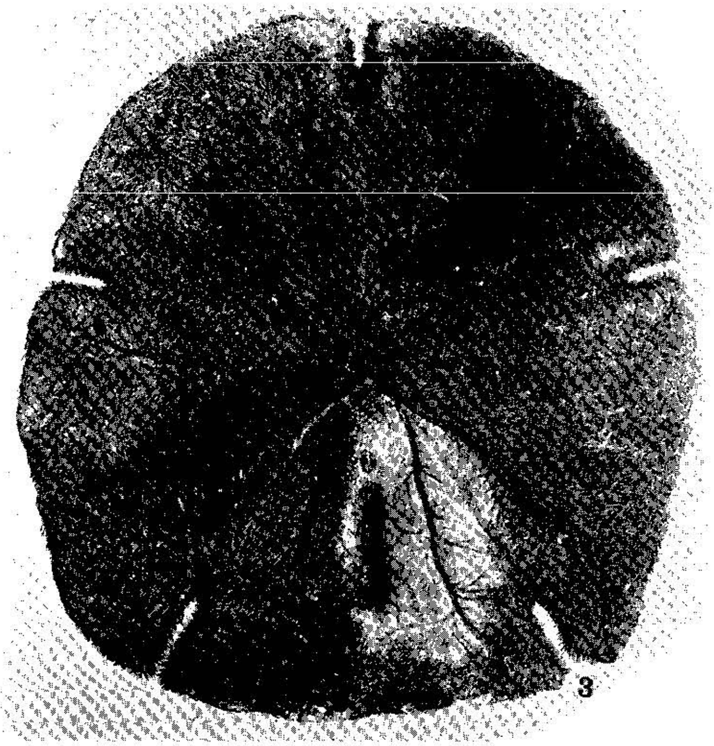
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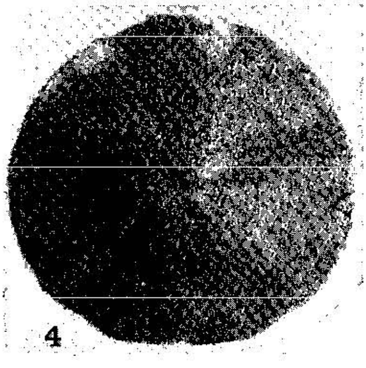
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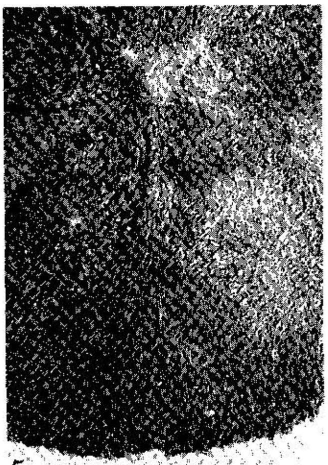
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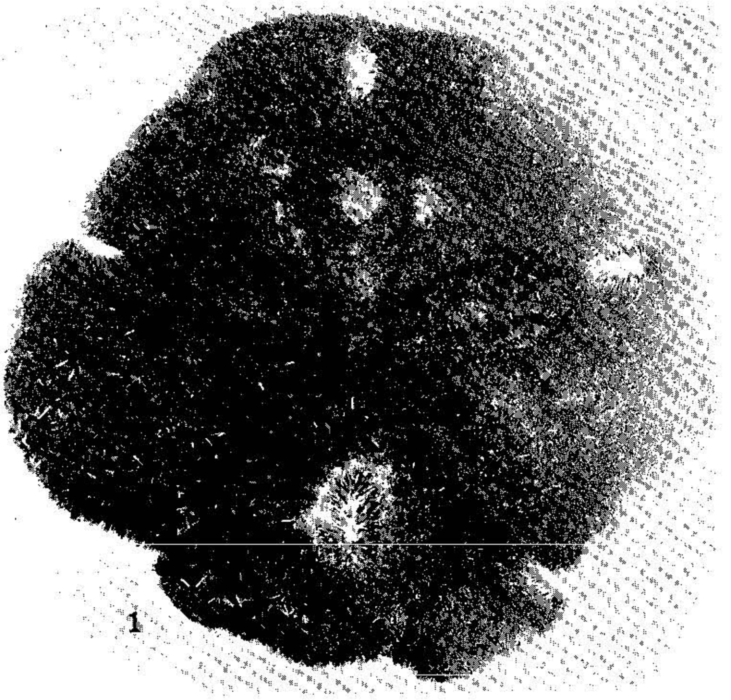

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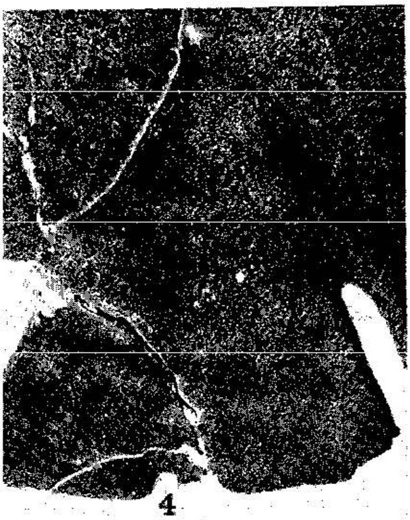

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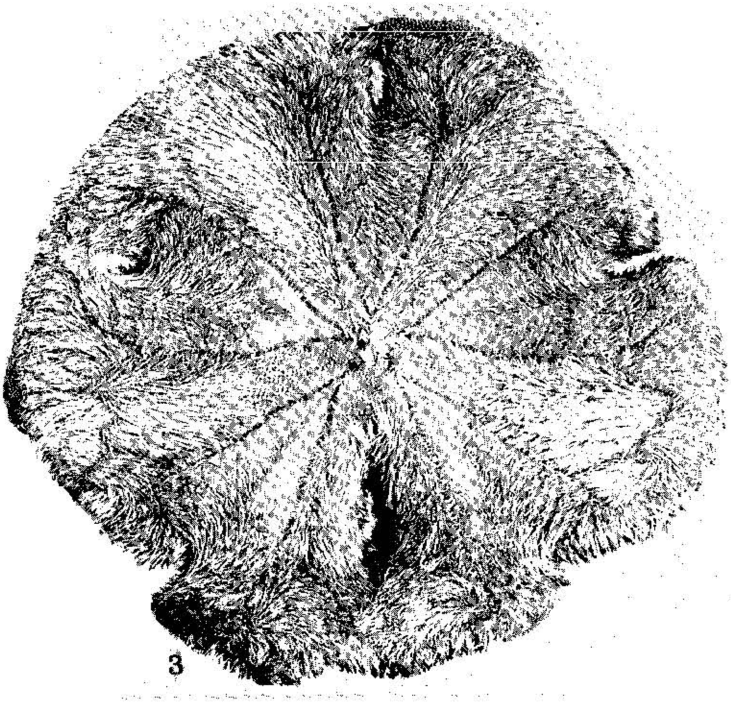

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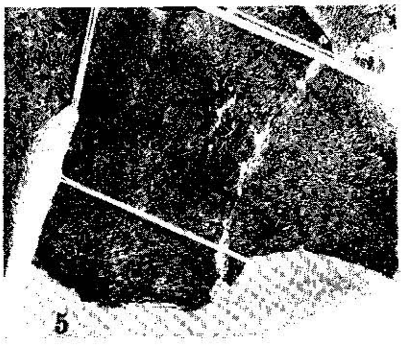

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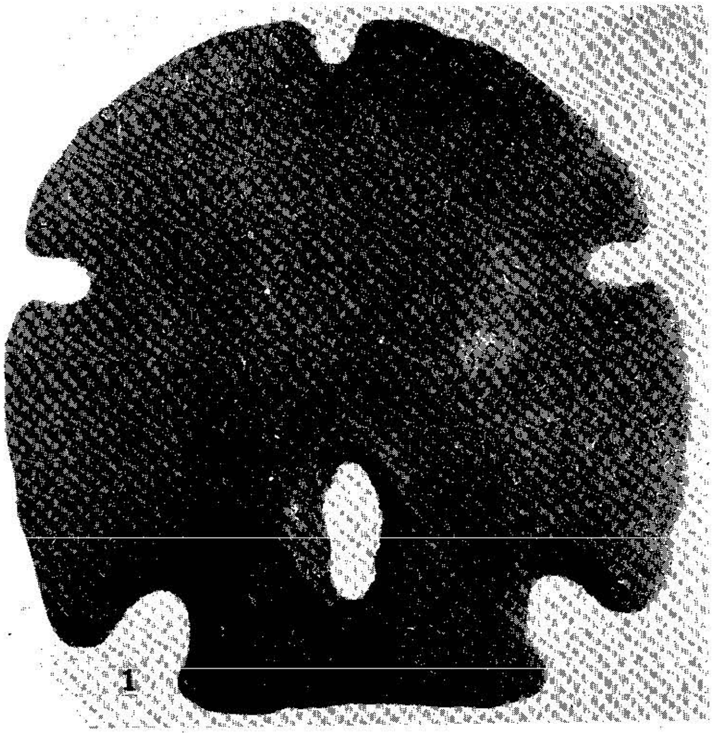
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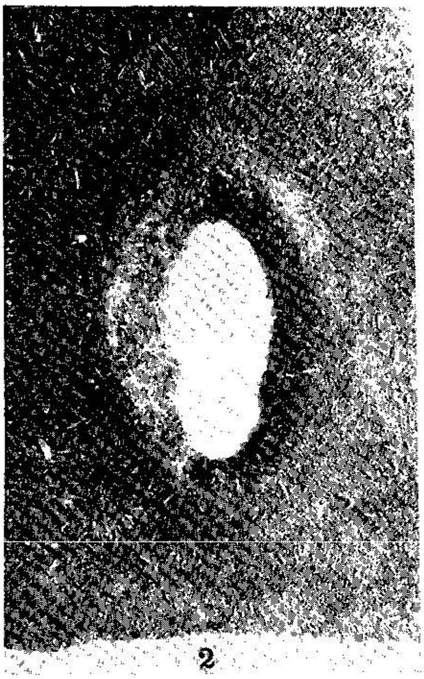
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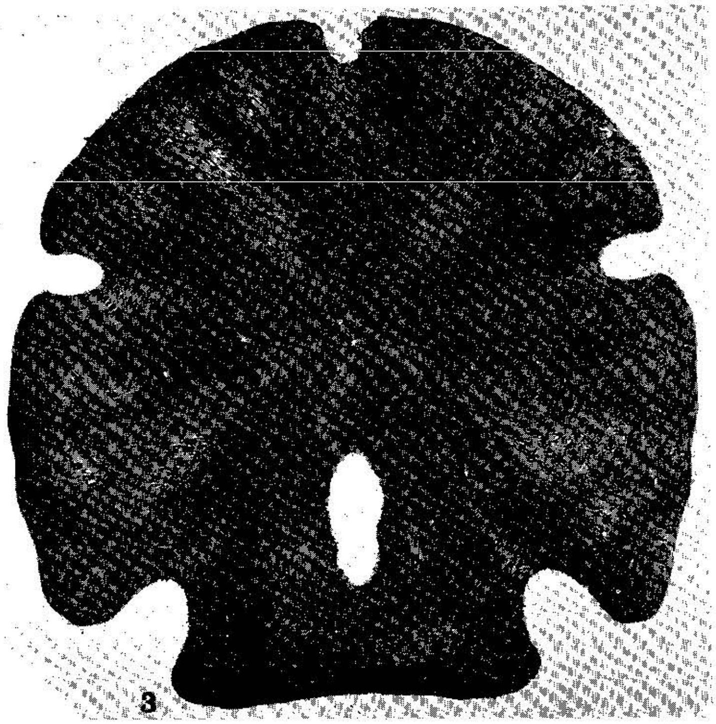
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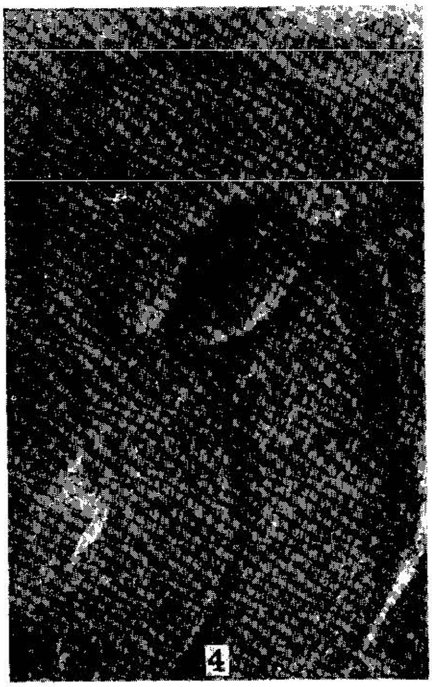
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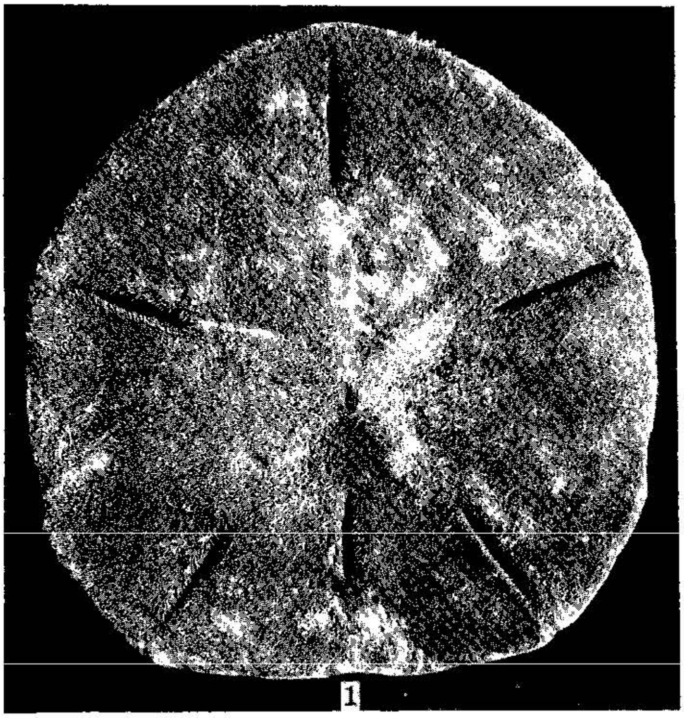

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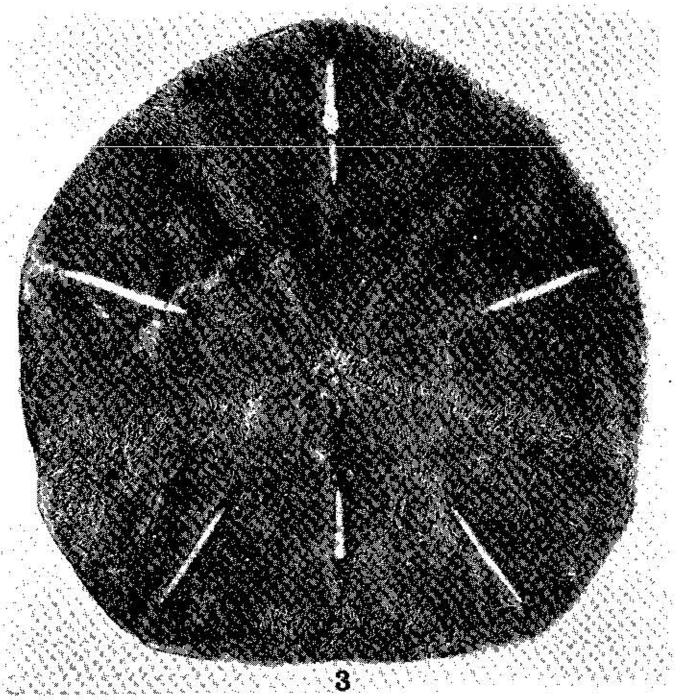

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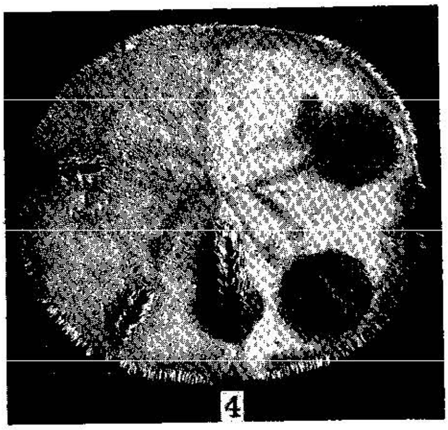

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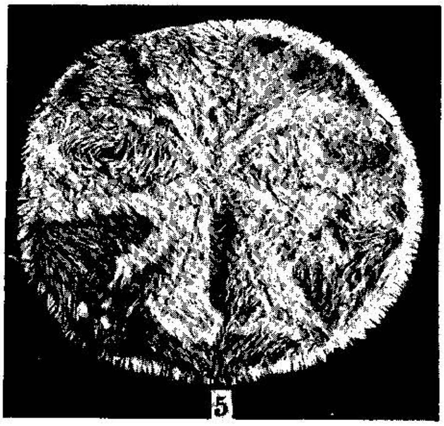

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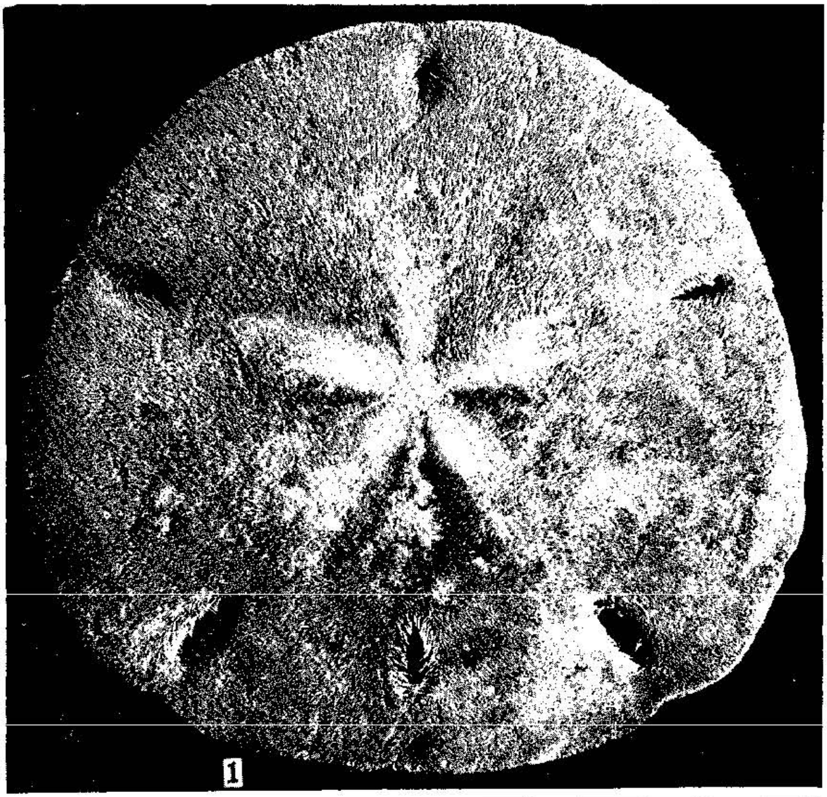
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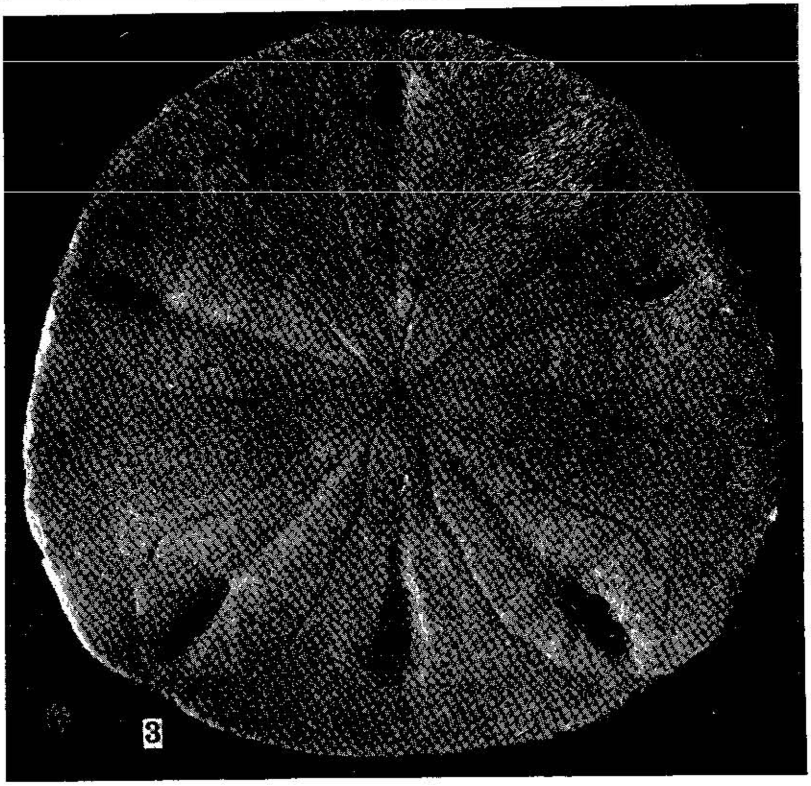
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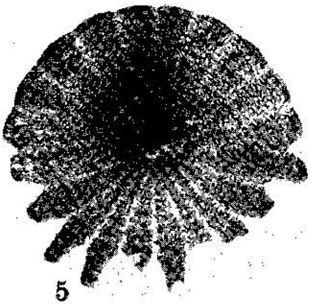
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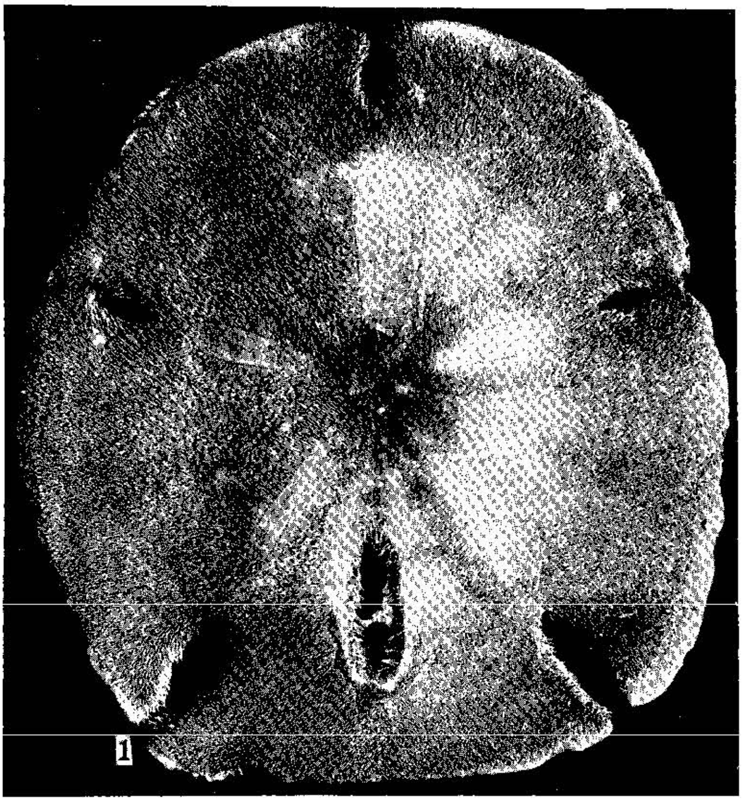
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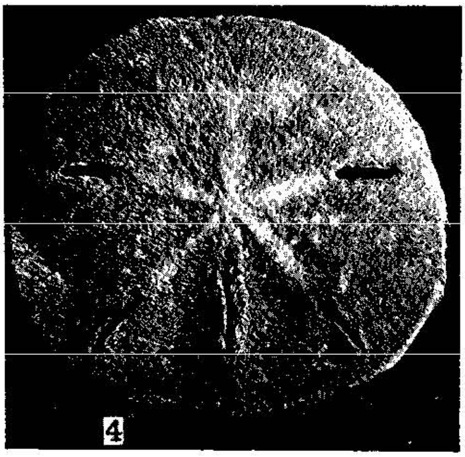
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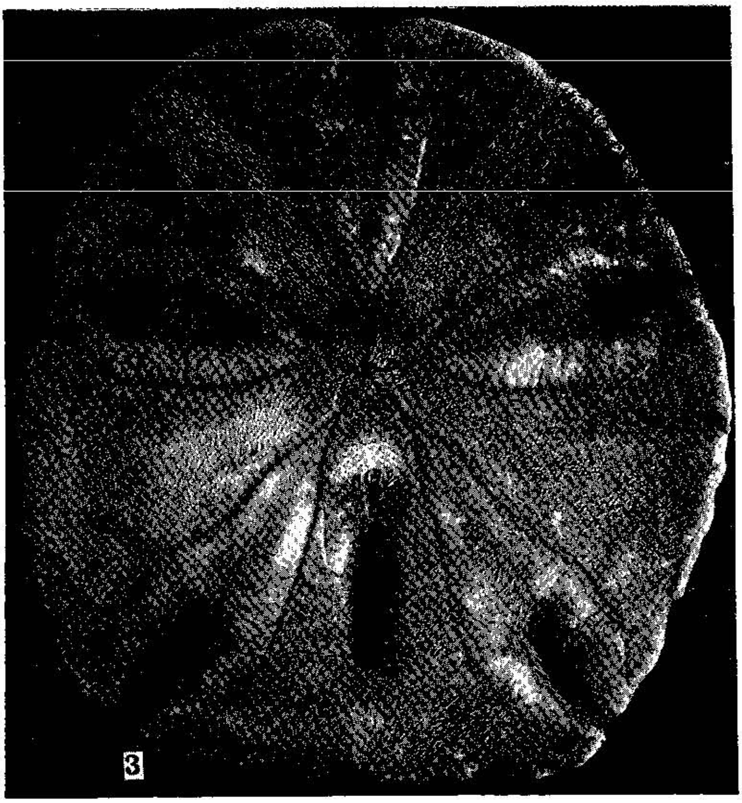
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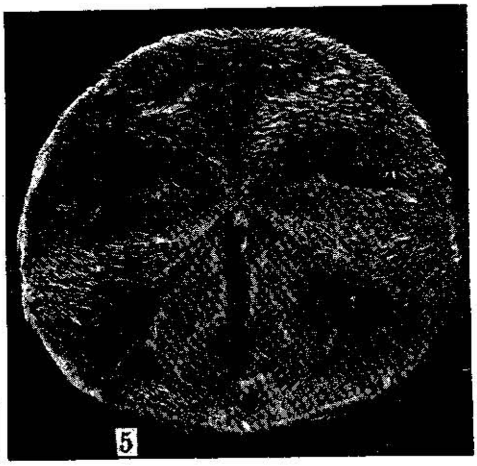
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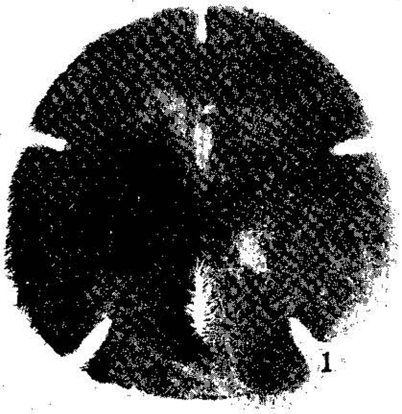
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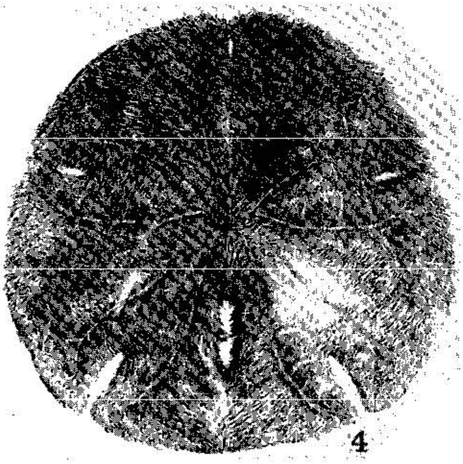
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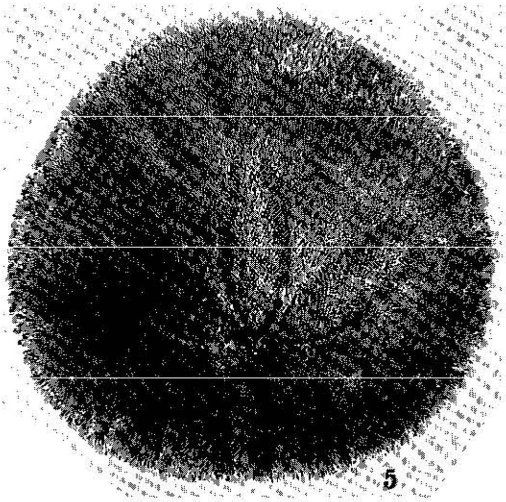
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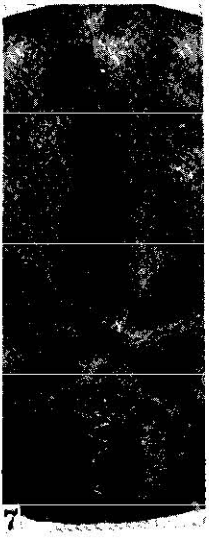
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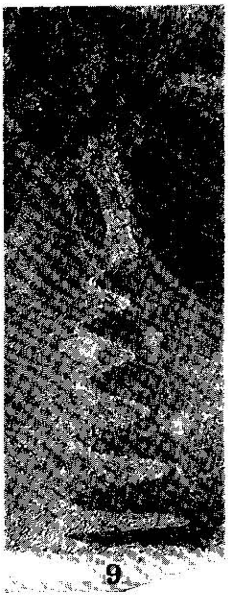
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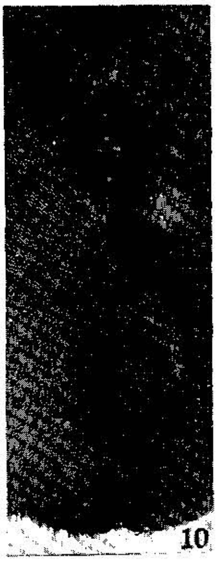
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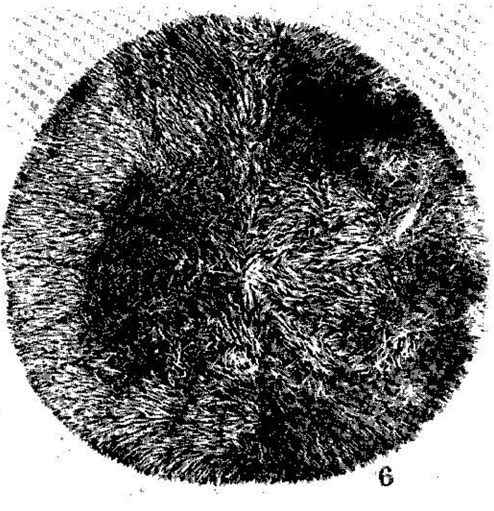
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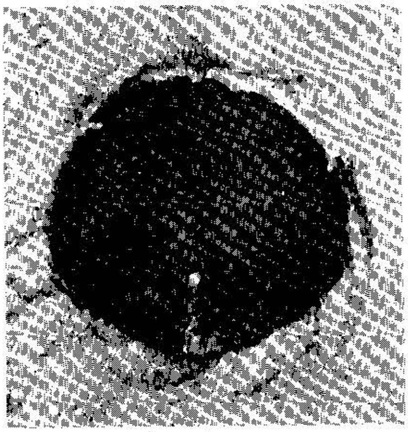

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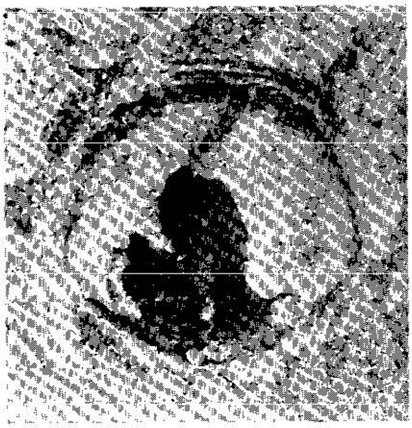

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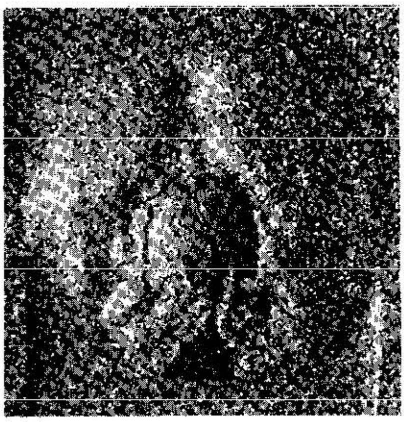

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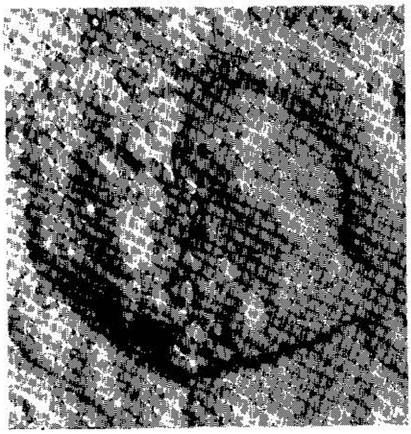

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