

THE SPINES AND DIFFUSE FASCIOLES OF THE  
CRETACEOUS ECHINOID *ECHINOCORYS*  
*SCUTATA* LESKE

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ABSTRACT. Four types of primary spine and one type of secondary spine are described, and probable functions suggested for them. Fragments possibly of pedicellariae are described. Previous descriptions of a 'diffuse fasciole' are extended, and their significance is discussed.

ALTHOUGH *Echinocorys scutata* Leske is a familiar fossil of the Chalk, descriptions of its spines are unusual. The first account of them, by Cotteau (1849), is the only one accompanied by figures. He showed two primary spines, which correspond to those here described as 'thorny spines'. He also figured, but did not describe, a number of secondary spines. Lambert (1903) quoted Cotteau's account of the spines, and also reported the occurrence of spatulate spines on the plastron.

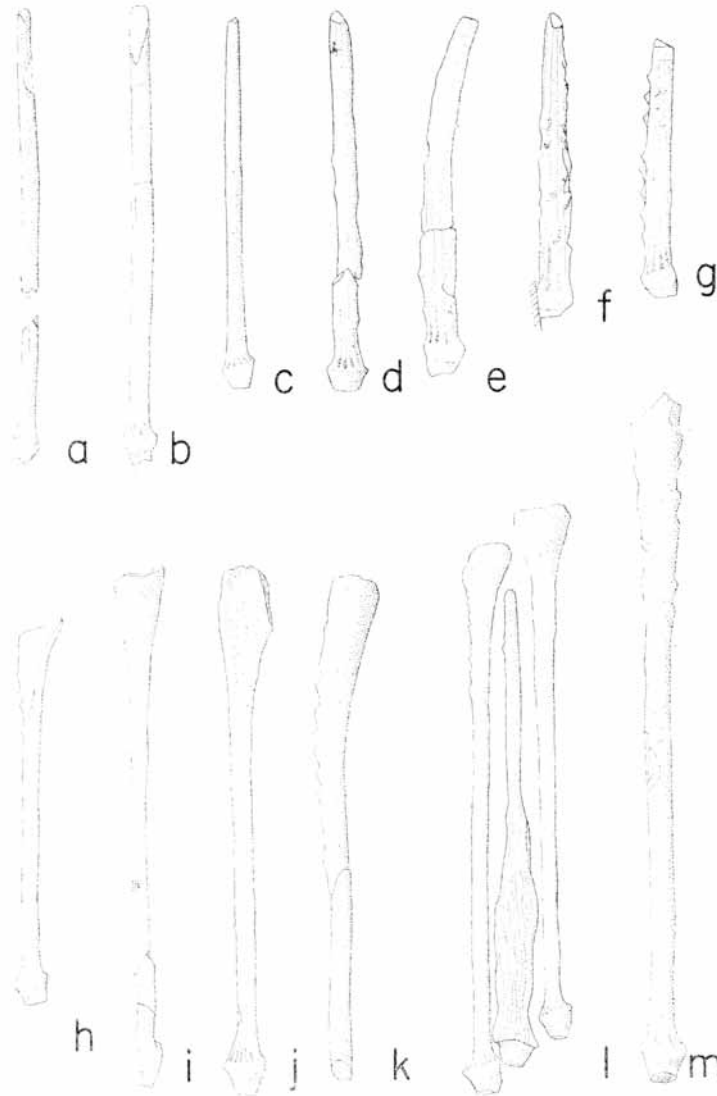
Four types of primary spine, named spatulate, simple, thorny, and swollen, were found among the material studied. The first three types are accounted for below in terms of their function on the living animal, but the fourth appears to indicate a pathological condition. There is only one type of secondary spine, which in places is arranged in 'diffuse fascioles'.

*Materials.* Two specimens were used in this work, one from the collection of the Geology Department of Reading University (E. 663: a complete test of *Echinocorys scutata*), the other from the Sedgwick Museum, Cambridge. Most of the matrix has been removed from E. 663, but primary and secondary spines are preserved in patches adhering to the oral surface and round the ambitus. Secondary spines are also preserved in smaller patches of chalk higher up on the aboral surface. E. 663 is described as collected by W. Wright from the *Actinocamax quadratus* Zone at Rottingdean. However, Brydone (1914), when he established the Zone of *Offaster pilula*, assigned the cliffs at Rottingdean to this zone. The specimen is not ascribed to any variety, but seems to be one of the 'non-descript forms of moderate size' recorded by Gaster (1929) from the subzone of *E. scutata* var. *depressula*. It is 49 mm. long, 42 mm. broad, and 33 mm. high.

The Cambridge specimen (B. 65040) is a fragment, 38 mm. long and 40 mm. wide, of the oral surface and ambitus of a large *E. scutata* with many spines preserved in the matrix adhering to it. The width of the complete test is estimated at 70 mm. It was collected by R. M. Brydone from the *Ostrea lunata* Zone at Trimingham, Norfolk.

*Simple spines.* These are found on both specimens (text-fig. 1a-c). None is complete, but the fragments remaining indicate that they are about 8 mm. long on B. 65040 and 3 to 4 mm. long on E. 663. The base is conical, narrowest at the acetabulum and widening to the milled ring, which is slightly asymmetrical. The shaft is straight and

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TEXT-FIG. 1. Primary spines. Camera lucida drawings. *a*. Simple spines, B. 65040.  $\times 11$ . *b*, *c*. Simple spines, E. 663.  $\times 22$ . *d*, *e*, *f*, *g*. Thorny spines, E. 663.  $\times 22$ . *h*, *i*. Spatulate spines, B. 65040.  $\times 11$ . *j*, *k*. Spatulate spines, E. 663.  $\times 22$ . *l*. Group of primary spines as preserved. The inner one is a swollen spine, the two outer ones are spatulate. B. 65040.  $\times 11$ . *m*. Spatulate spine, E. 663.  $\times 22$ .

slender, tapering gradually to a point. All simple spines are fluted where the shaft joins the base. On specimen B. 65040 this fluting continues as fine grooves along the length of the spine (text-fig. 1*a*), but on E. 663 the shaft is quite smooth (text-fig. 1*b, c*).

The distribution of simple spines is similar on both specimens. On B. 65040 a few occur on the flat basal surface, but they are concentrated on the small part of the ambitus which is preserved. On E. 663 also, they are concentrated round the ambitus—mainly on the aboral surface, but some on the adoral surface, especially anteriorly, between the ambitus and the peristome.

It will be shown that the spines on the under and upper surfaces of the test were specialized for functions which depended on conditions on those surfaces. But at the ambitus conditions would probably have been more varied, so an unspecialized type of spine was presumably better adapted to meet them.

*Thorny spines.* On specimen E. 663, on the adoral surface of the test, about twenty spines are preserved in a few small patches near the ambitus (text-fig. 1*d-g*). Though none is complete they seem to have been 2–3 mm. long. Instead of tapering as a uniform cone, the base narrows abruptly in a step; one of the most characteristic features of these spines. The shaft is straight or slightly curved, tapering distally. Each spine has seven or eight flutings on it, most marked just above the base, but continuing the length of the shaft. The ridges between the grooves carry the 'thorns'—small projections rising to an obtuse-angled point.

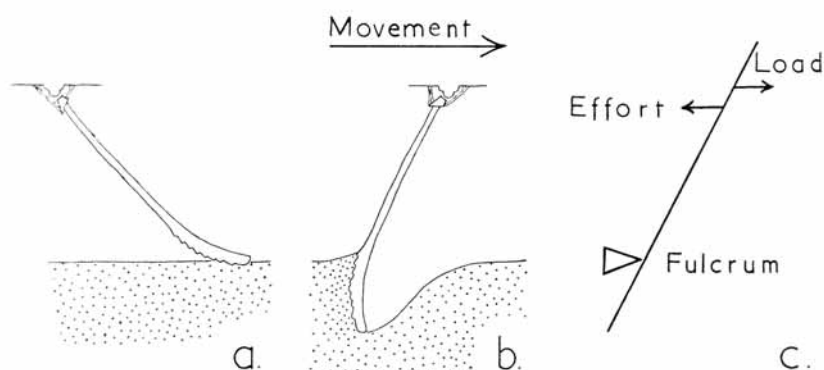
Thorny spines intergrade with the simple spines already described. As the spines become more thorny, their shafts become stouter; and it appears that the most thorny spines are shorter. There is also variation in distribution of the 'thorns'. On intermediate examples, most of the thorns are at the proximal end of the shaft (text-fig. 1*d, e*), but in the extreme examples most thorns are nearer the distal end (text-fig. 1*g*). There is a tendency for the more thorny spines to occur higher on the test than the smoother types, though none of the spines preserved is more than 1 cm. from the ambitus.

The form of these spines does not appear suited to any role in which they come into contact with the soft substratum, but it would serve well as a protection of the exposed test. That this is probably their function is confirmed by finding them only on the upper surface of the test. The distribution of the primary tubercles on this surface is also consistent with this function. Over the upper surface of the test, they average rather less than 2 mm. apart, but are closer along the ambulacra where the vulnerable tube feet were. With a spine rather over 2 mm. long, this was probably about the maximum separation allowing efficient protection on the surface. The graduation from simple spines on the ambitus to extremely thorny spines about 1 cm. above it, presumably indicates that spines near the ambitus may at times have had to move sediment. The concentration of thorns at the proximal end of intermediate spines can be seen as an adaptation to this, leaving a smooth tip for contact with the sediment. Higher on the test, where the spine had one function only, the concentration of thorns at the tip of the spine might have been more efficient for protection.

The normal reactions of living echinoids to local stimulation of the epidermis involve both sets of muscles operating a spine. First, the outer muscles move the spine so that it points towards the stimulus. If the irritation is prolonged, the inner, or 'tonus', muscles hold the spines rigid in this position (e.g. Hyman 1955, p. 552). If the thorny

spines of *Echinocorys* protect the animal in this way, it follows that both sets of muscles would have been well developed. It seems likely that the 'stepped' base was related to the insertions for these sets of muscles (text-fig. 3).

*Spatulate spines.* Present on both specimens (text-fig. 1*h-m*). There are more on E. 663, but they are all damaged and are often fragmentary. It seems that the length was about 4.5–6 mm. On B. 65040 there are five complete spatulate spines, 6–9 mm. long. These longer spines have the extra length in the shaft, giving a more slender spine with a relatively shorter blade (text-fig. 1*i, j*). As is usual in spatangoids, the base of the spine is bilaterally symmetrical, with the milled ring running obliquely across the distal end



TEXT-FIG. 2. The mode of action of the spatulate spines. *a*, The beginning of the working stroke. *b*, The end of the working stroke. *c*, The spine as a lever.

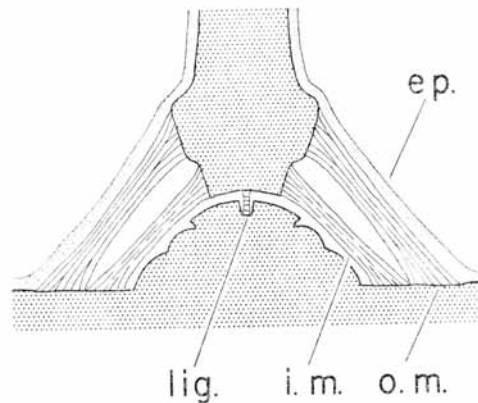
of the base, e.g. in the two outer spines in text-fig. 1*h* (cf. Mortensen 1951, pls. xlv and xlvii). The shaft is cylindrical, widening distally into a fan-shaped blade, concave on one face (text-fig. 1*h, j*). The side of the blade has a saw-tooth edge (text-fig. 1*m*). The whole spine is curved so that the convex face is on the inside of the curve (text-fig. 1*k*).

On both specimens, the spatulate spines are restricted to the oral surface, where they are most dense on the plastron. But they are not found only on its extremity as Lambert (1903) said. Nichols's (1959*a*) experiments showed that the spatulate spines on the plastron of *Echinocardium cordatum* (Pennant) and *Spatangus purpureus* (Müller) are primarily for locomotion and are not essential for burrowing. It is thus most probable that the spatulate spines of *Echinocorys scutata* were also used for locomotion.

The blade of a spatulate spine on the underside of the animal would have rested with its concave face on the sea-floor while the animal was at rest (text-fig. 2*a*). When the muscles on the posterior side of the spine contracted, the blade would have dug into the sediment on the sea-floor, pushing the animal forward (text-fig. 2*b*). Thus the spine acted as a lever of the third order (text-fig. 2*c*). On the return stroke, the muscles on the anterior side of the spine would have pulled it back to the starting position. The convex reverse face of the blade would have reduced the resistance offered by the water and by loose sediment which flowed into the hole dug by the blade on the working stroke.

The asymmetrical projections of the saw-tooth edge to the blades (text-fig. 1*k*, *m*) are also shaped so that they would have helped to grip on the working stroke, but would have offered less resistance on the return stroke. Though this is a satisfactory explanation of the action of any particular spine, the forward progress of the animal depended on the spines acting in combination. Von Uexkull's (1907) account of *Echinocardium cordatum* suggests that the spines on the underside of the echinoid beat in a metachronal rhythm. Nichols's (1959*a*) observations confirm this. It is a reasonable inference that *Echinocorys scutata* was propelled by a similar rhythmic movement of the spatulate spines.

The mechanical advantage of the spatulate spines acting as a lever may be calculated.



TEXT-FIG. 3. Reconstruction of the soft tissues at the base of a thorny spine to show the insertions of the two sets of muscles separated by the 'step'. Approx.  $\times 100$ .

To do this the following measurements were made with a travelling microscope, on a number of suitable spines:

(i) Length of shaft, i.e. distance of effort—the distance from the most distal part of the milled ring to the first serration on the blade.

(ii) Length of shaft and base, i.e. distance of load—the distance from the acetabulum to the first serration on the blade (text-fig. 2).

The tip of the blade is not the fulcrum, hence the somewhat arbitrary choice of the first serration of the blade as a suitable fixed point within the different blades to which measurements can be taken.

The mechanical advantage is the ratio of the length of shaft (*s*) to the length of shaft and base (*l*).

Spines from specimen No. E. 663:

<i>s</i> (mm.)	<i>l</i> (mm.)	Mechanical advantage ( <i>s/l</i> )
1.70	1.96	0.87
3.02	3.29	0.92
3.34	3.51	0.95
2.54	2.80	0.91

Mean of mechanical advantages = 0.91.

Spines from specimen No. B. 65040:

<i>s</i> (mm.)	<i>l</i> (mm.)	Mechanical advantage ( <i>s/l</i> )
5.42	5.79	0.94
6.11	6.55	0.93
3.84	4.21	0.91
3.73	4.14	0.90

Mean of mechanical advantages = 0.92.

The mechanical advantage of the spines on the two specimens is effectively the same. The increased length of the shaft relative to the blade in the larger and stratigraphically younger specimen is probably not an evolutionary change, but a change during the growth of the animal to allow the mechanical advantage to remain constant.

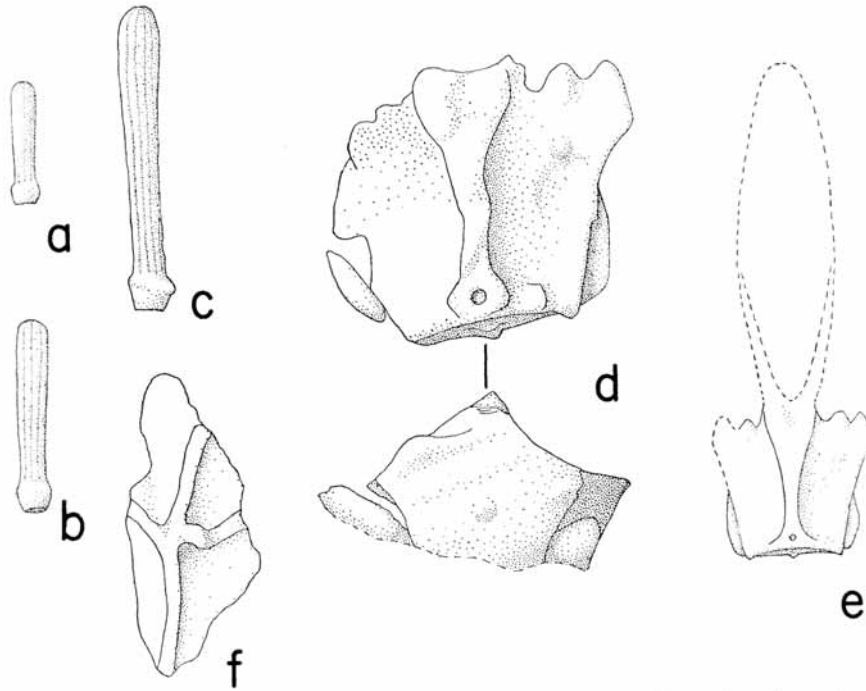
'Swollen' spines. Found only on B. 65040, on the oral surface and the ambitus (text-fig. 1f). The only well-preserved specimen is in the centre of the group in text-fig. 1f. It is 7.6 mm. long, but the tip is missing. The base is of the normal conical type, but set on the spine at a marked angle. Above this is a milled ring, but instead of the usual narrowing of the shaft, the diameter remains greater than that of the base for about half the length. This swollen part is marked by deep longitudinal grooves. The grooves and the ridges between them are not parallel, but anastomose at frequent, though irregular, intervals. Beyond the swollen section, the distal end of the spine has a smooth surface, which appears slightly flattened in cross-section.

There were also four fragments which had a similar combination of anastomosing longitudinal grooves and greater diameter than other primary spines. An attempt was made, by sectioning one of these fragments, to compare the structure of simple and swollen spines. Both types agreed with Hesse's (1901) 'Spatangus Typus', with an axial canal surrounded by radial septa. In transverse sections of swollen spines all the parts increase in size in the same proportion, but are more irregularly shaped than in the simple spines.

No satisfactory explanation in terms of function has been deduced for these spines. The only comparable structure that has been found in the literature is swellings in the spines of *Diadema antillarum*, figured by Mortensen (1940). He claimed to have found a parasitic organism, 'probably some sort of micro-fungus', to which he attributed the swellings. While the swollen condition in *E. scutata* cannot be definitely ascribed to a parasite, it does suggest a pathological condition. From the flattened tip, it may be inferred that the figured spine is an infected spatulate spine.

Secondary spines. Only one type is present (text-fig. 4a-c) and it is considerably smaller than the primary spines; 1.0 to 1.5 mm. long on B. 65040 and 0.5 to 0.8 mm. long on E. 663. Although short they are stout, with the length about six times the breadth, and a cylindrical shaft, rounded distally. The shaft has seven or eight longitudinal grooves, giving it the fluted appearance of the figures. The base is slightly different on spines from each specimen. On E. 663 it is as broad as it is high, with no milled ring. Instead the base is convexly curved, with its greatest width not far below the point where shaft and base join (text-fig. 4a,b). On the other specimen the base is slightly broader than its height, and the widest point is at the top, where there appears to be a rudimentary milled ring. About half-way up the base there may be traces of a 'step' similar to

that on the bases of the thorny spines (text-fig. 4c). On E. 663 there is no difference between spines preserved on the adoral and adapical surfaces. The small secondary tubercles which carried these spines have no scrobicule and are not perforate. This suggests that the secondary spines had no ligament for attachment, but were held in place by simple muscles, so that they had only a limited range of movement.



TEXT-FIG. 4. Camera lucida drawings. *a, b*, Secondary spines, E. 663.  $\times 50$ . *c*, Secondary spine, B. 65040.  $\times 25$ . *d*, Fragment of pedicellaria, E. 663.  $\times 75$ . *e*, Restoration of *d*.  $\times 36$ . *f*, Fragment of pedicellaria, E. 663.  $\times 75$ .

*Diffuse fasciole.* Though *Echinocorys* is usually considered to be without fascioles, Lambert (1898) reported the presence of a rudimentary perianal fasciole. Later (Lambert 1903), while denying the existence of true fascioles in *Echinocorys*, he described 'un fasciole diffus' surrounding the periproct in *E. vulgaris* var. *striata* and *E. meudonensis*. In the same work he described *E. ovata* as having a 'pseudo-fasciole diffus'. Hoffman (1914) described and figured the 'Fascioleanagen' (Lambert's 'diffuse fasciole') as 'ein hufeisenförmiger Bogen um den After'. In fact, the pattern of tubercles on the underside of *E. scutatus* is more complex than this. There are four distinct types of tuberculation, occupying the areas shown diagrammatically in text-fig. 5a. These types are (lettering as in text-fig. 5a):

(a) The 'diffuse fasciole' of Lambert, with very fine secondary tubercles so closely packed as to be almost touching.

(b) A type of pattern having secondary tubercles which are larger than type (a) but which are still very tightly packed together.

(c) An area of secondary tubercles which are slightly larger than in type (b) and much more widely spaced—about once or twice their own width apart.

(a), (b), and (c) all have primary tubercles spread over them at a uniform density, and without any definite pattern. The primary tubercles in area (a), however, are rather smaller than elsewhere.

(d) The pattern here has no primary tubercles, and the secondary tubercles are the largest and most widely spaced of any part of the test.

The tuberculation of the upper surface of the test is very similar to type (c). By analogy with the fascioles of more advanced echinoids, the pattern of type (a) will be called the 'anal diffuse fasciole' and the pattern of type (b) the 'marginal diffuse fasciole'.

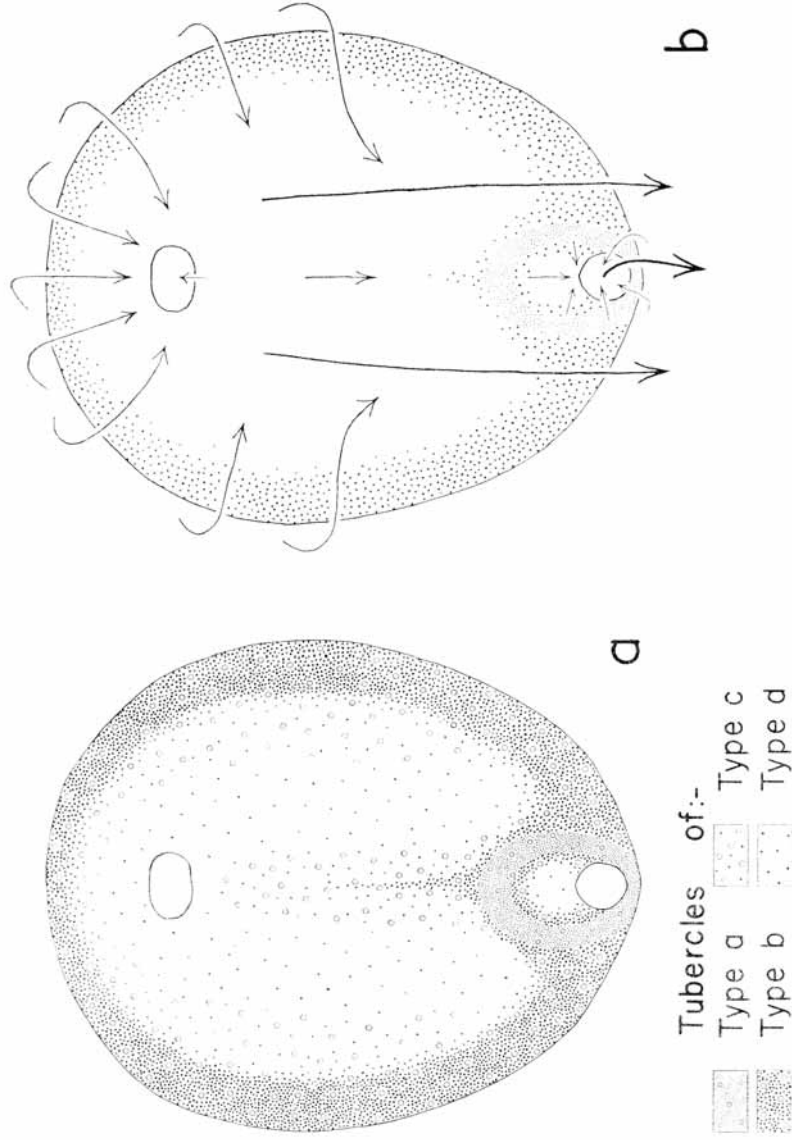
This pattern of tuberculation is present on suitably preserved specimens of *Echinocorys scutatus* from all horizons in the Chalk, but is best developed in specimens from the zones of *Micraster cor-anguinum* to *Actinocamax quadratus*. The findings of Lambert (1903) appear to confirm this. *E. vulgaris* var. *striata*, *E. meudonensis*, and *E. ovata* are all forms from the zone of *M. cor-anguinum* or above. Willcox (1953) says 'the most strongly tuberculate tests come from the *cor-anguinum* Zone'.

*Morphological relationship of diffuse to true fascioles.* Examination of the fascioles of an advanced spatangoid, such as *Echinocardium cordatum*, shows the following features:

- (i) The fine tubercles which carry the clavulae are set very close together in a hexagonal pattern which gives the greatest possible density. (The pattern is well shown in Nichols, 1959a, fig. 13.)
- (ii) Primary tubercles are absent in the area of the fasciole.
- (iii) The edges of the fasciole are sharply defined.
- (iv) In contrast to the fascioles, there are very few secondary tubercles elsewhere on the test.

However, *Echinocardium cordatum* is an advanced spatangoid, and examination of less highly developed species shows that not all fascioles have these four characters. On *Spatangus purpureus* other secondary spines besides clavulae are abundant. In *Stereopneustes relictus*, one of the living Meridosternata, the boundary of the subanal fasciole is not sharp; the secondary tubercles on the fasciole merely thin out as they grade into those on the rest of the test. *Micraster cor-anguinum* has primary tubercles on the midline of the fasciole, but they are fewer and considerably smaller than those on the rest of the test, so that they do not destroy the distinctness of the fasciole. Even the hexagonal 'close-packing' of the tubercles, one of the most constant features of all fascioles, is missing on much of the marginal fasciole of *Cardiaster granulosis*. The major difference in diffuse fascioles is that the primary tubercles are as abundant as elsewhere on the test. This distorts the close-packed pattern so that it is rarely hexagonal. Morphologically, the diffuse fascioles appear to represent the stage preceding the appearance of the most primitive true fasciole. The anal diffuse fasciole, with a finer tuberculation than any other part of the test, is presumably slightly more differentiated than the marginal diffuse fasciole.





TEXT-FIG. 5. *a*, Oral surface of *Echinocoryx scutata*, showing the pattern of tuberculation and the 'diffuse fascioles'. The representation of tubercles is diagrammatic only. *b*, Oral surface of *E. scutata* with a conjectural restoration of the water currents produced by the diffuse fascioles.

*The function of the diffuse fasciole.* This probably depended on the secondary spines carried on each tubercle. We can assume that at least part of each secondary spine was ciliated as in recent echinoids, so they probably produced currents in much the same way as the clavulae of the fascioles of more advanced spatangoids. If this were so, the secondary spines would not need a large range of movement. The clavulae of the recent *Echinocardium cordatum* have cilia in two bands on opposite sides (Nichols 1959b), but the secondary spines of *Echinocorys scutata* are circular in cross-section and give no evidence about the arrangement of cilia on them.

On the assumption that the diffuse fascioles have the same function as true fascioles in living echinoids, an attempt is made in text-fig. 5b to reconstruct the currents produced by the diffuse fasciole. It suggests that the diffuse fascioles were situated where the currents produced would be effective. In particular, it emphasizes the importance of the 'anal diffuse fasciole'. This runs round the slope of a raised part of interambulacrum 5, which was named by Lambert (1898) the 'anal plastron'. The periproct is at the far end, which slopes so that the periproct faces downwards and backwards. It seems likely that the inward flowing currents produced by the diffuse fasciole would have combined as a strong current away from the anus, as indicated in text-fig. 5b. It would have been particularly important to have carried off waste products in this way when the animal was stationary or moving slowly. This arrangement resembles that described by Nichols (1959a) for *Spatangus raschi* of which the mode of life resembles that postulated for *Echinocorys scutata*. Apparently the density of spines needed to produce a current strong enough for this sanitary function is more than can be obtained merely by packing normal-sized secondary tubercles as close as possible. Hence the very small tubercles in this area which first attracted attention as the 'diffuse fasciole'.

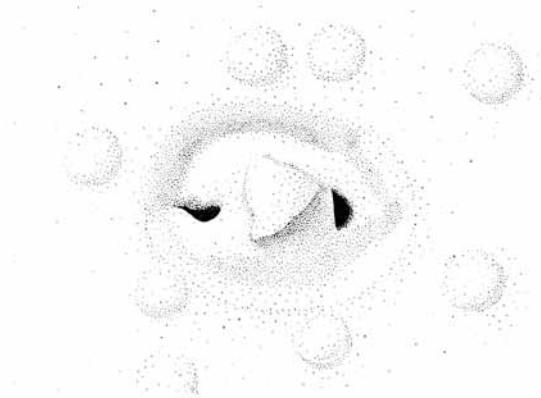
The occurrence and position of fascioles has been extensively used in the classification of spatangoids, although it has recently been shown that even in the Amphisternata this is not always justified (Nichols 1959c). From the phylogenies given by Mortensen (1951) and Durham and Melville (1957), it seems that fascioles were evolved independently several times in different spatangoid stocks. A search for diffuse fascioles or similar structures on primitive spatangoids where true fascioles are absent might throw some light on this process.

*Pedicellariae.* Some calcite fragments on E. 663 may represent parts of the valves of pedicellariae. The fragment shown in text-fig. 4d may be the basal part of the valve of a tridentate pedicellaria, of which the blade is missing. A restoration is shown in text-fig. 4e. The upper figure in text-fig. 4d is interpreted as being of the inner side of the valve, showing the prominent ridge of the muscle insertion. The serrated edges of the upper part suggest the 'irregularly dentate' edges of the tridentate pedicellariae of *Plexiechinus spectabilis* figured by Mortensen (1950). As this species is one of the few living Meridosternata, the likeness may support the reconstruction. The lower figure shows the base, with ridges and indentations which may be part of the articulations of the valves.

Another fragment (text-fig. 4f) may be part of another type of pedicellaria, seen from the inner surface, but it is so damaged as to be very difficult of interpretation. However, under strong oblique illumination it is translucent, like fragments of echinoid spine. This strongly suggests that it is a single crystal of calcite and hence if organic, an echinoid fragment.

*Ecology.* Kongiel (1949) discusses the ecology of *Echinocorys*. He concludes that it buried itself in the soft sediment of the sea-floor, but not to any great depth. Willcox (1953) considers that *E. scutata* at times showed a trend towards a partial burrowing mode of life, but he implies that most forms lived on the surface of the sediment. The present work confirms this. *E. scutata* did not burrow, but lived on the surface of the sea-bed, at most sunk into the sediment to just above the level of the ambitus. It propelled itself by means of the spatulate spines, and its upper surface was protected by the thorny spines.

Other evidence can be found to support this. The shape of the test with flat adoral surface and pyramidal adapical surface separated by a sharp ambitus is consistent with it.



TEXT-FIG. 6. Pore-pairs of a 'feeding tube-foot' adjacent to the peristome, showing ornament. In this example the central column of calcite is triangular, but this is variable. Camera lucida drawing.

As Kongiel (1949) pointed out, a less elevated form of test would be expected in a burrowing form.

Examination of the pore-pairs of *E. scutata* and the ornament surrounding them suggests a marked difference between the tube-feet of oral and adoral surfaces. But there are no pore-pairs which may be interpreted as supporting burrow-building tube-feet anywhere on the test.

On the underside of the test is a conspicuous group of pore-pairs round the peristome. Each is set on an oval depression, and out of this, between the pores, rises an irregular column of calcite (text-fig. 6). This ornament is similar to, though more pronounced than that around similarly placed pore-pairs in *Micraster*, which Nichols (1959a) considers carried the feeding tube-feet. But *Echinocorys* had more feeding tube-feet than *Micraster*: between 35 and 43, against an average of 22 in *Micraster*. The difference in the size of the ornament suggests that the feeding tube-feet of *Echinocorys* were also more muscular. This contrast with *Micraster* is to be expected from the ecology of *Echinocorys*. Both echinoids were microphagous, but *Echinocorys*, living on the sea-floor, must have had to pick up all its food with its tube-feet, while *Micraster*, living in a burrow, could have trapped food particles falling on to the surface of the test, and carried them to the mouth

by ciliary action. Nichols (1959a) describes an apparatus possessed by the urchin to remove from the tube-feet those particles which *Micraster* picked up. It consisted of a series of spines around and inside the mouth, by which particles adhering to the tube-feet were scraped off, and then caught by a projecting labrum. There is no trace of any comparable apparatus in *Echinocorys scutata*. The area round the peristome is relatively clear of spines. A projecting labrum is absent and the mouth is sub-central within the peristome (Hawkins 1912).

The remaining pore-pairs of the undersurface are a much smaller version of the feeding tube-feet. Each pore-pair is set in a pit as deep as those of the feeding tube-feet, but much narrower, with only a small bump of calcite between the pores. This type of pore-pair extends to the ambitus only, except in *E. scutata* var. *cineta*, where, as Willcox (1953) described, the first two pore-pairs above the ambitus are of this type. The ornament surrounding these pore-pairs suggests that they carried a feebly muscular tube-foot with a sensory function.

Willcox (1953) studied the pore-pairs of the aboral surface. He concluded that they supported respiratory tube-feet, and demonstrated changes in form which were correlated with changes in environment. One small point does not appear to have been remarked, but may be significant: in the petals of many irregular echinoids, the ribbon-like tube-feet and the corresponding pore-pairs are not perpendicular to the axis of the ambulacrum, but converge adapically. The ciliary current in the living animal is described as flowing down the axis of the ambulacrum and *out* between the tube-feet. A typical example is *Spatangus purpureus* (Nichols 1959a). The pore-pairs of the respiratory tube-feet of *E. scutata* converge adorally (see Willcox 1953, fig. 6). This is not always marked, but I have seen no specimen with the opposite convergence. It would have been an inefficient arrangement for the current system described. Possibly the ciliary currents in *Echinocorys* flowed *in* between the tube-feet and continued down the axis of the ambulacrum. Kongiel (1949) suggests that because of the structure of the apical disk, with relatively small genital plates and large ocular plates, the Holasteridae were unable to develop petaloid ambulacra. The development of the ambulacral pattern seen in *Echinocorys* may provide increased aeration of the tube-feet in another way.

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