CHANGES IN THE CHALK HEART-URCHIN *MICRASTER* INTERPRETED IN RELATION TO LIVING FORMS

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[Plate 9]

CONTENTS

The fossil genus *Micraster* from the Chalk gives an excellent example of continuous evolution of individual characters. The changes, however, appear to be independent of changes in those environmental conditions which have left their mark in the formation of the sediment (changes in depth at which it was deposited, particle size, temperature, etc (Nichols 1956)). Consequently, these changes in the urchins probably reflect either a change in niche or an improvement in the adaptation of the animal in an effectively unchanged niche. To discover the significance of the changes, the following seven living species of British irregular echinoids have been studied in detail, both morphologically and functionally.

Order Spatangoida: *Spatangus purpureus*, *S. raschi*, *Echinocardium cordatum*, *E. pennatifidum*, *E. flavescens*, *Brissopsis lyrifera*.

Order Clypeastroida: *Echinocyamus pusillus*.

The ciliary currents on the tests of these urchins are in general similar, except at the fascioles. Features not previously reported are, first, the existence in all the urchins of an apical eddy of currents to ensure that the genital products are not wafted into the mouth, and secondly, forwardly directed currents into the mouth flowing over the lip.

The normal burrowing of three of the urchins, *S. purpureus*, *S. raschi* and *E. cordatum*, was observed. *S. purpureus* can burrow with its dorsal surface some 5 cm below the surface of the substratum, with no visible connexion with the sea water; water currents for respiration are apparently obtained through the interstices of the gravel particles in which it lives. The prehensile tube-feet of its subanal region build a double sanitary tube, each element originating at one lobe of the bilobed subanal fasciole. *E. cordatum*, observed both in aquaria and in the field, burrows to a maximum depth of about 18 cm, and maintains contact with the sea water via a respiratory funnel built by the tube-feet of the dorsal part of the anterior ambulacrum. A single sanitary tube is built, originating at the shield-shaped subanal fasciole. From the configuration of their subanal regions it is inferred that *E. pennatifidum* and *E. flavescens* also build single sanitary tubes, whereas *B. lyrifera* builds a double one. The main factor governing the number of tubes for sanitation is suggested to be the coherence of the substratum, those living in shell gravel and mud requiring only the same number of tube-feet to build two tubes as those living in sand require to build one; in consequence the shell-gravel and mud forms can attain a larger size. Some experimental evidence is presented for this hypothesis. *S. raschi* ploughs through the substratum with about half of its corona exposed above the surface; it attains a larger size than any other urchin studied, yet apparently builds only one subanal tube. The reason for this seems to be that since the respiratory tube-feet are not confined in a burrow, there is no need for a large soak-away for the respiratory water, and the sanitary device can be correspondingly smaller in cross-section.

The feeding of all six spatangids was observed; in general they grasp a particle or cluster of particles of the substratum with the oral prehensile tube-feet, convey the material with its covering of organic matter to the mouth, and scrape it off against the spines surrounding the peristome so that it passes into the gut. Selection of food particles by weight occurs in those urchins normally inhabiting shell gravel (*S. purpureus*, *E. pennatifidum*, *E. flavescens*).

The functional significance of the following morphological features of all the urchins is discussed: (i) number and arrangement of the fascioles providing augmentation of the ciliary currents on the test where they are specially needed; (ii) shape and arrangement of spines, for use in scraping, locomotion and burrow-building; (iii) division of labour among the tube-feet for feeding, burrow-building, respiration and sensation; (iv) depth of the anterior groove providing a channel for the passage of food currents from the dorsal surface to the mouth; (v) arrangement of the respiratory organs in the most efficient way for the type of burrow.

The morphology of the various tube-feet of *E. cordatum*, and the pores from which they arise, is described. The disks of the feeding tube-feet have a velvet-like pile of papillae for collecting the sediment, whereas those of the burrow-building tube-feet tend to allow space in the centre so that the fringe of papillae can fold in during retraction. The feeding tube-feet, extending at all angles to the test, have wide bases to their stems, whereas those whose extensions are mainly perpendicular to the test are much narrower.

The main features of *Micraster* and the closely related subgenus *Isomicraster* are described, and the work of Rowe and Kermack on the evolution of the group is reviewed. The probable effect of other animals living in or feeding on the sea bottom at the time of these fossils is described.

The number of pore-pairs in the petaloid parts of the paired ambulacra (those which gave rise to the respiratory tube-feet) have been examined in specimens from successive stages of the *Micraster* and *Isomicraster* series. There is a progressive increase in number in the main *Micraster* line with time, while the *Isomicraster* series have many more than the highest number of these. The increase in the main line is interpreted as enabling successive populations to burrow more and more deeply and is confirmed by changes in other features, particularly the increase in surface area by ornamentation to increase the concentration of cilia. The higher number in the isomicrasters is interpreted as enabling a reduction in size of the tube-feet as a countermeasure to predation, thus paralleling such living forms as *S. raschi*, and this is also supported by other features, particularly the reduction in ciliary currents in the subanal region.

In the main *Micraster* phylum changes in the peristomial region, in the position of the mouth, degree of development of the labrum and the depth of the anterior groove suggest by comparison with the mode of life of living urchins a gradually increasing reliance on a ciliary mode of feeding at the expense of that of using tube-feet.

When *Micraster* appears in the *cuvieri* zone as *M. leskei* it is a rare urchin. Its features suggest that it burrowed only shallowly. In the next two zones the shallow-burrowing features are retained by extremes on one side (*corbovis*), while features suggesting deeper burrowing gradually become more common and more pronounced on the other (*cortestudinarium*). At the top of the *planus* zone the shallow-burrowing forms die out, but the deeper burrowers persist up to the *testudinarius* zone, the features that suggest deeper burrowing becoming even more marked (*coranguinum*). At the same time, following the disappearance of the shallow burrowers, a partial burrower, *senonensis*, appears, probably by immigration. Considerable interbreeding occurs between this, the so-called *Isomicraster* line, and the main line and at the most it should only be considered subspecifically distinct from the micrasters. Similarly, in the *mucronata* zone of Norfolk intermediates occur between *glyphus* and its contemporary member of the isomicrasters, *stolleyi*, though from the small sample available and because of the lack of evidence from intermediate strata it is not possible to say whether the situation parallels the micrasters and isomicrasters of the south of England (i.e. that *stolleyi* is an immigrant), or whether both these forms have re-invaded the English area after becoming subspecifically distinct outside it.

I. GENERAL INTRODUCTION

Probably the best example of continuous and directional evolution of individual characters occurs in the series of fossils of the genus *Micraster*, an irregular echinoid from the Chalk. To be able to assess the functional significance of serial changes of this sort one requires, first, a thorough knowledge of the morphology and behaviour of the form, or where this is impossible (as in this case), of closely related living forms in relation to their modes of life (§ II). In this study a very important aspect of the mode of life is the nature of the substratum in which the animals burrow, and many features of the urchins are shown to be correlated with its particle size. This is especially important, since quite a comprehensive picture of the conditions of sedimentation in the Chalk Sea can be obtained by a study of the Chalk itself. It has already been shown (Nichols 1956) that those changes which are detectable in the Chalk occur irrespective of changes in the micrasters, so that the changes in the fossils must either represent gradual improvement in organization of the animals' structure or a change in niche with an effectively unchanged habitat.

For building and maintaining a burrow the most important appendages of the living forms are the tube-feet. Their morphology has been only cursorily described previously, and is therefore dealt with here (§ III). The parts of the test which bear these structures show considerable variation related to the function performed by the appendages they bear, and these are well preserved in the fossils and can be used for comparative purposes.

Next, the exact sequence of evolutionary change within the group and the interrelations of other animals in its vicinity must be established (§ IV). The first detailed study of *Micraster* considered from evolutionary aspects is that of Rowe (1899); recently Kermack (1954) has augmented and modified Rowe's work by a statistical approach to the group. One changing feature of the test not dealt with by either Rowe or Kermack is the nature of the petaloid paired ambulacra, which is treated statistically in this paper (§ V).

With the information obtained from these various sources a possible functional significance can be ascribed to the serial changes in *Micraster* (§ VI); the changes in nearly every feature of the test strongly suggest that this form changed its niche appreciably during the period studied, the main result being that high-zonal forms burrowed much deeper in the substratum than low-zonal ones. As those with low-zonal (shallow burrowing) characters die out another form appears, the features of which suggest that it ploughed through rather than burrowed in the substratum. This is the form which has been placed in a separate 'subgenus', *Isomicraster*.

II. THE MORPHOLOGY AND MODE OF LIFE OF SOME RECENT BRITISH IRREGULAR ECHINOIDS

1. Introduction

Seven species of irregular echinoids, which represent all the forms included in the fauna lists of the Marine Biological Stations at Plymouth (*Plymouth Marine Fauna* 1957), Port Erin (Jones 1950) and Millport (Chumley 1918), plus a form from deeper water, *Spatangus raschi* were investigated. Six of these (all of the order Spatangoida) are classified within the same family (Spatangidae) as *Micraster*, while the seventh (of the order Clypeastroida) shows important comparative features, and has been included on this account. The evidence obtained shows that their special modes of burrowing, feeding, sanitation and locomotion are closely correlated with the particle size of the substratum in which they live, and this adaptation is expressed in many features of their tests, in particular the position and degree of development of the fascioles (special bands of heavily ciliated spines), and the division of labour in the tube-feet, which, more than those in regular urchins, show a marked specialization in different parts of the ambulacra.

2. MATERIAL AND METHODS

The irregular urchins studied were:

Order Spatangoida: *Spatangus purpureus* O. F. Müller, 1776; *S. raschi* Lovén, 1869; *Echinocardium cordatum* (Pennant), 1777; *E. pennatifidum* Norman, 1867; *E. flavescens* (O. F. Müller), 1776; *Brissopsis lyrifera* (Forbes), 1841.

Order Clypeastroida: *Echinocyamus pusillus* (O. F. Müller), 1776.

Some of the rare forms could not be obtained in good enough condition for all their behaviour to be observed. The observation of moribund sea-urchins, or those denuded of some of their important spines, is worse than useless when they are burrowing; indeed, it is abundantly clear that the activity of moribund material has been described as normal in past literature, and it has therefore been considered necessary to repeat many previous observations in this study. *Spatangus purpureus* and *Echinocardium cordatum*, which are very unlike, were obtained in good condition and could be kept in aquaria. The numbers of each species studied are given in the appropriate sections below.

The observations on these forms were made in three parts:

(1) Plotting the external ciliary currents.
(2) An examination of burrowing activity.
(3) An examination of feeding behaviour.

The animals used for plotting ciliary currents were sent to Oxford from Plymouth and Millport. To avoid over heating and abrasion of the specimens, they were despatched from the Marine Stations, two only to a breffit, in the late afternoon, and were received in Oxford first thing the following morning, when they were immediately placed in a marine aquarium with circulating sea water maintained at 6 °C, and left for a few days. At first, a small quantity of the diatom *Phaeodactylum* was pipetted once a day into the aquarium, but later it was found that natural sea water, changed periodically, contains enough organic matter to feed the urchins for at least 9 months without any addition from cultures of this sort. In fact, on one occasion the shell-gravel substratum of one form (*S. purpureus*) was sterilized by boiling for $1\frac{1}{2}$ h before being put into the tank to obviate losses by disease. The urchins in it lived for 8 months without the addition of food, and in the end death appeared to be due to an epidemic through the whole tank during very hot weather in the summer of 1955.

For observations on the ciliary activity the urchins were placed in a shallow dish of sea water and observed under a low-power binocular microscope, the temperature of the water being kept as low as possible. This meant that a normal bench lamp could not be used for illumination, so a $3\frac{1}{2}$ V pencil-torch bulb, of the type with a built-in lens, was run off a mains transformer. This could be placed at such a distance above the microscope stage that a disk of light thrown on to the urchin illuminated only that part of the test covered by the field of view. In this work, when currents are being followed and the animal is moved about on the stage, it is necessary to be able to see at a glance exactly where the binocular is focused on the test, and this method of illumination, in addition to keeping down the temperature, has been found excellent.

Several kinds of particulate material for following the currents were tried, including small glass balls, Perspex shot, purified *Sepia* melanin and carmine particles. The latter were found by far the most satisfactory material for this work. The particles (or aggregations of them) could be made as fine or as coarse as convenient by grinding with sea water in a mortar, and the colour makes them easily visible at a glance under reflected light.

Where currents are less vigorous, it sometimes happens that a stream of carmine-plus-mucus veers round a tubercle or other projection from the test, and continues for a short distance at right angles to, or even against, the main current. In some cases in the literature (e.g. Gislén 1924), these local deviations have been included in the plots with confusing results. In figures 7, 8, 9 and 10, therefore, the main trends of the currents only have been plotted.

The examination of burrowing activity was carried out at the Marine Biological Stations at Plymouth, Millport and Port Erin. At each Station a circulating sea-water aquarium was prepared with a plane-glass bottom, mounted about 1 ft above the bench. Under this tank two prisms were arranged on a wooden block, so that a view could be obtained of the tank bottom. An advantage of this method was that a lens could be placed between the tank bottom and the first prism, at a fixed focus, and moved with the prisms as a unit to watch any part of the tank bottom. For photography, the optical system and its supporting wooden block was removed, and a single-lens reflex camera was placed on the bench looking up at the tank.

It is essential that the animals are observed as soon after removal from their natural surroundings as possible, and, of course, that most of their spines are still intact. It is very difficult to control the dredging operation for the deeper forms, and so it is a matter of luck whether an offshore specimen suitable for observation is obtained. For example, in the case of the shore-living *E. cordatum*, once a population-cluster has been located, careful digging with the fingers yielded specimens in good condition at once, and this made the sand urchin particularly suitable for study; but 10 or 12 specimens of *S. purpureus* were dredged before one was obtained which still had most of its spines; this specimen had been cushioned as the dredge was hauled up by an accidental covering of weed.

Specimens obtained at sea were immediately placed in circulating sea water on board; those dug up on the beach were carried back to the laboratory in breffits, not more than three to each. As the specimens were collected, a large sample of the substratum was also taken. At the laboratory, a convenient thickness of the natural substratum was placed in the bottom of the tank. For studying burrowing from below a fairly shallow layer was used so that the urchin would come into view through the tank bottom, but for studying depth of burrowing and the construction of the side-walls a deeper layer was used. One or two specimens were then placed on top of the substratum and the initial burrowing activity was observed. The urchins were then left to burrow to the bottom of the tank.

The examination of feeding behaviour was started at Oxford, on some of the specimens used for plotting ciliary currents, and confirmed later on fresh material at the Marine Biological Stations.

3. Habitats and main features of the urchins

The main test features and the arrangement of the tube-feet are illustrated in figures 1, 2, 3 and 10, and the main spine arrangements in figures 4, 5, 6 and 10. *S. purpureus* and *E. cordatum* are illustrated together because the principal comparison is between them.

(i) *Spatangus purpureus*

(figure 1*a*, *b* and *c*; figure 4*a*, *b* and *c*)

The specimens examined were taken from the shell gravel of the Eddystone *Amphioxus* grounds, south of Plymouth, and from the shell gravel to the south-west of the Isle of Man.

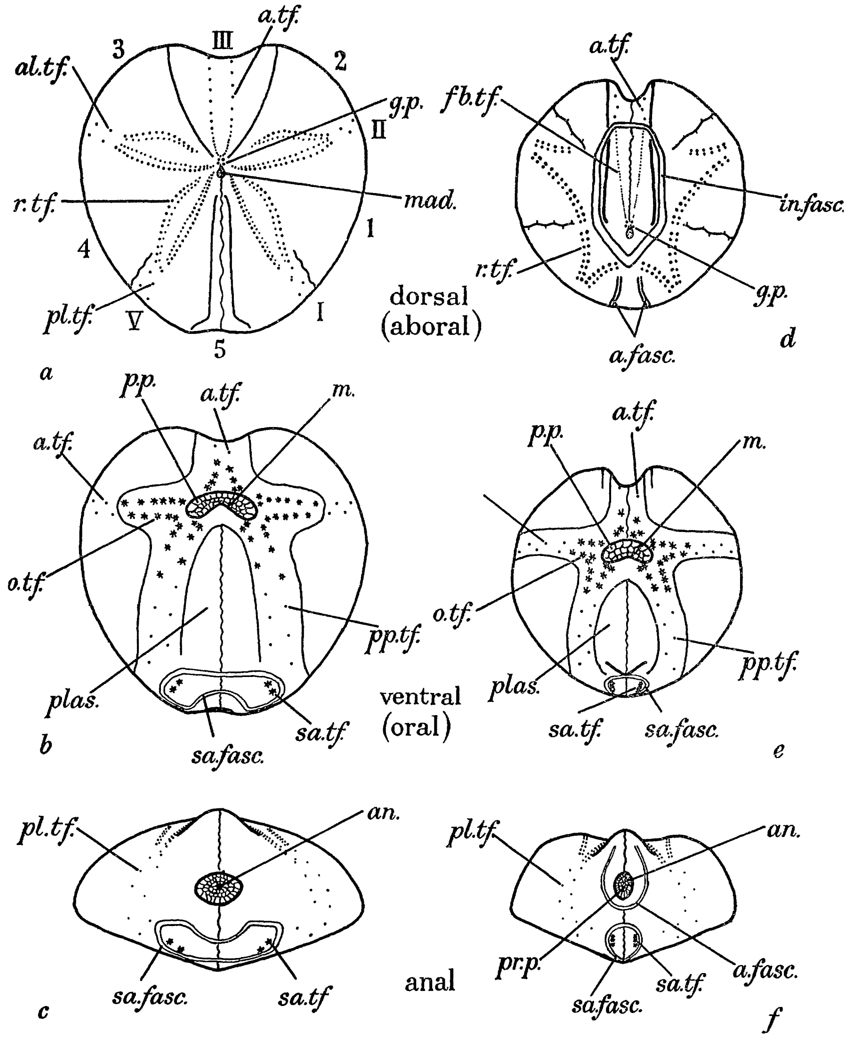


Figure 1. Diagrams of the main features of the tests of *Spatangus purpureus* (*a*, *b* and *c*) and *E. cordatum* (*d*, *e* and *f*), drawn without the spines and with the tube-feet retracted or removed. For list of abbreviations used in the figures see p. 428.

This urchin has respiratory tube-feet in petaloid areas in the dorsal regions of Amb. I, II, IV and V (of Lovén's scheme, 1874, figure 222). Large spines arise from the interambulacral areas of the dorsal surface and form a crest on top of the animal (figure 4*a*, *c*). The anterior ambulacrum (Amb. III) has much-reduced tube-feet running down the anterior groove and protected by an outer arch of medium-sized spines and two inner arches of small spines. Round the peristome all the tube-feet are large, and each bears a fringe of finger-like processes round its terminal disk; these have been termed penicillate tube-feet. Below the anus on the posterior side is the subanal fasciole, a special band of ciliated spines (clavulae). This encloses a bilobed space, within each lobe of which are two penicillate tube-feet externally similar to those round the peristome, and representing modified tube-feet of Amb. I and V. Also within the subanal fasciole (figure 4*b* and *c*) are two tufts of spines projecting backwards. Between the subanal fasciole and the mouth on the oral surface is the plastron, the main if not the only locomotory organ of the animals, consisting of an area of the test carrying a large group of slightly flattened spines, parted in the middle and slightly splayed out sideways. Around the peristome all available space (including the lip on the posterior side of it) is packed with small spines which arch across it.

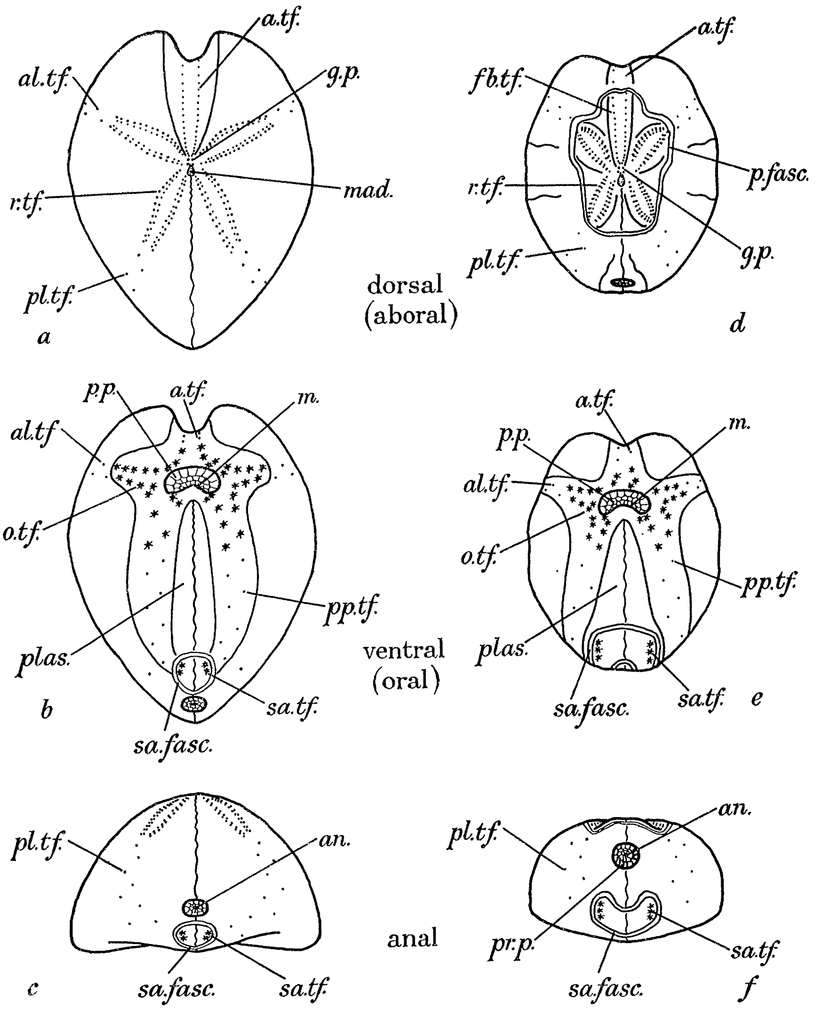


FIGURE 2. Diagrams of the main features of the tests of *Spatangus raschi* (*a*, *b* and *c*) and *B. lyrifera* (*d*, *e* and *f*) drawn without spines and with the tube-feet retracted or removed.

(ii) *Spatangus raschi*

(figure 2*a*, *b* and *c*; figure 5*a*, *b* and *c*)

This is from deeper water, occurring in sandy mud at about 100 to 150 fathoms, but occasionally coming closer inshore. Compared with *S. purpureus*, this species is more tapered posteriorly, and the anus is clearly visible from underneath (figure 2*b*), since it is borne on an undercut posterior surface (figure 5*c*). The anterior groove is more pronounced and more angular and from the front the test is more conical towards the apex.

The spine arrangement (figure 5*a*, *b* and *c*) differs markedly from *S. purpureus*, the largest spines being arranged in horizontal lines on the oral side of each ambulacral plate, and on the aboral side of each interambulacral plate, except in the anterior ambulacrum where they are more or less randomly distributed. The spines of the plastron are markedly flattened distally. The subanal fasciole is almost circular, and within it is a single tuft of spines, borne on a fairly pronounced hump in the centre.

(iii) *Echinocardium cordatum*

(figure 1*d*, *e* and *f*; figure 4*d*, *e* and *f*)

This, the common sand urchin of British waters, has respiratory areas of a very different shape and configuration from the two species of *Spatangus*, as can be seen from figure 1*d*, and the number of tube-feet in the dorsal section of the anterior ambulacrum is large, because of plate-crushing (Hawkins 1913). This region of the anterior ambulacrum is enclosed in an inner (sometimes called 'internal') fasciole, within which the spines form a dorsal tuft (figure 4*d* and *f* and figure 26*a*). The subanal fasciole in this form is shield-shaped, and bears a single tuft of spines. There is a third fasciole, the anal fasciole, surrounding the anus and periproct in a horseshoe-shaped band.

The tube-feet around the peristome, three pairs of tube-feet within the subanal fasciole and all the tube-feet within the inner fasciole, are penicillate, and capable of considerable extension.

(iv) *Echinocardium pennatifidum*

(figure 3*d*, *e* and *f*; figure 6*d*, *e* and *f*)

Compared with those of *E. cordatum* the respiratory tube-feet of its ambulacra are in more obvious double columns, but the anterior row of Amb. II and IV have only four or five functional respiratory tube-feet, towards the ambitus. The anterior groove is absent, and, although there is a very narrow inner fasciole, only a few of the tube-feet of the anterior ambulacrum within it are penicillate. There are no large spines above the ambitus.

(v) *Echinocardium flavescens*

(figure 3*a*, *b* and *c*; figure 6*a*, *b* and *c*).

In many respects this urchin is intermediate between *E. cordatum* and *E. pennatifidum*; the anterior groove is present but shallow, the inner fasciole fairly well marked and enclosing a few penicillate tube-feet (figure 3*a*), and there are a few large spines above the ambitus (figure 6*a* and *c*). The anal fasciole is a branch of the subanal, passing up on each side of the periproct and forming a nearly complete circle round it. Mortensen (1951) describes the anal fasciole as a branch of the subanal for the whole genus of *Echinocardium*, but only *E. flavescens* has this arrangement.

(vi) *Brissopsis lyrifera*

(figure 2*d*, *e* and *f*; figure 5*d*, *e* and *f*)

The respiratory tube-feet in this mud-burrowing form are arranged in four sunken petaloid areas on the dorsal surface (figure 2*d*), and the dorsal tube-feet of the anterior ambulacrum (Amb. III) are penicillate and very extensile. The whole region containing respiratory and extensile tube-feet on the dorsal surface is enclosed by a peripetalous fasciole, which has re-entrant angles in the interambulacral areas. The subanal fasciole is bi-lobed (figure 2*f*), but there is no anal fasciole. Penicillate tube-feet also occur round the peristome and within the subanal fasciole. There are two tufts of medium-sized spines within the subanal fasciole, one to each lobe. The spines of the plastron are flattened distally.

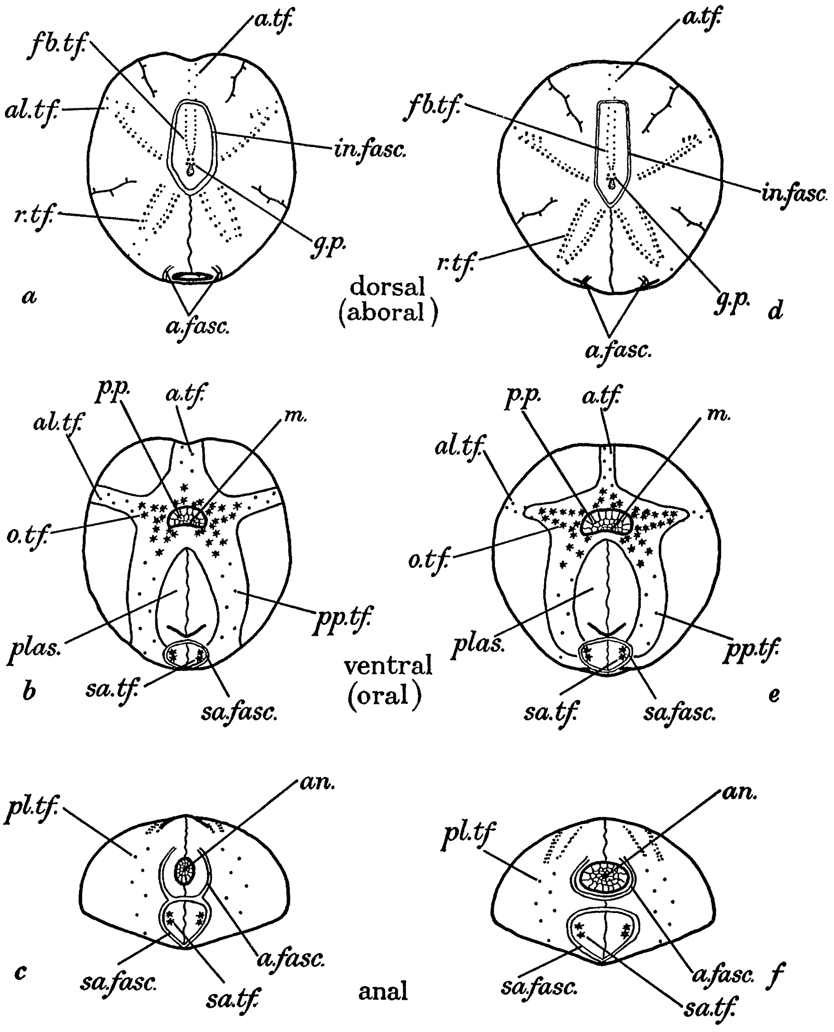


FIGURE 3. Diagrams of the main features of the tests of *E. flavescens* (*a*, *b* and *c*) and *E. pennatifidum* (*d*, *e* and *f*) drawn without spines and with the tube-feet retracted or removed.

(vii) *Echinocyamus pusillus*

(figure 10)

This tiny clypeastroid sea-urchin (maximum size about 1 cm long, normal size about $\frac{1}{2}$ cm) lives usually in shell gravel at about 20 to 30 fathoms, that is to say, in the same substratum as *S. purpureus*. In fact some authors (e.g. Gauthier 1874) report finding the dead tests of *Echinocyamus* among the gut contents of *S. purpureus*, and I have also found several in *S. purpureus*, *E. flavescens* and *E. pennatifidum*.

TABLE 1. SUMMARY OF HABITATS AND MAIN FEATURES OF THE TESTS OF THE URCHINS STUDIED IN § II

	specimens examined taken from			
	location	substratum	depth (fm)	fascioles
Spatangus purpureus	Eddystone shell gravel	shell gravel	25	subanal (bi-lobed)
S. raschi	Bay of Biscay	sandy mud	120	subanal (not lobed)
Echinocardium cordatum	1. Fairlie Sands, Ayrshire 2. Derby Haven, Isle of Man	sand	inshore	1. subanal (not lobed) 2. anal 3. inner
E. pennatifidum	Rame-Eddystone Grounds	shell gravel	25	1. subanal (not lobed) 2. anal 3. inner
E. flavescens	Off Calf-of-Man	shell gravel	25	1. subanal (not lobed) 2. anal 3. inner
Brissopsis lyrifera	Arran Basin, Firth of Clyde	mud	80	1. subanal (bi-lobed) 2. peripetalous
Echinocyamus pusillus	1. Eddystone shell gravel 2. Off Calf-of-Man	shell gravel	25	none

	division of labour in the tube-feet—approximate number per animal					
	respiratory	feeding	burrow-building		sensory only	
Spatangus purpureus	200	50	subanal	4	1. anterior ambulacral 2. lateral 3. peri-plastronal	32 50 12
S. raschi	200	40	subanal	4	1. anterior ambulacral 2. lateral 3. peri-plastronal	54 73 14
Echinocardium cordatum	70	40	1. subanal 2. anterior ambulacral	6 70	1. anterior ambulacral 2. lateral 3. peri-plastronal	8 40 16
E. pennatifidum	95	45	1. subanal 2. anterior ambulacral	4 6	1. anterior ambulacral 2. lateral 3. peri-plastronal	24 22 16
E. flavescens	55	32	1. subanal 2. anterior ambulacral	4 5	1. anterior ambulacral 2. lateral 3. peri-plastronal	14 45 12
Brissopsis lyrifera	120	35	1. subanal 2. anterior ambulacral	6 30	1. anterior ambulacral 2. lateral 3. periplastronal	7 45 22
Echinocyamus pusillus	45	none	none		buccal	10

The respiratory tube-feet are arranged in five double rows, radiating out from the apical disk. The other tube-feet, the accessory tube-feet, differ from those of spatangoid sea-urchins, since they arise in the sutures between the ambulacral plates, in groups of between five and twenty. All these other tube-feet are morphologically alike, except for a pair in the mouth region of each ambulacrum which are larger than the rest. There are no fascioles and no penicillate tube-feet. The spines, except for two round the mouth in each interambulacrum, which are slightly larger than the rest and project across the mouth, stick out more or less radially from the surface of the test (figure 10*h*).

All the more important differences of the urchins described above are summarized in table 1.

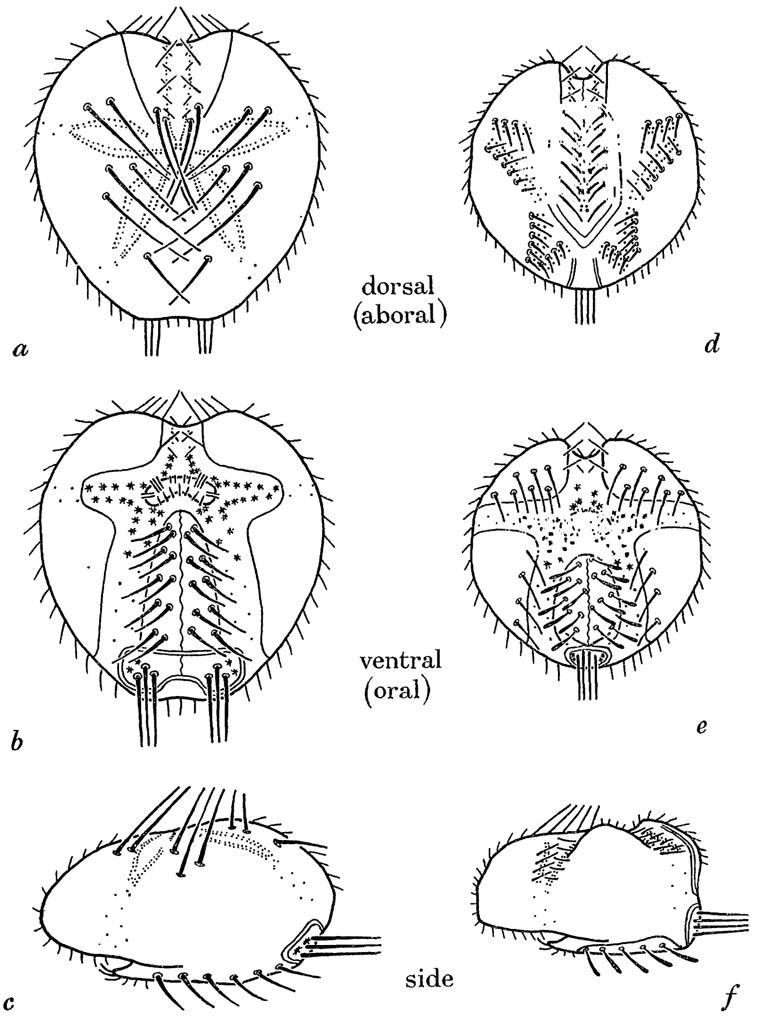


Figure 4. Diagrams to show the arrangement of the spines in *S. purpureus* (*a*, *b* and *c*) and *E. cordatum* (*d*, *e* and *f*). Only a few of each series of spines have been included for clarity.

4. Observations

(*a*) *Ciliary activity*

Features common to all urchins studied

The cilia are confined to the bases of the spines and the epithelium between them (Gislén 1924), except on the clavulae (the special spines of which the fascioles are composed) the stems of which have cilia on two sides. On the dorsal (aboral) surface of the test the direction of beat is mainly centrifugal (i.e. away from the apical disk). Currents pass down each respiratory ambulacrum and over the ambitus to the oral surface. In each of these ambulacra the respiratory tube-feet are not perpendicular to the longitudinal axis of the ambulacrum, but set at an angle to it. This angle decreases towards the ambitus in most urchins, so that down the whole length of the petaloid areas the respiratory tube-feet are diverting small streams out of the petal (e.g. figure 12). In the anterior ambulacrum, however, the current is centrifugal only from a point some distance anterior to the apical disk (figures 7*a*, 8*a*, 9*a* and 10*d*). Between this point and the apical disk there is a posterior (centripetal) current passing towards and over the apical disk; other currents lateral to this current pass round on either side of the disk, forming an apical eddy of currents. The function of this is considered below (page 388).

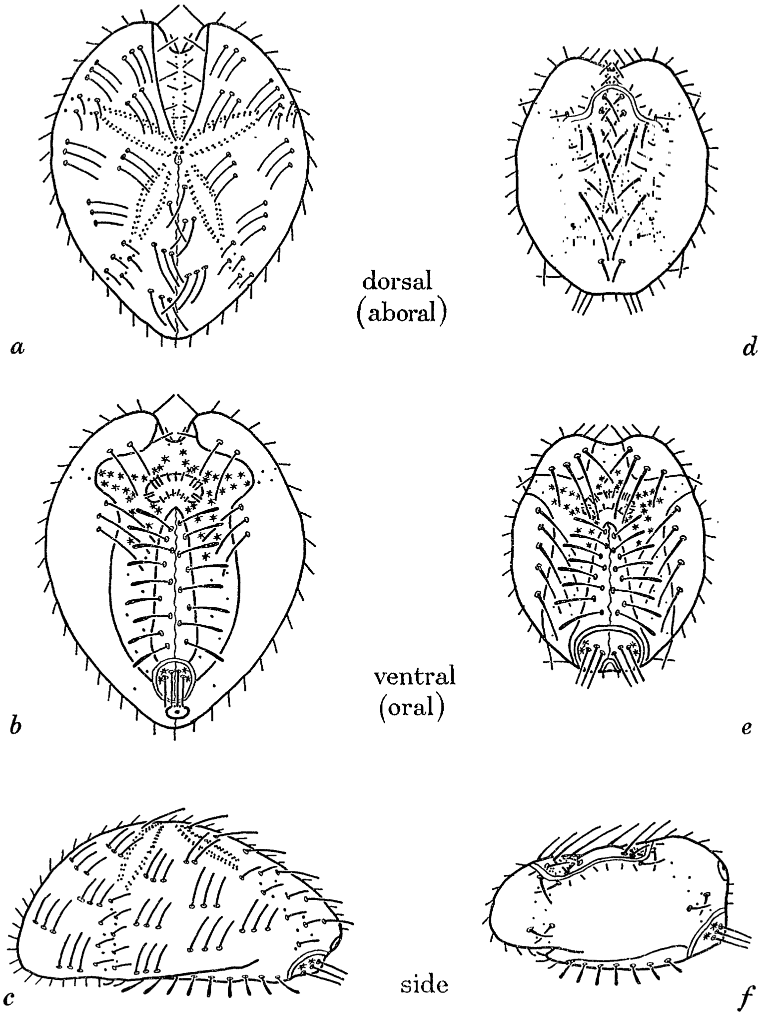


FIGURE 5. Diagrams to show the arrangement of the spines in *S. raschi* (*a*, *b* and *c*) and *B. lyrifera* (*d*, *e* and *f*). Only a few of each series of spines have been included for clarity; the primary spines of *S. raschi* are in linear groups of up to fourteen on each plate, of which two or three have been drawn on a few plates.

On the ventral (oral) surface the main trend of the currents is towards the posterior side. However, in the anterior trivium (Amb. II, III and IV) and in the interambulacra between them (Interamb. 2 and 3) there are currents towards the peristome. Near the margin of the peristome the more posterior of the currents along Amb. II and IV veer off and pass backwards down the periplastronal areas of Amb. I and V. Nevertheless, there is a distinct flow in the anterior region of the animal towards the peristome, although there is no ciliary activity on the peristomal plates themselves. In all the Spatangoida there is a lip, formed by the distal plate of Interamb. 5, on the posterior border of the peristome. Currents are in an anterior direction over this lip, that is, towards the mouth, but the main flow in Interamb. 5 is in the opposite direction. There are thus two places on all the spatangids examined at which there is a reversal of direction, namely, in the anterior ambulacrum anterior to the apical disk, and in the posterior interambulacrum, just behind the lip. In *Echinocyamus* there is a reversal of current direction only in the anterior ambulacrum.

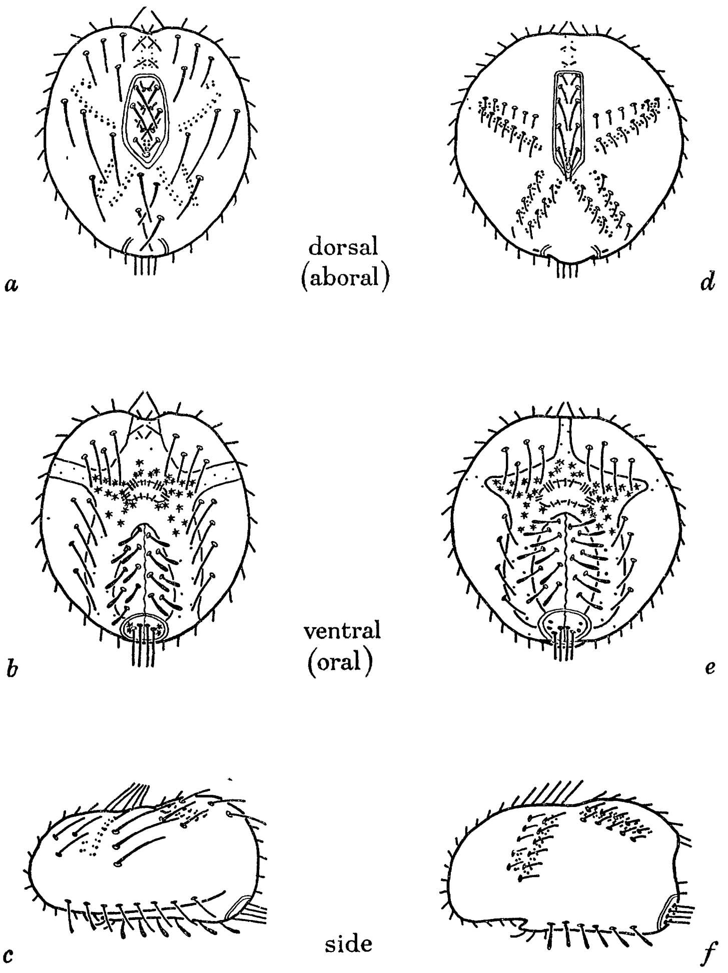


FIGURE 6. Diagrams to show the arrangement of the spines in *E. flavescens* (*a*, *b* and *c*) and *E. pennatifidum* (*d*, *e* and *f*). Only a few of each series of spines have been included for clarity.

In all the spatangids the ciliary currents converge to the subanal fasciole. There is a strong current produced here, beating inwards towards the centre of the region enclosed by the fasciole (*S. raschi*, *E. cordatum*, *E. pennatifidum*, *E. flavescens*) or to the centre of each lobe if it is bi-lobed (*S. purpureus* and *Brissopsis lyrifera*). The effect of this is to produce a resultant current or currents away from the animal (figures 11 and 12).

Specific features of the ciliary currents

Spatangus. Both species of this genus have a peculiarity not found in the others; there are cilia on the plates of the dorsal half of the periproct, and these produce a series of currents towards the anus (figures 7*c* and 8*c*). Four specimens of *S. purpureus* and 1 of *S. raschi* were examined.

Echinocardium. In addition to the inward-beating subanal fasciole, all three species possess two other fascioles. Of these, the inner fasciole, surrounding part of the anterior ambulacrum and the apical system, beats outwards and causes currents away from the apex, and is so arranged (figure 13) that the currents emerge perpendicular to the line of the fasciole and pass straight down the ambulacra (figures 7*d*, 9*a* and *d*). This fasciole produces currents which are roughly proportional to the thickness of the fasciole bands in the three species; i.e. *E. cordatum* has the strongest current in this region, *E. pennatifidum* the weakest, and *E. flavescens* is intermediate (compare figures 7*d*, 9*a* and 9*d*).

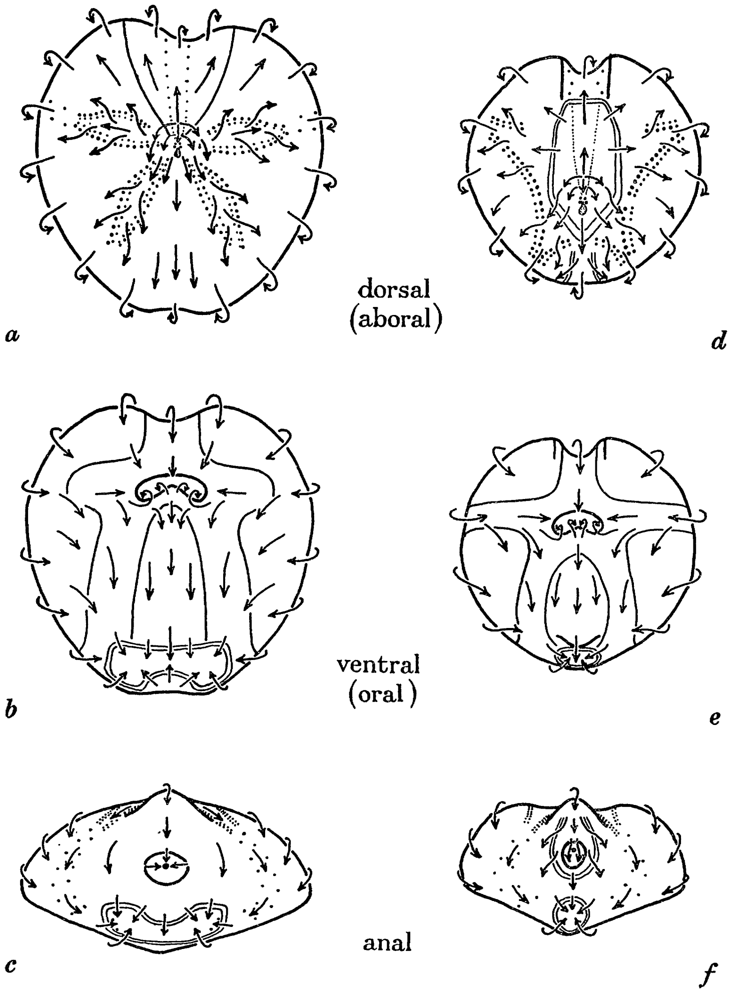


FIGURE 7. Diagrams to show the course of the ciliary currents on the tests of *S. purpureus* (*a*, *b* and *c*) and *E. cordatum* (*d*, *e* and *f*).

The anal fasciole produces outward currents, the merging currents converging into the subanal fasciole almost at once (figures 7*d* and *f*; 9*a*, *c*, *d* and *f*). In *E. flavescens* the oral side of the anal fasciole and the aboral side of the subanal are confluent (figure 9*c*).

In all three species there is ciliation on the periproctal plates, but no current towards the anus; the periproctal currents move towards the subanal fasciole, via the anal fasciole.

Four specimens of *E. cordatum* were examined, two specimens of *E. pennatifidum*, and four of *E. flavescens*.

Brissopsis lyrifera. This has, in addition to the inward-beating subanal fasciole, a peripetalous fasciole surrounding the respiratory petals, apical disk and part of the anterior ambulacrum, and causing currents outwards. The arrangement of this fasciole is such that its portions adjacent to the oral ends of the petaloid parts of the ambulacra are perpendicular to their longitudinal axes. Consequently, the currents passing directly down each petal are speeded up when they reach it. It has re-entrant angles in all the interambulacra except the posterior one, so that in these areas the line of the fasciole band is at right angles to the currents passing between the respiratory tube-feet, and assists them to bathe the respiratory surfaces. Four specimens were examined.

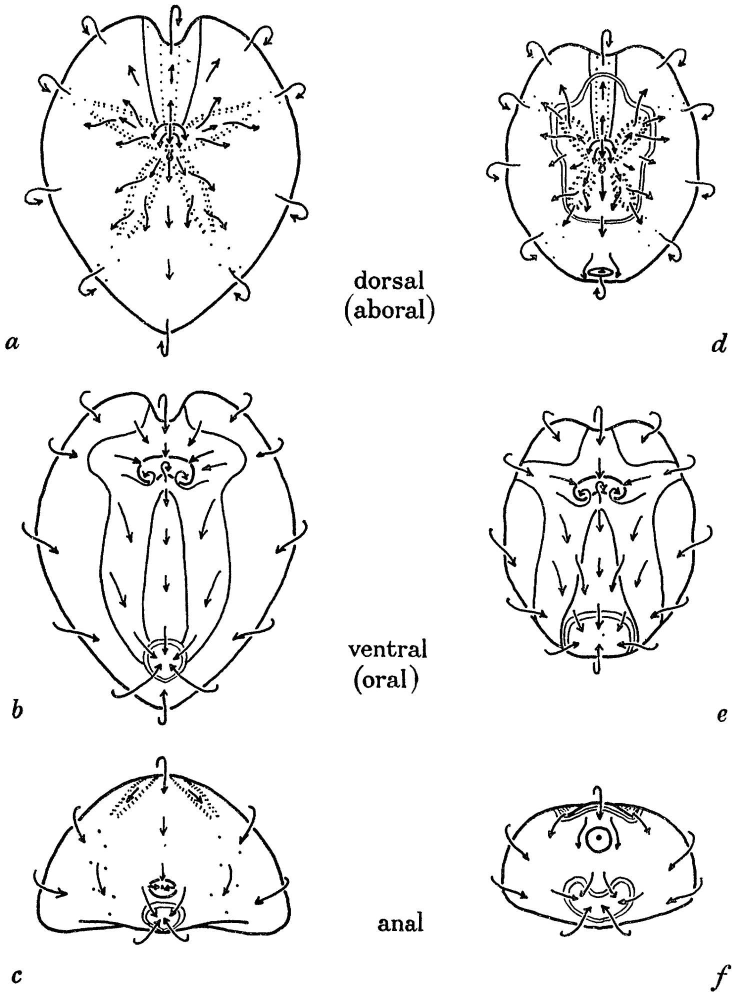


FIGURE 8. Diagrams to show the course of the ciliary currents on the tests of *S. raschi* (*a*, *b* and *c*) and *B. lyrifera* (*d*, *e* and *f*).

Echinocyamus pusillus. In this clypeastroid the apical eddy of currents (figure 10*d*) is slightly different from that in the spatangoids: there is a centripetal element to the current in the anterior ambulacrum, but the lateral currents do not pass round the disk towards the rear; they move straight to the sides of the animal. The ciliation on the rest of the urchin bears little resemblance to that on the spatangoids. There are no fascioles, and the currents converge to the anus, from which a downward resultant current flows away from the animal. The currents pass over the peristome, and are not diverted round it, nor, as far as could be seen, into the mouth at all. Four specimens were examined.

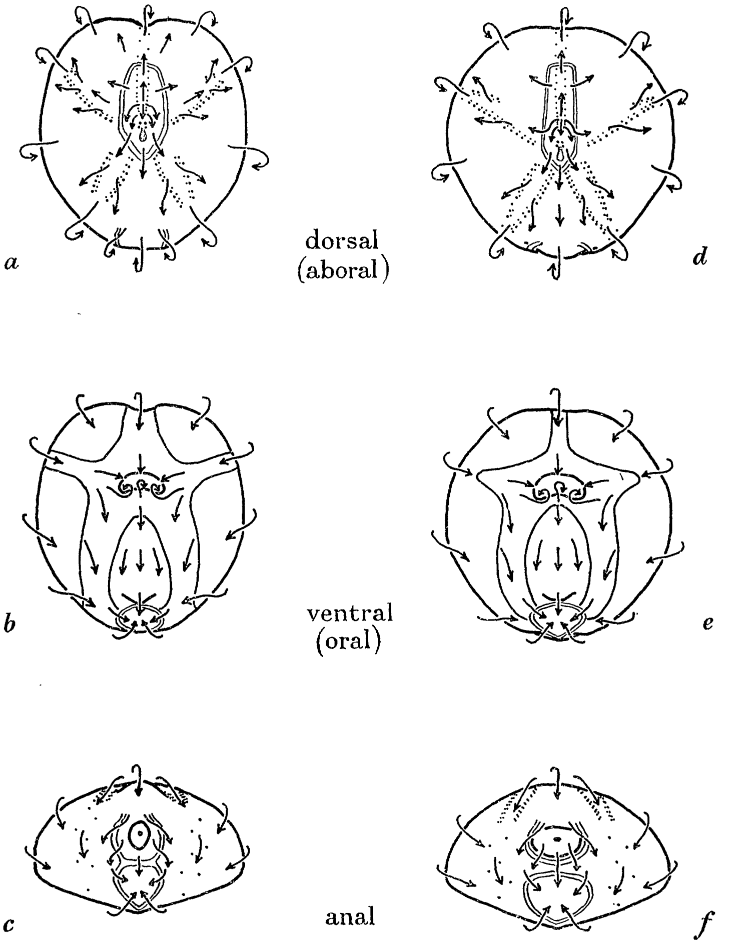


FIGURE 9. Diagrams to show the course of the ciliary currents on the tests of *E. flavescens* (*a*, *b* and *c*) and *E. pennatifidum* (*d*, *e* and *f*).

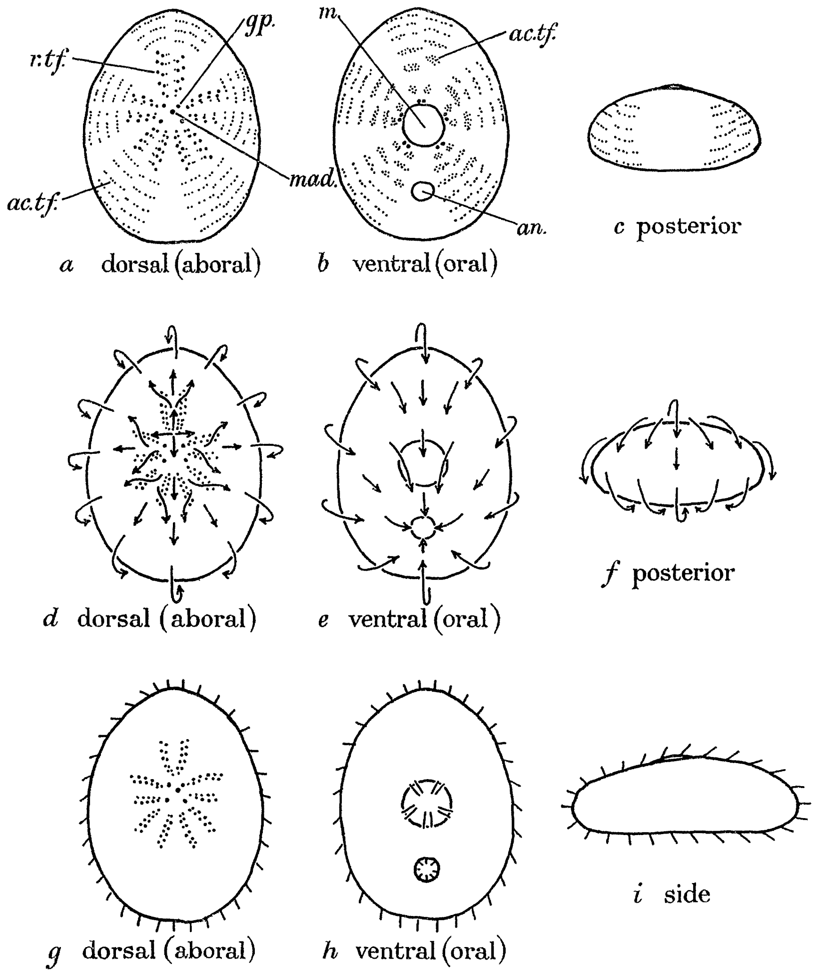
(*b*) *Burrowing activity*

(i) *Spatangus purpureus*

The one specimen I obtained in good condition showed the following burrowing activity (repeated several times):

When the urchin was placed on the surface of the shell gravel in the aquarium its spines and tube-feet remained motionless, usually for about $\frac{1}{2}$ min. Then the spines of the plastron and the lateral interambulacra started to move in such a way as to shift material from under the animal and cast it up in mounds on either side and in front (figure 15). Gradually, and without moving forward more than about a centimetre, the urchin became completely buried as these mounds joined above it, i.e. the ventral surface sank down approximately 5 or 6 cm.

While the animal was still on top of the gravel, the tube-feet round the peristome were retracted, but those within the subanal fasciole commenced activity about 10 min after burrowing began. They were extended up the spines of the two subanal tufts (figure 4*b* and *c*) and retracted again repeatedly. The spines of these tufts made ceaseless circular movements, each outlining a cone of about 15° apex. At first there was nothing solid within their reach, but as the animal sank deeper the spines came into contact with the gravel particles, their activity making at first a single groove in the surface. As the gravel of the lateral mounds fell in towards the mid-line behind the burrowing animal, the groove became a tube, leading forwards and downwards towards the subanal region of the burrowing animal. Meanwhile, the dorsal part of the test had disappeared beneath the surface of the gravel, but contact with the water above was maintained at first by the large spines of the dorsal interambulacra (figure 4*c*) which kept open a hole of about 1 cm diameter above the animal for about 10 or 15 min (figure 14*a*). As the animal burrowed deeper, however, this hole could not be maintained, and, except for the open end of the subanal tube, there was no sign of the animal at the surface of the gravel. Sometimes the burrowing animal disturbed the gravel and closed up the end of the subanal tube, so that not even this could be seen, and under normal conditions on the sea bottom this would most likely be the usual state of affairs.



a dorsal (aboral) *b* ventral (oral) *c* posterior

d dorsal (aboral) *e* ventral (oral) *f* posterior

g dorsal (aboral) *h* ventral (oral) *i* side

FIGURE 10. Diagrams of the clypeastroid *E. pusillus* to show the main features of the test (*a*, *b* and *c*), the ciliary currents (*d*, *e* and *f*) and the arrangement of the spines (*g*, *h* and *i*).

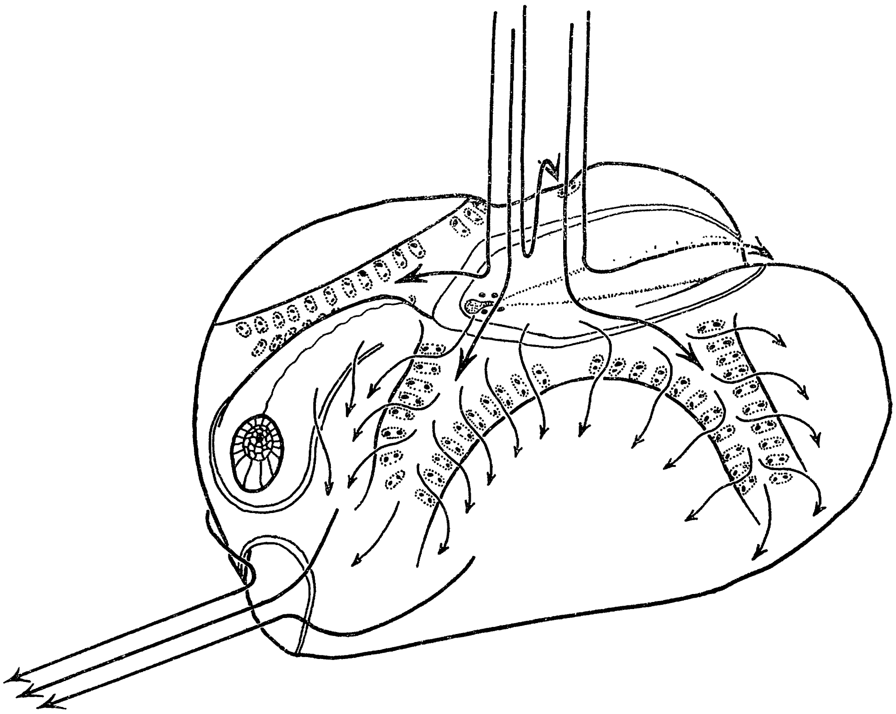


FIGURE 11. Perspective diagram showing the course of the respiratory currents in *E. cordatum*. The currents are drawn down a respiratory funnel by the ciliation of the body, augmented by that of the inner fasciole, pass down the ambulacra and between the respiratory tube-feet, and are collected within the subanal fasciole, which augments the body ciliation in passing the currents away from the animal down the sanitary tube. The outlines of the respiratory surfaces have been dotted in round the pore-pairs which bear them. By Lovén's (1874) scheme of numbering, the ambulacra facing the reader are, on the left, Amb. I, and on the right Amb. II.

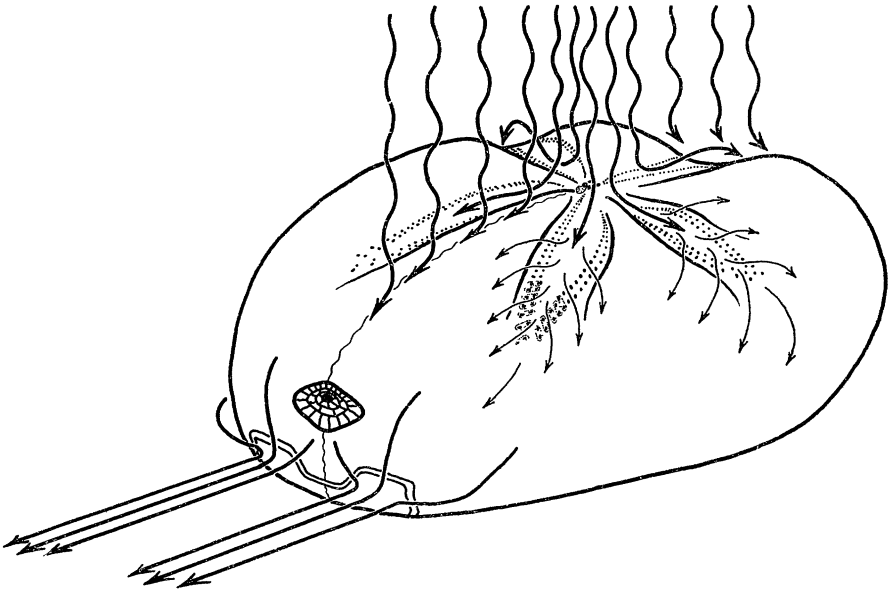


FIGURE 12. Perspective diagram showing the course of the respiratory currents in *S. purpureus*. The currents are drawn down through the interstices of the gravel particles by the ciliation of the body, then pass down the ambulacra and between the respiratory tube-feet, and collect within each lobe of the subanal fasciole, which helps the currents to pass away from the animal down the double sanitary tube. In this case the respiratory tube-feet are so numerous and close together that the outlines of only a few at the distal end of Ambulacrum I have been dotted in round the pore-pairs which bear them. Some of the other currents drawn down through the interstices, not destined to become respiratory currents, are also included.

After an hour or so, with the gravel some 6 cm deep in the tank, the animal could be seen through the glass bottom, the first part of it to appear being the spines of the plastron. The animal had usually moved about 5 or 6 cm forward from the position in which it disappeared from the surface. Because of the large size of the gravel particles the spines could clear them from beneath it and the glass bottom, so that a good view could be obtained of the burrowing and feeding activity. Although the smooth glass bottom of the observation tank now replaced the irregular and moveable gravel particles of the sea bottom, there were usually sufficient particles falling down from the side-walls of the burrow and collecting underneath the animal for the plastron spines to obtain enough purchase for movement and for feeding to go on. Since, therefore, the animal was carrying

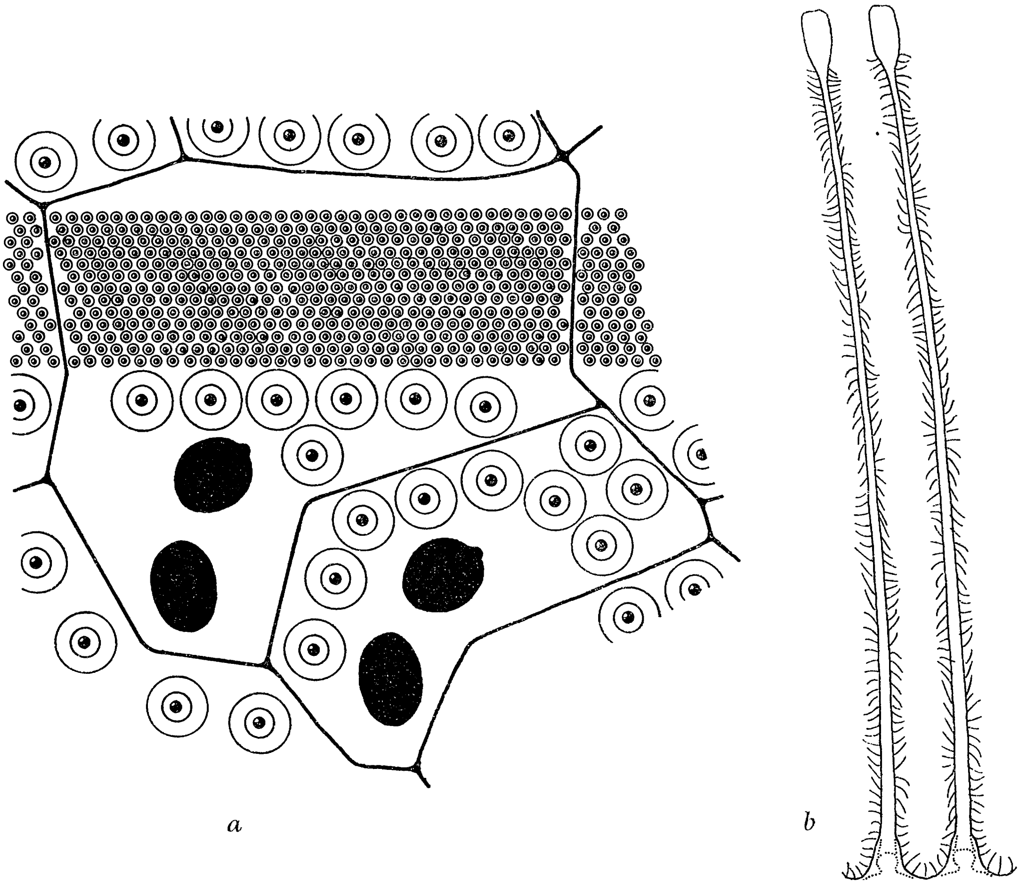


FIGURE 13. Drawings to illustrate the structure of a fasciole. (*a*) Plan view of two plates of an ambulacrum (left-hand column of Amb. II) of *E. cordatum* from which the spines, clavulae and tube-feet have been removed. A densely packed band of small tubercles, which bear the clavulae, and which are in fairly regular horizontal and diagonal lines, runs across the uppermost plate. A pore-pair, which bears a respiratory tube-foot, is present in each plate; the irregularity in the upper pore of each pair bears the tributary of the radial water-vascular canal to each tube-foot. A number of larger tubercles, which bear medium-sized spines, are also present on each plate. The width of the fasciole is about 1 mm at this point. (*b*) Side view of two clavulae, drawn to a larger scale. The height of each clavula is about 2 mm; the cilia are in two bands on either side of the stem, but these do not extend to the club-shaped terminal portions.

out its normal activities of locomotion and feeding, and lived under these conditions for 9 months, it seems reasonable to assume that the behaviour was normal.

As the urchin came further into view from below the subanal region became visible, and construction of the sanitary device could be observed. This was seen to consist of two separate tubes, backward prolongations of the burrow, which extended horizontally from the posterior side of the animal. One originated at each lobe of the subanal fasciole (figure 14), and each tuft of large spines in the area enclosed by the fasciole extended into the tube on its side. The method of construction was as follows. The subanal tube-feet in each lobe were extended and rubbed against the tuft spines, presumably wiping mucus on to them, and then retracted. The tuft spines made circular movements (as seen in the initial burrowing) and appeared to be plastering a lining of mucus on to each tube. In one or two instances the subanal tube-feet were extended beyond the tips of the spines, and presumably wiped their mucus direct on to the walls of the tube, but in the majority of extensions this did not happen. The two tubes were remarkably permanent and their dimensions constant; they were situated about 8 mm apart, and were about 4 mm in

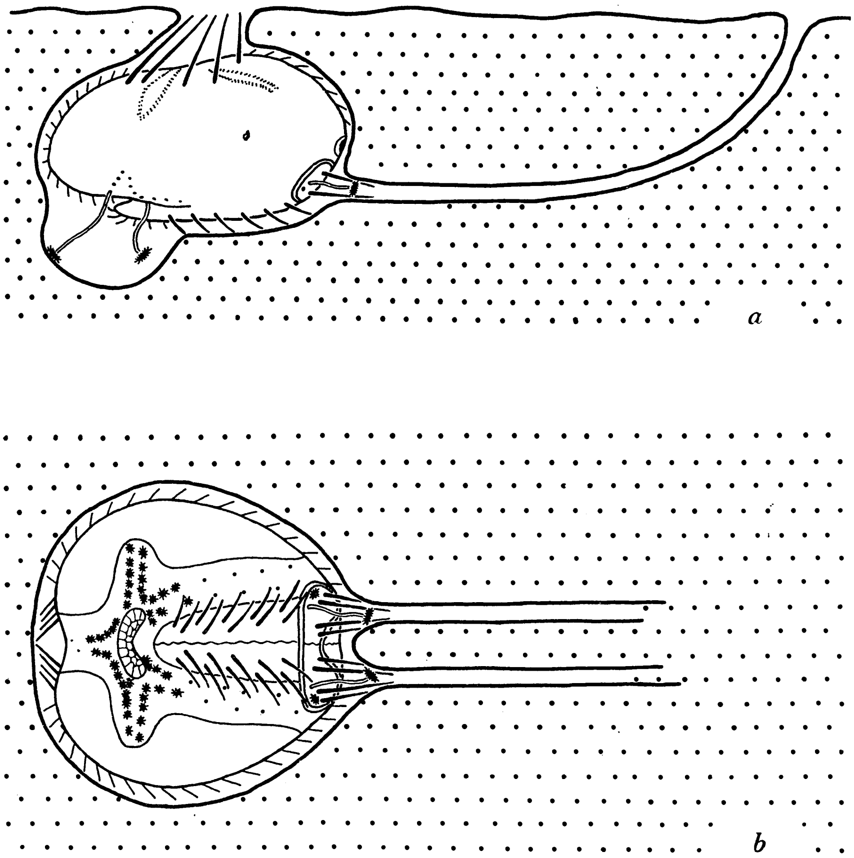


FIGURE 14. Diagram to show the burrowing activity of *S. purpureus* in side view (top) and oral view (bottom). In the top picture the urchin has been burrowing for about 15 min, and the dorsal spines are still keeping open a funnel to the top of the substratum. Later, this funnel will not be maintained, but merely a space above the dorsal surface of the animal. Also, it is quite likely that the opening of the sanitary tube at the surface will become blocked later. Two of the oral feeding and one of the subanal burrow-building tube-feet have been included.

diameter. The length of the specimen was 55·7 mm, and the dimensions of the subanal fasciole 23·3 by 11·1 mm (maximum width and height, respectively). Each tuft of spines had a diameter of between 6 and 7 mm.

There is an obvious current away from the animal down the two tubes. I was able to introduce carmine particles into each tube by means of a small pipette, gently inserted into the gravel from above. The current is not very rapid, even close to the animal; only the smallest particles of carmine were moved any distance at all before dropping to the floor of the tube. Their speed was less than 1 mm/s.

No field observations could be made on this urchin, because it normally lives at between 5 and 30 fathoms.

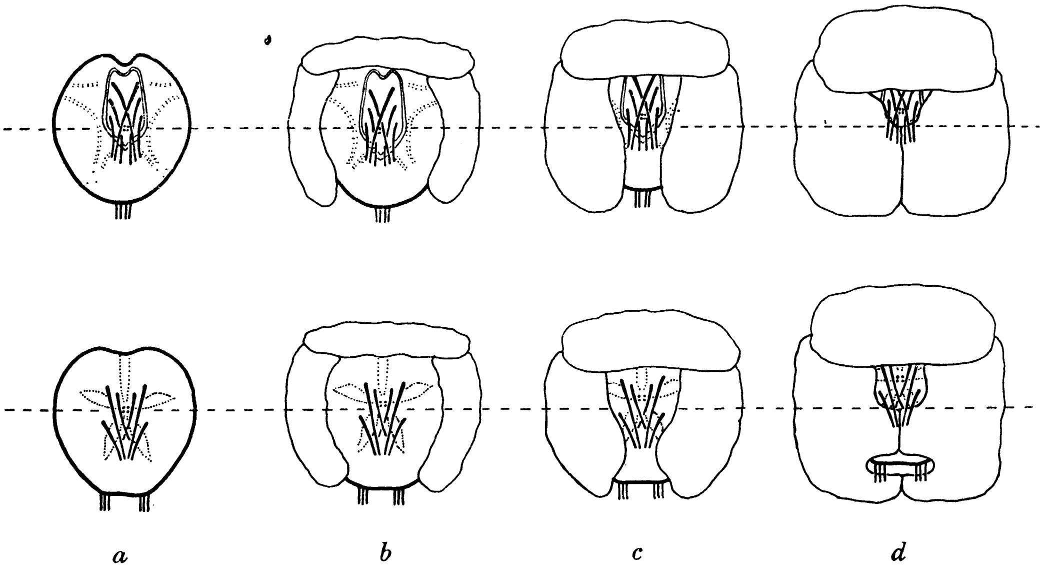


FIGURE 15. Diagrams of the successive stages in the initial burrowing of *E. cordatum* (top line) and *S. purpureus* (bottom line) showing the side and front walls thrown up by the spines. In each case a datum line (dotted) has been drawn through the apical disk to show the amount of forward movement (if any) which occurs during the initial stages of burrowing.

(ii) *Echinocardium cordatum*

Observations in aquaria. The initial burrowing of this sand-living form (figure 15) was similar to that of *Spatangus*. Mounds were thrown up at the front and sides of the animal (cf. Tornquist 1911, Fig. 9) and there was little, if any, forward movement until it was invisible from above. The subanal tube-feet commenced slight activity after 10 min or so, as they did in *Spatangus*, and there was no appreciable activity of the tube-feet around the mouth. The main difference between the two forms was in the activity of the dorsal region. The tuft of large spines here (figures 4 *f* and 26) became active, and the penicillate tube-feet of the dorsal region of the anterior ambulacrum extended slightly at this stage, apparently wiping mucus on to these spines. These went through motions suggestive of plastering it on to the walls of a wide hole, which is a respiratory funnel opening to the surface immediately above the animal. As the animal burrowed deeper and the dorsal spines were unable to reach the surface, the hole, instead of simply falling in, as happened in *Spatangus*, was maintained by the dorsal tube-feet, which could be extended a considerable distance beyond the ends of the dorsal spines (figure 16). Consequently, it became much narrower, and after a time sand invariably blocked the top end of it. But later, generally about 10 min after it had closed, the same funnel would be opened again by the tube-feet, and kept open for a while by the extension of one tube-foot at a time at intervals of about 15 s. The funnel usually remained in the same position for some time, falling in and being remade several times; but then there would come a time when the interval between falling in and rebuilding was much longer. As one watched the depression marking the position of the old funnel, the tube-feet would suddenly break surface about 2 cm in front of it, as shown in figure 17 and figure 47, plate 9 and the falling-in and rebuilding process would be started again. In about 15 or 20 min another new funnel was built as the animal moved forward. All trace of the former funnels was removed by the disturbance caused by the animal burrowing. As the animal burrowed deeper, however, its forward movement disturbed the surface less and less, so that a series of depressions, marking the position of former funnels, was left along the course taken by the burrowing urchin.

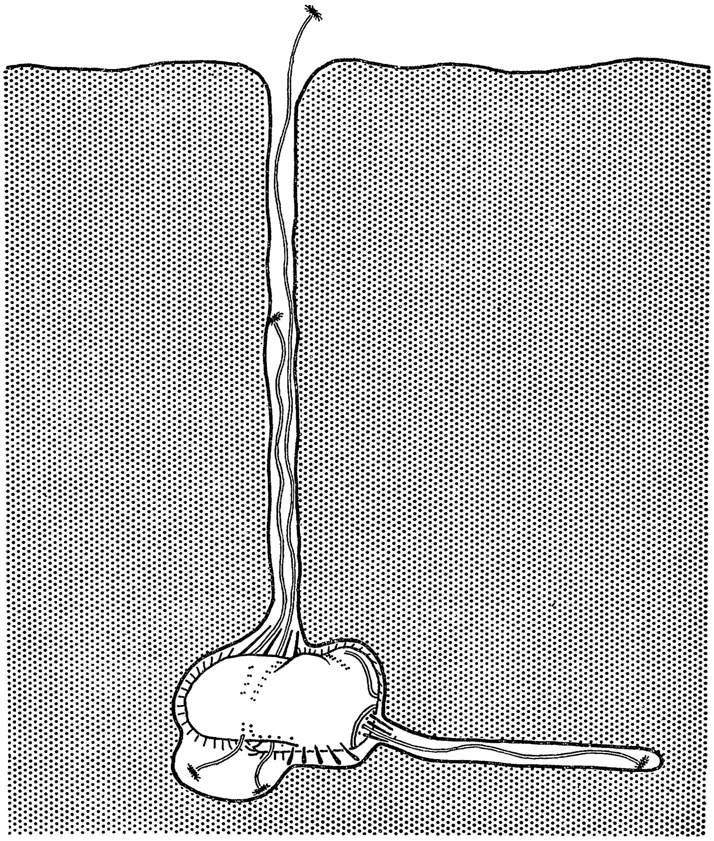


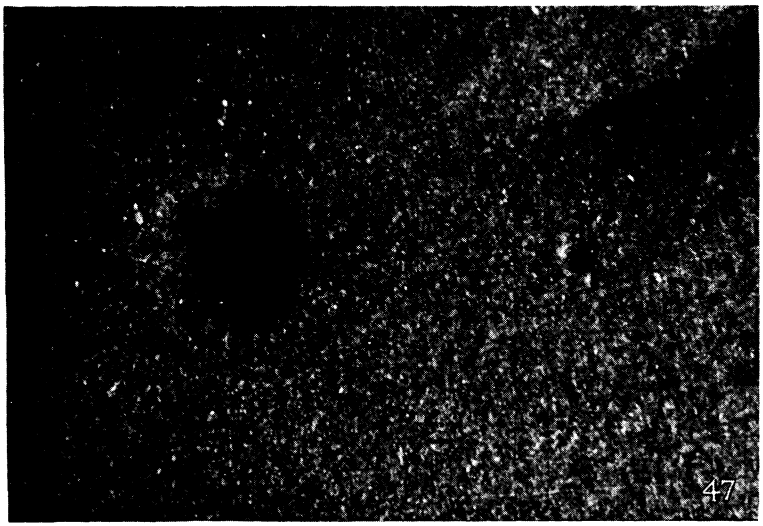
FIGURE 16. Diagram to show *E. cordatum* in its burrow from side view. This urchin normally maintains a respiratory funnel to the surface of the substratum by means of the penicillate tube-feet of the dorsal region of the anterior ambulacrum, two of which have been drawn. Two of the oral feeding and one of the subanal burrow-building tube-feet have also been included.

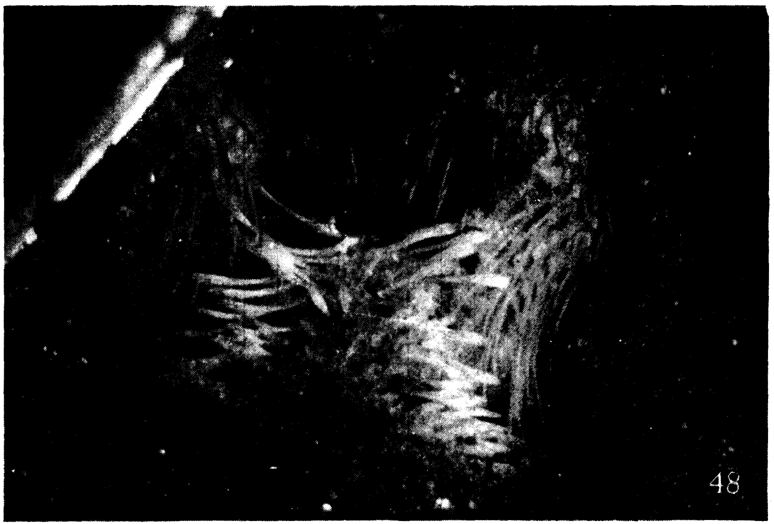
Although some activity was sometimes shown by the subanal tube-feet before the animal disappeared, no opening of the burrow, as was sometimes seen in *S. purpureus*, remained. When the animal came into view through the bottom of the tank, its spines cleared away the substratum from between its ventral surface and the glass, as in *S. purpureus*, but the substratum for this species has a much smaller particle size and clearance was never very complete. Figure 48, plate 9 shows a specimen of *E. cordatum* which has just appeared, and is about to move along with its lateral surface against the side wall of the tank. The paddle-shaped plastron spines still have some sand to move from under them, but the long lateral spines of the animal have cleared two areas on either side, these apparently being the main sand-moving spines for shifting the sand excavated from the front of the burrow to the space left behind the animal as it moves forward (see p. 389 below).

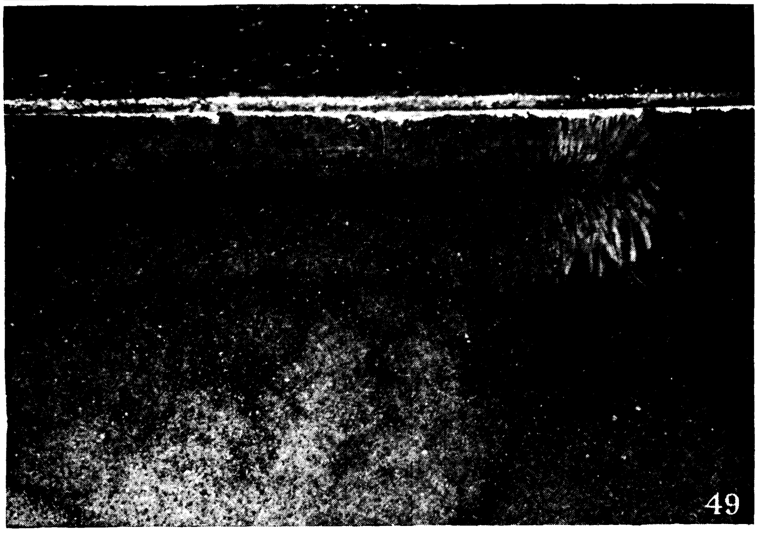
As burrowing along the bottom continued, the activity of the subanal region could be observed. The tube-feet, like those of *S. purpureus*, were extended backwards, but in this species they normally extended much farther than the tips of the tuft spines as shown in figure 19. The subanal fasciole in *E. cordatum* is not lobed, and there is only one tuft. Correspondingly, the backward prolongation of the burrow is single. This sanitary tube differed from the double tube of *S. purpureus* also in that it ended blindly at a distance of between 8 and 12 cm from the posterior side of the animal. The tube-feet were seen to extend up to 12 cm to maintain the tube, but apparently could stretch no farther; in consequence as the animal moved forward, and they could no longer reach the blind end, the roof soon fell in. In figure 49, plate 9, an urchin, of which only the plastron spines are visible, is shown excavating a subanal burrow. The end of this tube is too far from the end of the animal to be reached by the subanal tube-feet, and at its distal end a small collection of sand can be seen, which has fallen in from the roof. Running backwards from the blind end a darker line of sand can be seen curving away from the tank wall. This is a mixture of sand and mucus, which once formed the walls of the subanal tube and which has progressively fallen in as the animal moved on.

On most occasions the subanal tube-feet collected sand on their penicillate processes and disks as they wiped mucus on to the walls of the tube. This sand was carried back as they retracted, but was never on them when they extended again. How it was removed has not been directly observed, because, as shown in figure 49, plate 9, there is always a collection of sand just hiding the posterior side of the body. I assume, however, that when they retract, the subanal tube-feet are applied to the spines of the subanal tuft wiping some mucus, plus the sand, on to them. This mixture may then be used to line the beginning of the subanal tube by a plastering action of the subanal tuft, as seen in *S. purpureus*. It will be shown elsewhere (Nichols 1959*b*) that the histology of the spatangid burrow-building tube-feet is unique among the echinoderms I have studied, the individual mucus glands having thin muscle fibres running between them. It seems very likely that these act in squeezing out the mucus from the glands, so that the transfer of the mucus sheet, plus the sand, to the spines of the subanal tuft or the walls of the burrow is not entirely passive, but may be assisted by the tube-feet themselves.

The current within the subanal tube was again detected in this species, but after considerable difficulty. It was even weaker than in the tubes of *S. purpureus*, and the walls collapsed more readily when a pipette was introduced. Consequently, the only way to introduce carmine particles was to feed them into the top of the respiratory funnel. A few escaped being incorporated in the wall of the burrow (see under Field Observations below) and appeared in the outgoing current of the subanal tube. Another difficulty was to detect against the background of sand in the burrow even those few carmine particles which did get through, and it was only on two occasions that this was possible. In both these cases







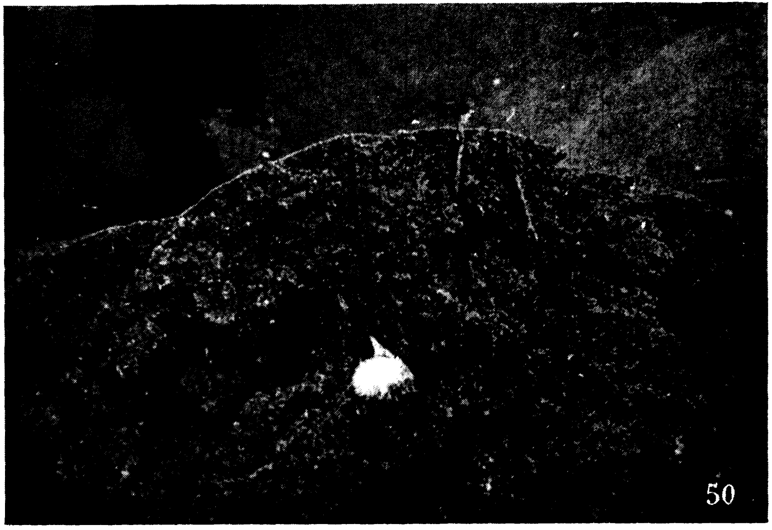


FIGURE 47. Surface view of the openings of two successive funnels built by a burrowing *E. cordatum* in sand in an aquarium. The pit on the left is the remains of the first-formed funnel, which has filled in and been discarded; the small hole on the right has just been opened by the urchin, and the tube-feet of the dorsal anterior ambulacrum will now be maintaining it. The distance between the two pits in this case is about 4 cm.

FIGURE 48. Ventral view, looking upwards at the bottom of an aquarium, of a burrowing *E. cordatum* which has just appeared, and is about to move along the side of the tank. The long scraping spines of Interambs. 1 and 4 have cleared two areas on either side of the plastron, of which some of the paddle-shaped spines can be seen. The urchin is feeding, and the oral tube-feet are blurred in consequence; however, the disk of one, pressed to the glass bottom of the tank, can be seen posterior to the mouth.

FIGURE 49. Ventral view, looking upwards at the bottom of an aquarium, of a burrowing *E. cordatum* moving along the side of the tank, and of which only the plastron spines are visible, showing the single sanitary tube extending from the posterior side of the animal for a distance of about 8 cm. An explanation is given in the text, p. 368.

FIGURE 50. Photograph of a spadeful of sand which has been dug up on the beach. The sand has cleaved across the burrow of an *E. cordatum* and the urchin can be seen in its burrow 10 to 12 cm below the surface of the sand. The respiratory funnel to the surface is also visible, with the dorsal tuft of spines extending up it for about 1 cm. The anterior side of the urchin is to the right: the subanal tube is not visible.

a small cockle shell formed part of the roof of the tube close to the animal, and this acted as a background against which the occasional passing carmine particle could be seen.

One specimen out of the ten or so I examined in this way produced an abnormal subanal burrow. Quite often, the subanal tube-feet of one side of this animal would curve away from the straight course of the tube and push through its side wall. The result in this case was a Y-shaped burrow. As the animal moved forward, both arms of the Y would eventually fall in, and the process would be repeated a little further on.

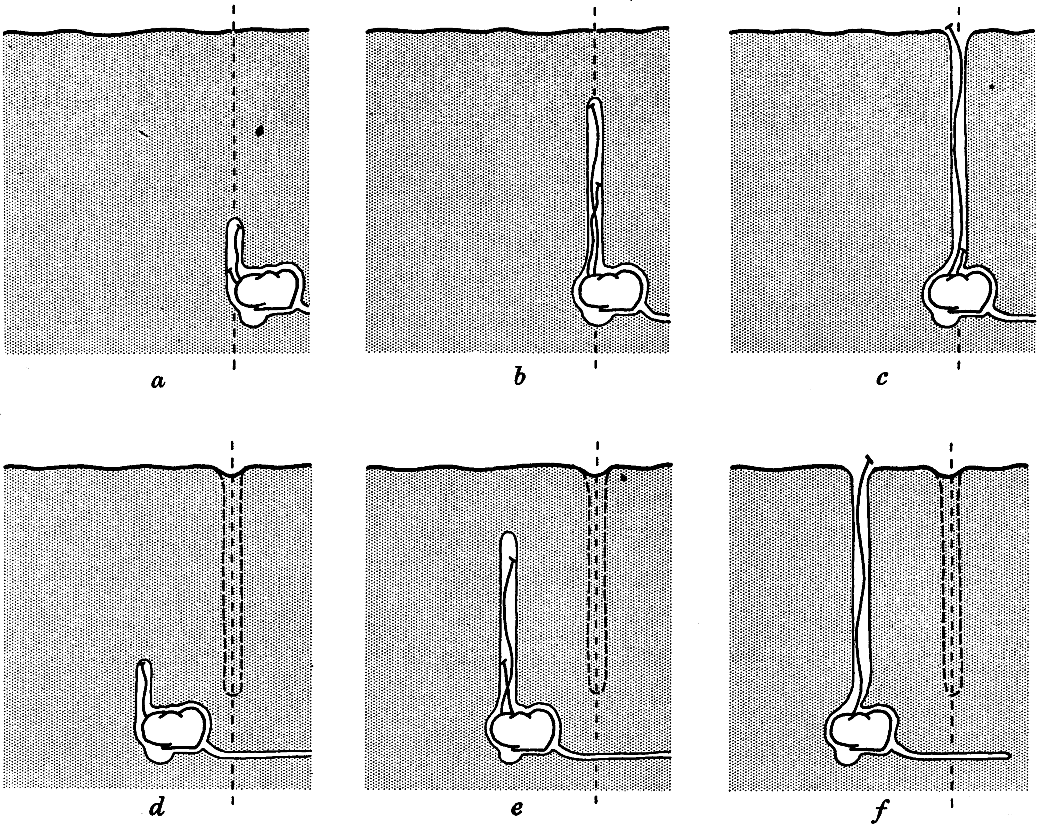


FIGURE 17. Series of diagrams of *E. cordatum* to show the successive stages in the building of a burrow in pure sand. (*a*) The more anterior of the penicillate tube-feet of the anterior ambulacrum are excavating the lower part of the funnel. (*b*) The middle tube-feet are continuing the excavation. (*c*) The funnel is completed and maintained for some time by the tube-feet nearest the apical disk. (*d*) As the urchin moves forward the adapical tube-feet cease to maintain the first funnel, it becomes filled in, and the more anterior tube-feet start to excavate another funnel in front of the first. (*e*) and (*f*) The excavation of this second funnel is completed and maintained for some time by the adapical tube-feet. A dotted datum line has been drawn through the first funnel in each case. (See also figures 47 and 50, plate 9).

Urchins from two widely separated localities were used in this study; some were taken from Fairlie Sands, on the Ayrshire coast, and some from Derby Haven, Isle of Man. The sand at Fairlie is extremely pure, whereas that at Derby Haven contains much clay. This makes the Derby Haven sand more mouldable, a property which is reflected in the behaviour of the urchins burrowing in it. The respiratory funnels and subanal tubes of urchins in purer sand (Fairlie) fell in unless they were constantly maintained by the tube-feet, as shown in figure 17, and the urchins built new respiratory funnels every few centimetres as they moved forward; but the funnels and tubes of those in sand-with-clay (Derby Haven) remained open for much longer with less maintenance, and the first vertical funnel could be used for considerably longer (see figure 18). The urchin in this case built a horizontal connexion to the vertical part as it moved forward. Normally this

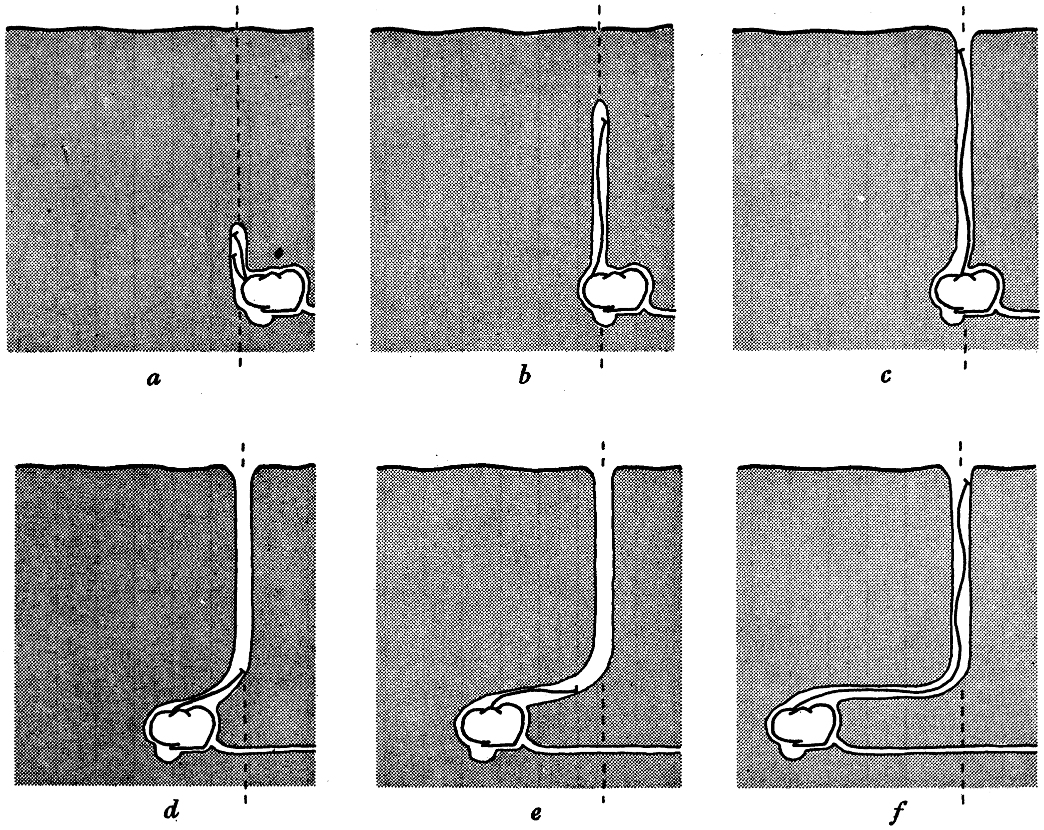


FIGURE 18. Series of diagrams of *E. cordatum* to show the successive stages in the building of a burrow in sand-with-clay. (*a*, *b*, *c*.) The first stages follow the same pattern as in figure 17, except possibly that in this case less activity of the tube-feet is necessary. (*d*, *e*.) As the animal moves forward the maintaining tube-feet near the apical disk slide backwards into the first vertical funnel. (*f*.) The result is the production of a horizontal connexion from the top of the animal to the first vertical funnel.

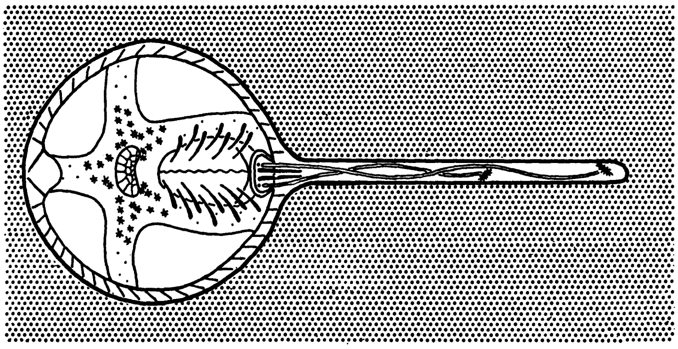


FIGURE 19. Diagram to show the burrowing of *E. cordatum* in oral view. The single sanitary tube must be constantly maintained by the subanal tube-feet (two of which are shown). Thus, the end of the tube is blind, its length being determined by the degree of extension of the subanal tube-feet. Compare the lower diagram of figure 14.

connexion could be used until the animal was about 10 cm further on, and although the tube-feet could extend to the top of the vertical funnel, as shown in figure 18*f*, they very seldom did so. Similarly, the subanal sanitary tube in purer sand fell in about 8 cm from the animal, but the tube built in sand-with-clay often extended 15 or 20 cm from the animal.

Field observations. I have excavated the burrows of these urchins in their natural habitat at both Fairlie Sands and Derby Haven, and have confirmed the observations made in aquaria (see figure 50, plate 9). Under natural conditions burrowing activity of *E. cordatum* continued until the animal was as much as 15 to 20 cm below the surface in purer sand (Fairlie), but only to 10 to 15 cm in sand-with-clay (Derby Haven). In both, observations on a large number of specimens (about fifty in each case) dug out in the field showed that they always burrowed below the water-table. At both Fairlie and Derby Haven the relatively pure sand overlay blue muddy sand underneath; the transition was normally deeper at Fairlie (about 15 to 20 cm) than at Derby Haven (about 10 to 15 cm), and apparently the low rH of this blue muddy sand kept the urchins burrowing just above it, or only in its upper layers. Consequently, they could burrow deeper at Fairlie, and may have been able to inhabit a region further up the beach, than at Derby Haven. The penicillate tube-feet of the dorsal region of the anterior ambulacrum are extensile enough still to reach the surface and keep open the dorsal funnel (figure 16 and figure 50, plate 9) even when the animal is 20 cm below. They can be seen from above, slightly protruding from the hole at the surface (Allen & Todd 1900). Of course, no tube-feet can be seen at the surface unless the respiratory funnel opens in a pool left behind by the receding tide.

Looking down from above at holes in such small pools I have frequently seen sand falling into the respiratory funnel, so that the spines of the dorsal tuft, while plastering mucus on to the walls of the proximal part of the respiratory funnel, are constantly rained on by sand loosened by the tube-feet or by water-movements, or received direct from the tube-feet as they retract. The fate of this sand was determined both in the field and in the aquarium by dropping red ballotini (grades 6, 8 and 10) into the respiratory funnel from above, and subsequently excavating the burrow. The ballotini, and therefore presumably the sand grains, were moulded into the walls of the burrow in which the animal lived, and this must have been done by passing them from the dorsal tuft over the dorsal and lateral spines. It is as though a coal-mine shaft were being excavated from below, the material brought down in doing so being used to line the galleries.

(iii) *Spatangus raschi*

One living specimen of this form from deeper water was obtained by the crew of the Marine Biological Association's trawler from Plymouth, but unfortunately I was not present when it was dredged. At the Marine Laboratory the specimen had been placed in a tank containing fine shell gravel to a depth of about 8 cm to await my arrival. When I first saw it, the specimen, which measured about 4 cm in height, was buried to a depth of about $2\frac{1}{2}$ cm only, and I was told that it had maintained this depth for 2 days or so, the devious path it had taken, while ploughing through the gravel, being clearly marked as a groove in the surface running for a total distance of 80 to 100 cm. Although its activity was not observed in its natural substratum, evidence will be put forward later (p. 387 below) which indicates that partial burial only during burrowing, and to about the depth I observed, is probably its normal position.

(iv) *Echinocyamus pusillus*

The term 'burrowing' applied to the behaviour of this urchin would be misleading; many particles of the substratum are larger than the urchin itself, and though the five specimens I have watched in aquaria usually succeeded in nestling in the interstices between the particles, none was seen to push itself actively under the substratum. Concealment in this species is brought about in another way: between the ambulacral plates there are many accessory tube-feet (figure 10*a*, *b* and *c*); these are used to pull very small gravel particles over the animal and so form a covering. I have placed red ballotini in the vicinity of specimens of *Echinocyamus* and have seen some of the balls being passed from tube-foot to tube-foot over the animal, and dropping off again, while others remained on the animal for some days.

(*c*) *Feeding*

All the urchins studied appear to feed on the organic matter which adheres to the particles of the substratum in which they burrow. The spatangoid urchins take particles of mud, sand or shell gravel into the gut and later pass out the particles, but the nature of the food has not been determined. During my observations I have seen the clypeastroid scraping off food with its teeth, and microscopical sections of whole specimens have shown that diatoms, radiolarians, fragments of sponges, etc., are all taken in. The feeding processes have been observed on at least three specimens of each of the urchins whose feeding patterns are described below, except *S. raschi*, of which only one was examined.

(i) *Spatangus purpureus*

Some of the gravel from between the ventral (oral) surface of the specimens and the glass bottom of the aquarium was removed by the spines of the lateral interambulacra, which incorporated it into the walls of the burrow; but quite a large proportion was cleared by the oral penicillate tube-feet (figure 1*b*) during the feeding operation. This consisted of picking up particles by means of the sticky disks and processes of the penicillate tube-feet and conveying them straight to the mouth. A tube-foot was extended randomly (it appeared) until a solid object was touched, then it was withdrawn. If nothing had stuck to the disk, it was extended again and the operation repeated. When a piece of gravel or a collection of pieces adhered as the tube-foot was retracted, it bent round and was extended again, this time into the mouth. All available space not taken up by the tube-feet round the mouth is occupied by small spines (figures 4*b* and *c*). These arch over the mouth, and acted as a grill through which the tube-feet carrying the particles extended into the mouth, and against the inner surface of which the particles were wiped off as the tube-feet withdrew again. There was considerable jostling among the tube-feet in an actively feeding urchin, and it was difficult to see whether more than one tube-foot was extended through the grill simultaneously. A loaded tube-foot never hesitated on its journey from the point of pick-up to the mouth, though after depositing its gravel and retracting, some time (about 10 to 15 s) often elapsed before it was extended again. There was no question of gravel particles being passed from tube-foot to tube-foot during feeding, since even the tube-feet furthest from the peristome can reach the mouth.

This urchin may exercise selection of the particles taken in while feeding in various ways, e.g. by the limiting size of the mouth, the closeness of the small peristomial spines, the power of the tube-foot muscles, or the stickiness of the mucus. Two animals of approximately the same size were kept in different aquaria, one in natural shell gravel taken from the Eddystone Shell Gravel with the animals, the other in an artificial shell gravel made from chicken grit. In the natural shell gravel the particles were mostly flat, or long and thin, but in the chicken-grit gravel the particles were rounder. After some days in the tanks the animals' gut contents were removed by dissection. The twelve largest pieces in each animal were weighed, and it was found that the tube-feet could cope with almost any shape (up to about 1·1 cm length), but there was a maximum weight which they could lift (about 100 mg) which was approximately the same for each type of substratum (see Appendix, table 2). This is considerably lower than the maximum weight of particles available in the substratum.

Observations in the glass-bottomed aquarium showed that two particles, which both together had the appearance of being fairly near the maximum weight, could easily be lifted by a tube-foot, but one particle, slightly above the maximum, would drop off in transit. It is therefore concluded that the limiting factor in particle-size selection is the stickiness of the mucus. Furthermore, the maximum size of gravel particles which can be lifted by the oral tube-feet increases in direct proportion to the size of the animal, as shown in the following experiment.

Twenty-eight specimens of *S. purpureus* were dredged from shell gravel to the south-west of the Isle of Man. After measurement (length and breadth) their gut contents were removed. The six heaviest particles of gravel in the gut of each were weighed (see Appendix, table 3), and the logarithm of the average was plotted against a size-number obtained by multiplying length by breadth for each specimen. The results from the two specimens used for the previous experiment were also included in the graph (figure 20), and the regression line calculated.

The details are as follows:

equation of regression line	S.E. of b	S.D.	correlation coefficient (r)
$Y = 0{\cdot}58 + 0{\cdot}0002218x$	0·0000293	0·243	0·8201

The regression is highly significant ($P \ll 0{\cdot}001$), and shows that in the larger animals heavier particles can be coped with, probably because a greater sticky area in the tube-feet can be used for lifting them.

(ii) *Echinocardium cordatum*

In this species too the spines and tube-feet cleared a roughly crescent-shaped area round the mouth in a glass-bottomed tank, though the clearance was less complete than in *Spatangus* because of the small size of the sand grains. The mode of operation of the tube-feet was very similar, but in this case no particle-size selection could be observed, all the particles in the substratum being so small and the strength of the tube-feet being such that any single grain could be transported. Presumably the total amount transported by any one tube-foot on one occasion is limited.

The sand particles were conveyed to the mouth on the sticky penicillate disks, and it is assumed that the small peristomial spines (figure 4*e* and *f*) acted as a scraper in the same way as those of *Spatangus*, but this was not actually seen, because of the presence of sand which always collected on the glass bottom immediately below the peristome, presumably as a result of this very process.

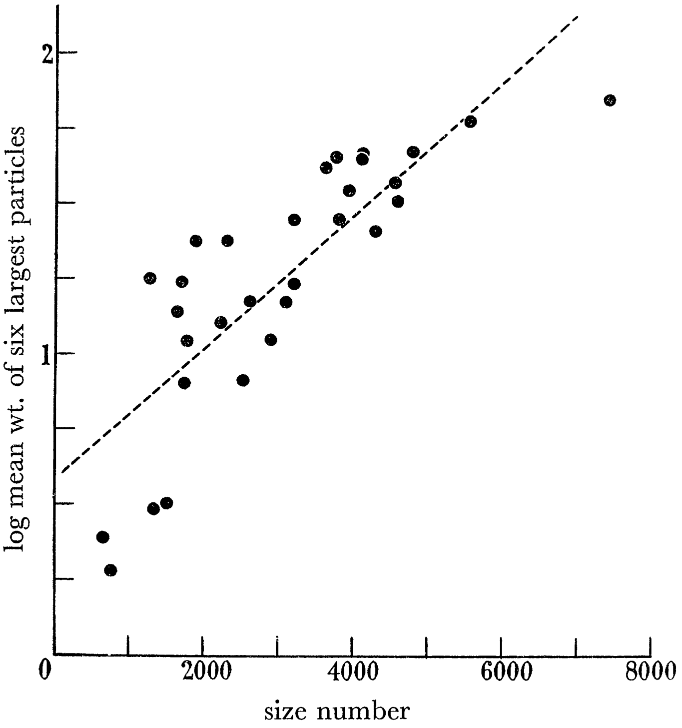


FIGURE 20. Graph to show particle-size selection in a sample of thirty specimens of *S. purpureus*. The logarithm of the average weight of the six heaviest particles lifted by the oral tube-feet of each specimen has been plotted against a size number obtained by multiplying length by breadth of each specimen (see Appendix, table 3). The calculated regression line has been dotted in.

(iii) *Echinocardium pennatifidum*, *E. flavescens*

Although the two specimens of each of these two shell-gravel species which I examined lacked many of their important spines, and consequently did not exhibit their normal burrowing activity, I was able to observe enough of their feeding behaviour in a glass-bottomed tank with a sprinkling of shell gravel in it to ascertain that they show a pattern of feeding behaviour closely similar to that of *S. purpureus*, also from shell gravel. The gut contents of one specimen of each species was examined, the specimens chosen being of closely similar dimensions. Both showed a selection for particle weight, and the average weight of the twelve heaviest particles from the gut of each was also closely similar (see Appendix, table 4).

(iv) *Brissopsis lyrifera*, *Spatangus raschi*

The feeding of these two urchins from muddy substrata was found to be closely similar to that of *E. cordatum*, the particles of mud being picked up, a cluster at a time, by the sticky disks and processes of their peristomial penicillate tube-feet. The particles were presumably wiped off on the inside of the grill of small spines round the mouth, though this was not actually seen. As in *E. cordatum* there can be no particle-size selection in these urchins, the maximum size of individual particles being far below that which can be lifted by tube-foot.

(v) *Echinocyamus pusillus*

This clypeastroid has a pair of large tube-feet in each ambulacrum round the mouth (figure 10*b*) which appear to function only while the animal is feeding. In the three specimens I observed feeding these touched particles of the substratum, and further work (Nichols 1959*c*) suggests that the particles were being tasted, after which the teeth rasped off the encrusting organic matter. There is also a pair of large spines in each interambulacrum round the mouth (figure 10*h*), and these appeared to be working in conjunction with tube-feet to hold the smaller gravel particles up to the mouth during the feeding operation. Particles which were lifted were held up for between 10 and 20 s only.

5. Discussion and further observations

The preceding observations show that there are marked differences between the modes of life and the structure of *S. purpureus* and *E. cordatum*, the two forms most studied. These include:

(*a*) Depth of burrowing and nature of the respiratory device.

(*b*) Number of tubes in the sanitary device, its mode of construction and maintenance, and its permanence.

(*c*) Mode of feeding.

(*d*) Number and arrangement of the fascioles.

(*e*) Shape and arrangement of the spines.

(*f*) Division of labour among the tube-feet.

(*g*) Depth of the anterior groove.

(*h*) Arrangement of the respiratory organs.

It will now be shown that these differences are controlled or influenced, among other factors, by the particle size of the substratum in which the urchins live, and are closely connected with the ciliary activity on their external surfaces. In each section *S. purpureus* and *E. cordatum* will be considered first, followed by the evidence offered by the other forms.

(*a*) *Depth of burrowing and nature of the respiratory device*

S. purpureus, a shell gravel and, where I have found it, an offshore form, does not burrow deeper than about 2 cm or so beneath the surface of the substratum. It appears from observations in aquaria (p. 364 above) that the normal ciliation of the body is sufficient to draw oxygenated water down through the large interstices between the gravel particles and over the respiratory surfaces; consequently, it is not odd that this urchin has no dorsal fasciole. *E. cordatum*, on the other hand, usually inhabits sandy beaches, and might be left high and dry in the sand at times by the receding tide if it burrowed only a few centimetres below the surface. It may be because of this, or some other unknown factor, therefore, that this form builds a long breathing funnel to its deep burrow (figure 16), and therefore needs an inner fasciole on its dorsal surface to help draw water down the funnel and across the respiratory surfaces. The petaloid shape of each respiratory ambulacrum of *Spatangus* (figure 12) is replaced by a funnel shape (figure 11), the line of the fasciole along its whole length being such as to direct the current straight into each funnel.

Though none of the other urchins studied could be induced to burrow, from the results obtained on *S. purpureus* and *E. cordatum*, it is highly probable that those equipped with dorsal fascioles and burrow-building tube-feet in their anterior ambulacra build respiratory funnels similar to *E. cordatum*. But it is extremely doubtful whether any burrow as deep as *E. cordatum*, since the degree of extension of their funnel-building tube-feet (p. 382 below) was observed to be much less.

There is a correlation between the strength of the dorsal fasciole and the number of funnel-building tube-feet used in conjunction with it, and this throws some light on the burrowing activity of these urchins. Four of the urchins studied have such an apparatus on their dorsal surfaces: *E. cordatum* has a wide inner fasciole (figure 1*d*) used in conjunction with about seventy penicillate tube-feet within it; *E. pennatifidum* has a very narrow inner fasciole (figure 3*d*) enclosing about six penicillate tube-feet; *E. flavescens* has a fasciole intermediate in width between the first two (figure 3*a*) enclosing about five penicillate tube-feet; and *B. lyrifera* has a wide peripetalous fasciole, and there are about thirty penicillate tube-feet in the dorsal region of the anterior ambulacrum. In order to estimate this correlation more precisely, some measurement of the strengths of the various fascioles in the different forms is required. As shown on p. 361 above, the strength of a fasciole is roughly proportional to its area, and this assumption is further strengthened by the fact that the clavulae (the ciliated spines of which a fasciole is composed) are of approximately constant size and density from species to species. Thus, a measure of the area of each fasciole is necessary.

Since the dorsal surfaces of the urchins are not flat, it is impossible to measure the area with a planimeter. Consultation with the National Physical Laboratory and the British Scientific Instrument Research Association revealed no instrument capable of measuring such an area directly, so a method was devised which involved covering the fasciole of a dried and denuded test with paper of a known weight per unit area, removing and weighing the paper. By direct proportion the area of the fasciole could be determined. The details of the method are as follows.

A strip of transparent sticky paper (music-mending tape) of area 10 cm^2 was washed for 10 min in water to remove the adhesive, dried for 10 min on a hotplate, then weighed accurately. This was done three times, using tape from different parts of the roll, and the average was taken. The tape was found to be remarkably uniform in weight, the three readings being identical to an accuracy of 0·1 mg. The dorsal surface of the specimen was covered with untreated tape and that not covering the fasciole was cut away with a sharp scalpel. The tape covering the fasciole was now removed, washed for 10 min to remove the adhesive, dried for 10 min and finally weighed. This method was repeated ten times on a single specimen, and the results were consistent to an accuracy of $\pm 5\,\%$. The funnel-building tube-feet enclosed by the fasciole were counted. In some cases this was difficult, since not all the pore-pairs present in the region bear functional or funnel-building tube-feet. For instance, in *E. cordatum* there is a region of up to fifty very small pore-pairs near the apical disk which examination of living specimens showed not to bear fully grown penicillate tube-feet. The point in the column of pore-pairs from which the tube-feet are functional is clearly marked, however, by an abrupt change in the size of the pore-pairs. From this point to that at which the inner fasciole passes across the anterior ambulacrum all the tube-feet are penicillate for funnel building. Likewise, in *B. lyrifera* there are about fifteen immature tube-feet adapically, the change to functional ones being marked by the point after which the pore-pairs are surrounded by ridges for the attachment of the tube-foot muscles. In *E. pennatifidum* and *E. flavescens* there is a region of about ten immature tube-feet adapically, then a region of about five or six penicillate tube-feet and finally a region of about ten non-penicillate tube-feet with very little extensibility, which can be assumed to be non-funnel-building. Each specimen was measured with vernier calipers and a size-number obtained by multiplying length by breadth.

Fourteen specimens of *E. cordatum*, fourteen of *B. lyrifera*, nine of *E. pennatifidum* and one of *E. flavescens* were examined using this technique, and the results, when plotted (figure 21) show three groupings: one for the sand-dwelling *E. cordatum*, one for the mud-dwelling *B. lyrifera* and one for the shell-gravel forms *E. pennatifidum* and *E. flavescens*. Regression lines representing the dependence of the average number of tube-feet per square centimetre (y) on the size-number (x) were fitted to each of the three groups, *E. cordatum*, *B. lyrifera* and *E. pennatifidum*, with the following results:

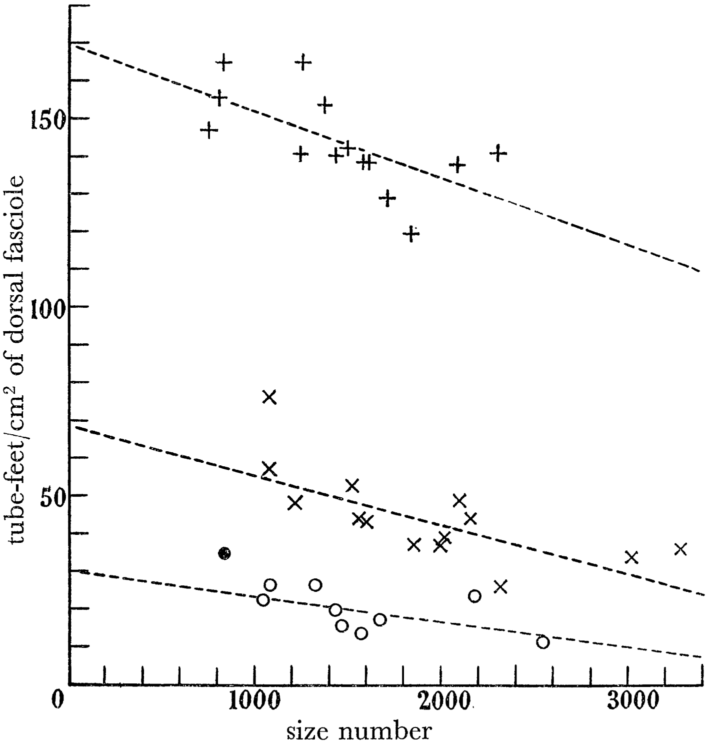


FIGURE 21. Graph to show the density of funnel-building tube-feet per unit area of dorsal fasciole in samples of *E. cordatum* from sand (+), *B. lyrifera* from mud (×) and *E. pennatifidum* from shell gravel (o) (Appendix, table 5, columns *a* and *d*). The regression lines have been dotted in. One specimen of *E. flavescens* has also been included (●).

group	equation of regression line	$s(b)$	$s(y.x)$
E. cordatum	$Y = 169{\cdot}25 - 0{\cdot}01760x$	$\pm 0{\cdot}00617$	10·28
B. lyrifera	$Y = 68{\cdot}52 - 0{\cdot}01306x$	$\pm 0{\cdot}00366$	8·64
E. pennatifidum	$Y = 29{\cdot}65 - 0{\cdot}006338x$	$\pm 0{\cdot}00314$	4·34

where $s(b)$ denotes the estimated standard error of the slope b of the line (coefficient of x in the equation), and $s(y.x)$ the estimated standard deviation of a value of y for given x. Assuming that the regression lines (dotted in on the graph) are linear, the slopes for *E. cordatum* and *E. pennatifidum* were tested against that for *B. lyrifera* and were found to be not significantly different ($P > 0{\cdot}5$ in each case), i.e. the true regression lines may be considered parallel. Only one specimen of the other shell-gravel form possessing a dorsal fasciole, *E. flavescens*, was available. This has been plotted on the graph for comparison, and lies very close to the group of *E. pennatifidum*. The graph shows, first, that in urchins which build respiratory funnels in any of the three substrata the bigger the animal the smaller the density of funnel-building tube-feet per unit area of the fasciole, and secondly, that urchins from different substrata separate out remarkably clearly in this feature.

That the difference in distribution on the graph is not due to differences in allometric growth is made clear by the graph in figure 22, which shows that in the sand-living *E. cordatum* and the mud-living *B. lyrifera* the regressions of the area of the dorsal fasciole, whether inner or peripetalous, on the size-numbers of the animals in each group are very similar, as shown in the following table.

group	equation of regression line	$s(b)$	$s(y.x)$	$\frac{\text{mean diff.}}{\text{S.E.}} = `t'$
E. cordatum	$Y = 0{\cdot}223 + 0{\cdot}000234x$	$\pm 0{\cdot}0000217$	0·03629	0·2184
B. lyrifera	$Y = 0{\cdot}016 + 0{\cdot}000330x$	$\pm 0{\cdot}000439$	0·1037	
E. pennatifidum	$Y = 0{\cdot}016 + 0{\cdot}000173x$	$\pm 0{\cdot}0000548$	0·0765	

The regression of the shell-gravel group has also been plotted on the graph for comparison, and the increase in area of the fasciole with increase in size is very much smaller than that of the other two groups. The difference between the regressions of the two nearly coincident groups was tested by means of 'Student's' *t*-test, and was found to be not significant. Thus, the bimodality of figure 21 must be due to a difference in concentration of burrow-building tube-feet per unit area of fasciole and not to the relative sizes of the fascioles. The concentration is of the order of 140 tube-feet/cm^2 of fasciole for *E. cordatum*, and 45/cm^2 for *B. lyrifera*. The shell-gravel forms group in the region of 20 tube-feet/cm^2. The factors which may give rise to this distribution will now be discussed.

Consider the same urchin burrowing to the same depth in different substrata. If this urchin built a respiratory funnel, then it is likely that different amounts of mucus would be required to maintain the funnels in the different substrata, because of differences in coherence, but the same fasciole could draw water down the funnel irrespective of the nature of the substratum. Thus, the distribution on the graph (figure 21) may be due to the different nature of the substrata. In the case of shell gravel some cohesion will be effected by the interlocking properties of the particles; in the mud some will be effected by the flocculation of colloidal particles by sea water; but in sand there are no physical cohesive properties, so it would be expected that more mucus would be needed to hold it together. More tube-feet per unit area of fasciole would therefore be expected to occur in *E. cordatum*, the sand-dwelling form.

If, now, the same urchin burrowed to twice the depth in each of the different substrata, then in each the strength of fasciole needed in theory would be nearly the same as that required at half the depth (the volume of water to be moved being the same), though in practice the greater eddying effect of water in the longer funnel would necessitate a stronger fasciole; the amount of mucus needed to build a respiratory funnel, however, is likely to be considerably greater than twice the original amount, since to reach the topmost sections of the funnel and line them adequately with mucus, the tube-feet would waste a certain amount on the previously excavated lower sections which probably already have sufficient covering (see figure 17). I am assuming that mucus is extruded the whole way up the funnel as each tube foot is extended for excavation; some justification for this assumption is given below (p. 382). Thus, in addition to the nature of the substrata the distribution on the graph may be due to the depth of burrowing. This feature of their activity has not been measured directly for all the urchins studied, since some could not be induced to burrow at all. Fortunately, however, some estimate of the depth of burrowing could be obtained as follows.

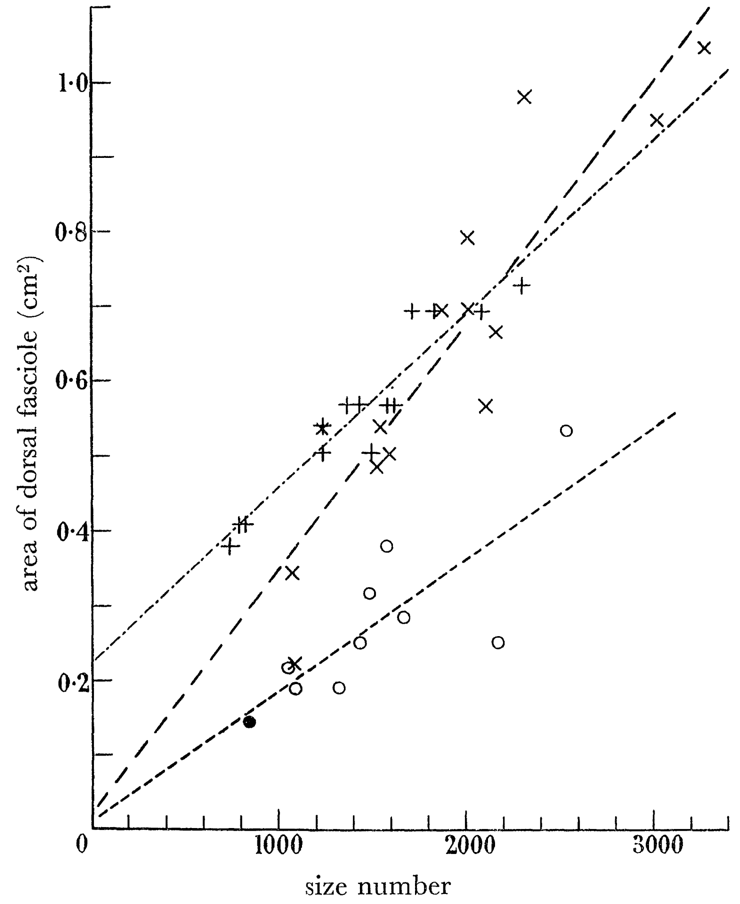


FIGURE 22. Graph showing the regressions of the areas of the dorsal fascioles on the size numbers (length by breadth) in samples of *E. cordatum* (+—·—·), *B. lyrifera* (×———) and *E. pennatifidum* (○ - - -) (Appendix, table 5, columns *a* and *b*). The calculated regression lines have been dotted in. One specimen of *E. flavescens* has also been included (●).

Under conditions of oxygen shortage (failure to aerate the tank for some hours) it was found that specimens of *E. cordatum* which were not burrowing could be induced to extend their dorsal funnel-building tube-feet. The length of extension of the penicillate tube-feet near the ambitus was only 4 to 6 cm, but that of the functional tube-feet nearest the apical disk was up to 18 cm, the depth at which I have observed them burrowing. Under similar conditions specimens of *B. lyrifera* extended the tube-feet of their adapical region only up to 6 or 8 cm, and it seems likely that this is the maximum depth to which they can burrow. Thus, specimens of *E. cordatum* probably burrow to about twice the depth of specimens of *B. lyrifera*, and if this were the only factor the area of fasciole would be expected to be slightly greater in *E. cordatum*, and the number of funnel-building tube-feet very much greater than in *B. lyrifera*. The number of these tube-feet per unit area of fasciole in *E. cordatum* would therefore also be expected to be greater than in *B. lyrifera*.

Specimens of *E. pennatifidum* and *E. flavescens* under similar conditions of oxygen shortage both extended their funnel-building tube-feet at best only to reach about 2 cm, i.e. just above the dorsal tuft of spines (figure 6*c* and *f*), but this is not likely to be the maximum depth to which they can burrow, for the following reason. If they are burrowing in clean shell gravel it seems likely that sufficient water for respiration will be drawn down the interstices between the particles (as in *S. purpureus*, figure 12), and therefore, from evidence on the activity of *E. cordatum* that their dorsal funnel-building tube-feet are not stimulated into activity, even when the dorsal spines are below the surface. If, however, they are burrowing in substrata which do not have the large interstices, their tube-feet are stimulated into activity, and probably keep open a respiratory funnel by working in conjunction with the dorsal tuft of spines, and perhaps on their own for a centimetre or so above the tuft. It is unlikely, therefore, that these animals can burrow as deeply in finer substrata as they can in coarse; but it would appear that they *can* inhabit the finer grounds. *S. purpureus*, on the other hand, is only equipped to maintain a respiratory funnel, if it needs to at all, by using its spines against the particles of a coarser substratum, and is likely, on this account, to be restricted to clean shell gravel. These theoretical conclusions are supported by the observed occurrence of these urchins, and probably explain certain differences in their known range of habitats. Of the three, *S. purpureus* is almost always found in clean shell gravel (*Plymouth Marine Fauna* 1957; Jones 1951), but *E. pennatifidum* and *E. flavescens* have been found in a range of substrata from their most usual habitat, clean shell gravel (Allen 1896; Hunt 1925; and records taken during the present work), to muddy shell gravel (Jones 1951), and even muddy sand (one specimen taken off Ardlamont, Arran Basin, during the present work).

The third factor which must be considered is the extrusion of mucus. In the argument above it was assumed that mucus is extruded on the upward journey of each tube-foot. The histology of the funnel-building tube-feet provides evidence in support of this assumption. It is shown elsewhere (Nichols 1959*b*) that the mucus glands in these tube-feet of both forms are concentrated on the disks and on the inside only of the finger-like processes; it seems unlikely, therefore, that the mucus is extruded as the tube-foot is withdrawn, when the non-glandular part is more likely to touch the walls of the funnel. Also, as was stated on p. 370 above, the individual mucus glands of all the spatangoid burrow-building tube-feet which I have examined histologically have been found to possess either thin muscle fibres running between them, or a sheet of muscle in the disk, and it is likely that these act in squeezing out the mucus. Whether the mucus is exuded all the way up the funnel or whether the muscles act at a certain point in the extension would be difficult to test experimentally, but it does seem most likely, both in the funnel building and in the sanitary tube-building tube-feet, that the mucus is exuded as soon as the tube-foot starts to extend. It would otherwise be difficult for them to maintain the proximal parts if they needed repair.

One further factor may have a bearing on the distribution in the graph. Of the four species building respiratory funnels three (all of the genus *Echinocardium*) usually burrow in fairly pure substrata, but one (*B. lyrifera*) inhabits thick blue mud in which sulphuration would be expected. It is likely, therefore, that this latter urchin requires a faster flow of water through its burrow to prevent fouling, and that in consequence its fasciole area is proportionately higher. This would mean that the number of tube-feet per unit area of fasciole would be comparatively lower than in the other urchins, so that possibly the grouping of *B. lyrifera*, if it were not complicated by this factor, would have a higher ordinate on the graph.

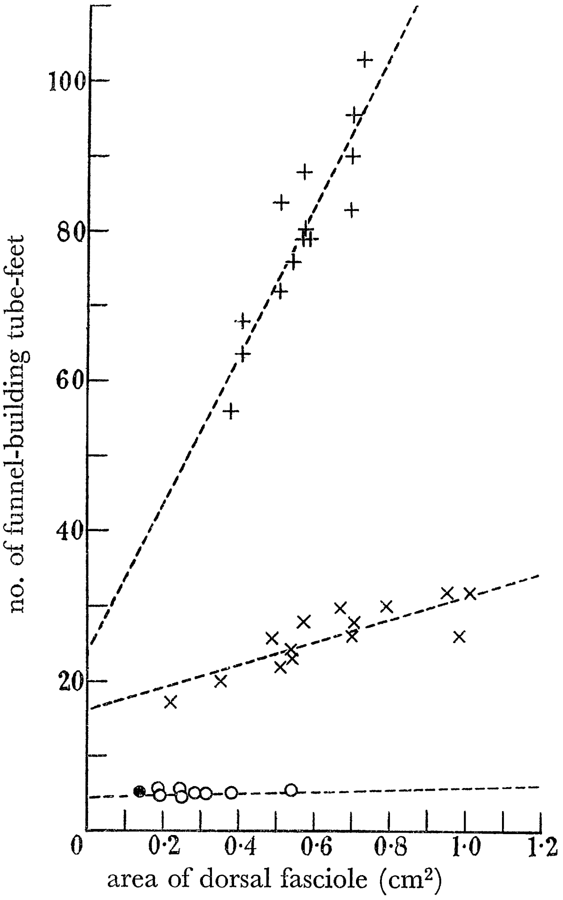


FIGURE 23. Graph of the number of funnel-building tube-feet plotted against the area of the dorsal fasciole in samples of *E. cordatum* (+), *B. lyrifera* (×) and *E. pennatifidum* (o) (Appendix, table 5, columns *b* and *c*). The calculated regression lines have been dotted in. One specimen of *E. flavescens* has also been included (●).

To summarize, it seems likely that the grouping of the species on the graph (figure 21) may be due to any of the following: the different physical and chemical natures of the substrata in which the urchins burrow, the depth to which they burrow, the mechanism of mucus extrusion, and the amount of mucus produced per tube-foot. Whatever the exact quantitative estimate of these interacting factors may be, it seems reasonable to conclude that the grouping is in the direction expected.

A similar grouping is shown in the graph in figure 23, in which regression lines representing the dependence of the number of funnel-building tube-feet per specimen (y) on the area of the fasciole (x) were fitted to each of the three groups with the following results:

group	equation of regression line	$s(b)$	$s(y.x)$
E. cordatum	$Y = 23{\cdot}71 + 99{\cdot}91x$	± 13·5	5·515
B. lyrifera	$Y = 16{\cdot}44 + 14{\cdot}78x$	± 3·053	2·698
E. pennatifidum	$Y = 4{\cdot}60 + 2{\cdot}12x$	± 1·275	0·399

The graph, in addition to emphasizing that in each group the larger the fasciole the more tube-feet must be present to work in conjunction with it, shows that the rate of increase in the ratio of number of these tube-feet to fasciole area in *E. cordatum* is greater than that in *B. lyrifera*, which is itself greater than in *E. pennatifidum*. The mechanism of this, in part at least, appears to be the mode of formation of the anterior ambulacra. Hawkins (1913) attributes the increase in number of anterior ambulacral tube-feet, during the life of *E. cordatum*, to the fact that in this species new coronal plates are developed throughout its life in Ambulacrum III only, increase in size in the other regions being brought about by an increase in size of the plates already in existence. My observations show that there is an increase in number of the anterior ambulacral plates in *B. lyrifera* also, but the increase is much less than in the case of *E. cordatum*, as shown in the graph in figure 24 and table 5, column *f* (Appendix). Regression lines were fitted to this graph also, with the following results:

group	equation of regression line	$s(b)$	$s(y.x)$
E. cordatum	$Y = 91{\cdot}6 + 0{\cdot}02437x$	± 0·003161	5·268
B. lyrifera	$Y = 29{\cdot}9 + 0{\cdot}00525x$	± 0·000693	1·638

Although there is an increase in the number of functional tube-feet of the anterior ambulacra in both *E. cordatum* and *B. lyrifera* (see Appendix, table 5, column *c*), in *E. cordatum* new plates are produced at the apical disk as the undeveloped tube-feet become functional for funnel building, but in *B. lyrifera* production of new plates does not keep pace with the rate at which undeveloped tube-feet become functional. This is shown in figure 25, where the functional funnel-building and the undeveloped tube-feet of both *E. cordatum* and *B. lyrifera* have been plotted on the same graph. The rate of increase of functional tube-feet in *E. cordatum* is greater than in *B. lyrifera*, as shown by the unbroken regression lines, but whereas the calculated regression for the undeveloped tube-feet of *E. cordatum* is parallel to the x-axis, that for *B. lyrifera* has a negative regression coefficient. The results of the calculations for this graph are as follows:

group	equation of regression line	$s(b)$	$s(y.x)$
E. cordatum functional tube-feet	$Y = 44{\cdot}88 + 0{\cdot}0241x$	± 0·003557	5·928
E. cordatum undeveloped tube-feet	$Y = 46{\cdot}72 + 0{\cdot}000292x$	± 0·003614	6·024
B. lyrifera functional tube-feet	$Y = 14{\cdot}52 + 0{\cdot}00600x$	± 0·000924	2·182
B. lyrifera undeveloped tube-feet	$Y = 18{\cdot}73 - 0{\cdot}00247x$	± 0·000828	3·083

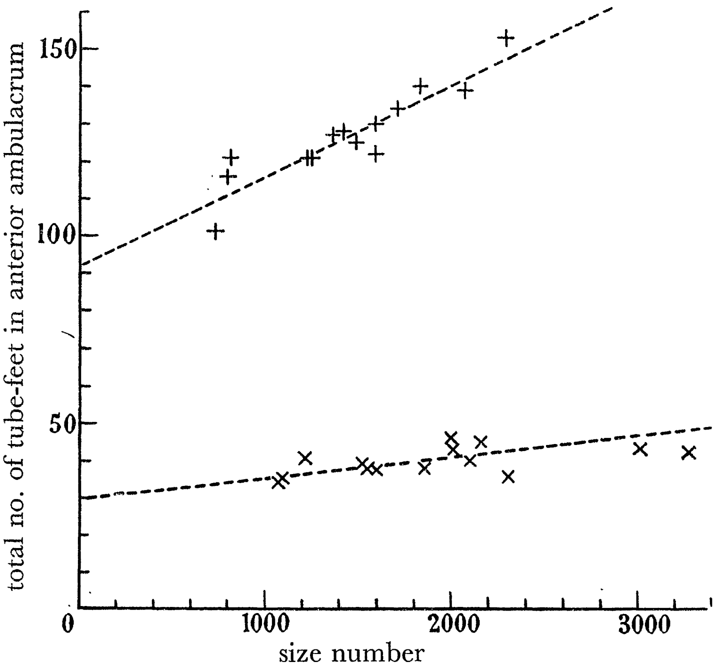


FIGURE 24. Graph of the total number of tube-feet in the dorsal part of the anterior ambulacrum in specimens of *E. cordatum* (+) and *B. lyrifera* (×) plotted against the size-numbers (Appendix, table 5, columns *a* and *f*). The calculated regression lines have been dotted in.

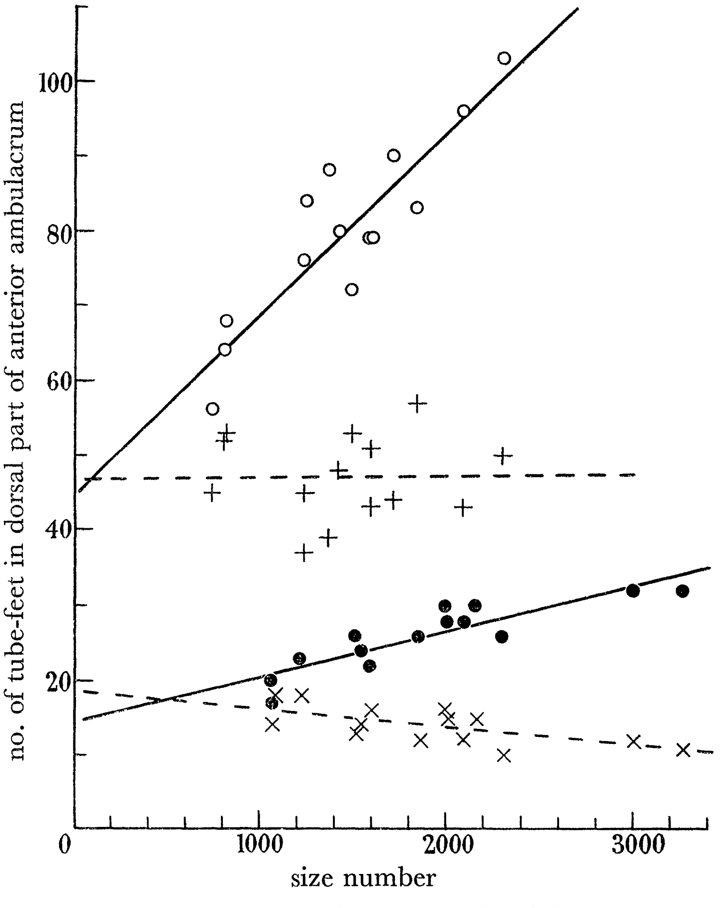


FIGURE 25. Graph of the number of functional funnel-building (○) and the undeveloped (+) tube-feet in the anterior ambulacra of *E. cordatum* and *B. lyrifera* (functional ●, undeveloped ×) plotted against the size number (Appendix, table 5, columns *a*, *c* and *e*). The calculated regression lines have been drawn in, the unbroken lines representing the functional tube-feet and the broken lines the undeveloped tube-feet of both forms.

The connexion between the maintenance of the burrow and the type of substratum is further emphasized by the differences in burrowing behaviour between specimens of *E. cordatum* from slightly different substrata described above. It seems likely that lack of oxygen is the stimulus causing an urchin to build a respiratory funnel to the surface; particles constantly falling in to block the funnel, as happens in purer sand, stop the flow of oxygenated water over the respiratory surfaces of the animal, and stimulate the more anterior of the penicillate tube-feet of the dorsal region of Amb. III to start building a new funnel, which is produced at first as a vertical excavation immediately above the front part of the animal (figure 17*a* and *d*). In contrast, a tube built in the more mouldable and coherent sand-with-clay does not fall in so easily, the flow of oxygenated water is not restricted, and the animal in this substratum is not stimulated to start building a new vertical funnel. Instead the more posterior of the tube-feet, which are extended to give periodic attention to the respiratory funnel as the animal moves forward, slide into the same vertical funnel, even if this means travelling slightly backwards at first (figure 18*d*). When the animal has moved still further forward, the maintaining tube-feet still slide into the backwards-directed tube, and thence into the vertical funnel (figure 18*e*). The result, in time, is to produce a horizontal connexion from the dorsal surface of the animal to the vertical respiratory funnel (figure 18*f*). I have observed this situation in urchins excavated on the beach at Derby Haven.

I have noticed that an urchin deprived of its oxygen will come to the surface of the substratum after some time. The respiratory funnel of a burrowing specimen of *E. cordatum* was systematically filled in with sand every time it was opened by the tube-feet. At first the interval between blocking up and re-opening was quite long (about 10 to 15 min), which is the normal interval, as mentioned above. After five or six attempts at re-opening, however (that is, after about 1 h), the interval gradually became shorter, and after $2\frac{1}{2}$ to 3h the tube-feet re-opened the funnel every 2 to 4 min. For the first hour the same funnel was re-opened, but subsequently the urchin started to move forward and opened a series of funnels every 2 cm or so at first, later decreasing to about 1 cm. Five such funnels had been opened when, after a little over 3 h, the urchin's dorsal tuft of spines broke surface, and thereafter kept a wide hole open.

The urchins used in this work were normally kept in aquaria with circulating sea water, and the water was kept well aerated. On one occasion the circulation and aeration were turned off for 24 h. At the end of this period the three specimens of *E. cordatum* which had been burrowing in the tank were on the surface of the substratum. Two of them had moved to the walls of the tank and were pushing against them, their front ends being forced up the sides of the tank. Strong metachronal waves could be seen passing down the plastron, so that it looked as though these two specimens were trying to climb the walls. The penicillate tube-feet round the mouth, although not actively feeding, were pressed against the walls as though they were clinging to them. MacBride (1935) had clearly witnessed an urchin in a similar distressed state, when he described a half-grown *E. cordatum* 'confined in a square glass tank' in which it was 'clinging to the walls with its tube-feet, using these in the same manner as does the regular sea-urchin'.

Another urchin from a sandy substratum, *S. raschi,* is not equipped to build a respiratory funnel, nor does it seem likely that it ever needs to, since, as described on p. 373 above, it probably ploughs through the substratum with most of its corona exposed above the surface. In this way the respiratory tube-feet are bathed in the currents on the sea bottom. Consequently, the sanitary device of *S. raschi* is only concerned with faecal waste and can be severely reduced, whereas those of total burrowers such as *S. purpureus* and *E. cordatum* help to get rid of respiratory water as well, and must be much stronger. This is in fact the case, the fasciole of *S. raschi* being single, and small at that, so that most likely only a single tube is built, even though the urchin is considerably larger than any other British burrowing spatangid.

(*b*) *Nature of the sanitary device*

Here again, the differences in substratum appear to hold the key to the type of burrow constructed. *S. purpureus* builds a fairly permanent double tube, and is equipped to provide a current down each limb of it, whereas *E. cordatum* builds only one very transient tube and its subanal fasciole is almost annular, to provide a current down this one limb only. The average size of adults of *S. purpureus* is about twice that of *E. cordatum*, and since the activity they display is very similar, more waste would have to be removed from the vicinity of *S. purpureus*. Correspondingly, the sanitary tube would need to be much bigger, but the engineering difficulties involved in the construction and maintenance of such a tube appear to make this impossible: the mucus 'mortar' would be unable to support large gravel particles in the roof, though it would be able to bind the same particles into the roofs of two tubes, side by side, which are small enough to utilize the interlocking properties of the particles, and which consequently require less mucus to hold them in place. The subanal tube-feet can therefore be divided between two tubes, whereas in *E. cordatum* they are all needed to supply the necessary mucus for the walls of one.

The other two urchins normally, though not invariably, inhabiting shell gravel, *E. pennatifidum* and *E. flavescens*, are each equipped to build a single tube only, and it may well be that their tolerance of a range of substrata (see p. 382 above) may be due to their ability to build a respiratory funnel (in contrast to *S. purpureus*), combined with their reliance on a single sanitary tube (as in *E. cordatum*). It may also be a consequence of this that their size is kept down to around that of *E. cordatum*.

B. lyrifera, inhabiting mud, also apparently builds a double tube and this may well be in part due to the help given by the substratum (flocculation of colloidal particles) to the building of the burrow. This is the only British urchin able to produce a respiratory funnel and a double sanitary tube, and these factors probably contribute to its singular ability among the urchins to colonize in large numbers the vast deposits of blue mud in the deeper waters.

The nature and size of the sanitary device in *S. raschi* has already been discussed (see this page); a comparison with other forms is scarcely valid, since this is only a partial burrower and does not rely on the device for ridding the burrow of respiratory water.

(*c*) *Mode of feeding*

The occurrence of particle-size selection in *S. purpureus* but not in *E. cordatum* has been discussed above (p. 375). In addition, there are features of the feeding common to both which are not directly affected by the nature of the substratum, and which have a marked effect on other functions of the animals. When either is burrowing fairly near the surface, particles of the substratum can be seen falling into the dorsal funnels, as described on p. 373

and other particles may be brought down from the surface accidentally by the tube-feet. These particles from the surface, with a covering of organic matter, are clearly a valuable source of food, and although most of the substratum particles are incorporated into the walls of the burrow, many of the minute particles of organic matter must become incorporated in the streams of mucus secreted on the dorsal surface of the animal and moved by its ciliary action. Some must pass down the anterior side of the body, particularly down the anterior groove, to the mouth (figure 7*a*, *b*, *d* and *e*). In the case of *E. cordatum* the forward current in the dorsal part of the anterior ambulacrum is augmented by the portion of the inner fasciole in that region (figure 7*d*). Thus, in all spatangids studied ciliary action would seem to be quite an important part of the feeding process. However, were the current down the anterior groove to originate at the apical disk, some of the genital products, when extruded, would pass down to the mouth. This is avoided by the apical eddy of currents found on all the forms studied (see p. 359 above), which tends to waft all the gametes towards the posterior side of the body (figures 7*a* and *d*; 8*a* and *d*; 9*a* and *d*). This precautionary measure has been verified directly in one of the urchins studied: a specimen of *B. lyrifera* in a shallow tank was seen to spawn and 10 min later the apical region was clear, and the genital products were on their way towards the subanal fasciole.

(*d*) *Number and arrangement of fascioles*

The differences between the subanal fascioles of the two forms have been described above, and it has been pointed out that a dorsal fasciole occurs in *E. cordatum* but not in *S. purpureus*. A third, the anal fasciole, is also possessed by *E. cordatum* but not *S. purpureus* (compare figures 1*c* and *f*). This appears to have the function of augmenting the surface ciliation in the anal region and thus helping to remove extruded waste matter. The current drawn down the respiratory funnel by the inner fasciole of *E. cordatum* passes over the surface of the animal and is helped along the sanitary tube and away from the animal by the subanal fasciole. The anus, therefore, opens into a blind part of the burrow which is not directly in the current (figure 16), and would become fouled very easily. The anal fasciole, beating outwards (figure 7*f*), helps to maintain a current in this part of the burrow and to pass these waste products into the main stream. Possibly the currents on the periproct of *S. purpureus* (figure 7*c*) and *S. raschi* (figure 8*c*), beating towards the anus, replace an anal fasciole by producing a resultant current away from the animal and out between the interstices of the gravel. Also, the currents produced by the surface ciliation for respiration (figure 12) are not restricted to a respiratory funnel, but filter down through the interstices of the gravel above the whole animal. These currents would also help to remove faecal matter.

Of the other spatangid urchins only *E. pennatifidum* and *E. flavescens* possess anal fascioles, and here again this is likely to be a device for clearing the anal region of faecal matter when these urchins are burrowing in a sandy substratum.

(*e*) *The shape and arrangement of spines*

The structural differences between the spines of the two main forms, *S. purpureus* and *E. cordatum*, also reflect the difference in substrata. The plastron spines of *E. cordatum* are markedly spatulate to obtain purchase on sand, whereas those of *S. purpureus* are only slightly flattened distally to work against the larger gravel particles. In both urchins the actual forward component is provided by the spines of the plastron; these are not essential for descending into the substratum, since their removal in two specimens of *E. cordatum* and one of *S. purpureus* did not hinder their burrowing. There was no appreciable difference between initial burrowing in these and in normal urchins, except that whereas normal ones sometimes moved forward about a centimetre before they disappeared, these specimens remained in the same place; neither did they move forward when they were completely buried.

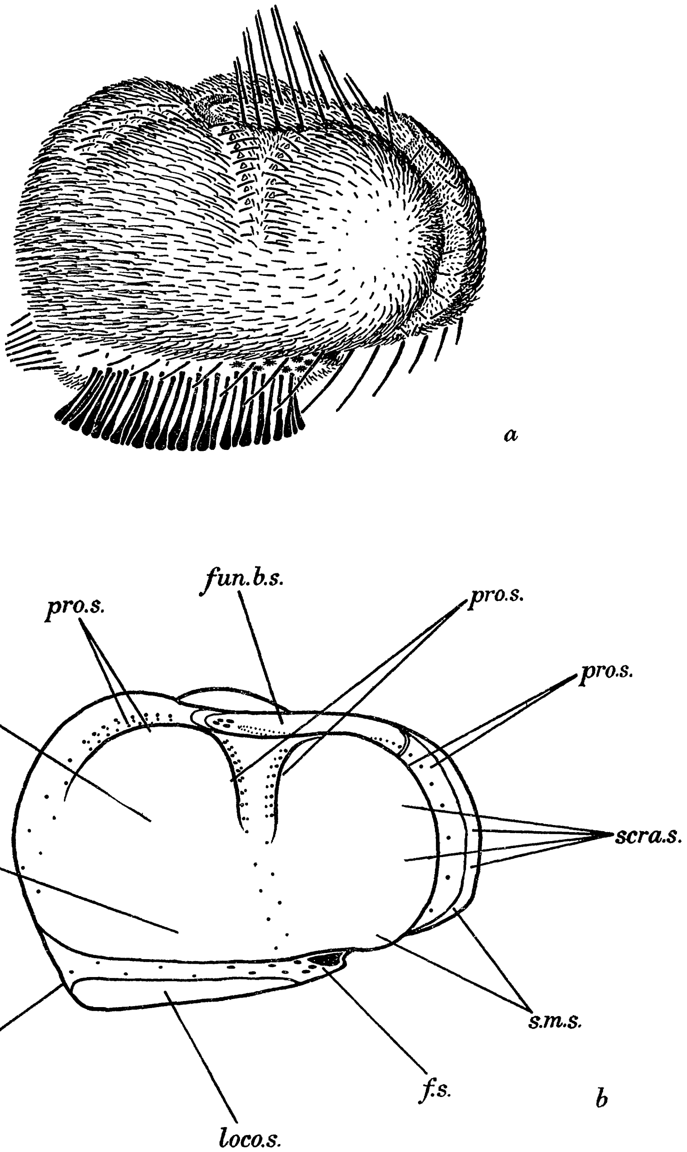


FIGURE 26. Diagram to show the main functions of the spines in various regions of the test of *E. cordatum*. This has been taken as an example of all the spatangids studied; there is only slight variation from this pattern in the others. (*a*) The test with its spines and tube-feet intact, (*b*) denuded of spines and tube-feet to show the regions of the test from which the spines arise.

During burrowing, the medium-sized spines in the anterior region of the animal scrape the front wall of the burrow (see figure 26) so that material is constantly being passed under and round the animal by the sand-moving spines to the posterior side, where it fills in the burrow again, except, of course, for the sanitary tube or tubes. It seems unlikely that much of this material is passed over the dorsal surface of the animals, since in both, first, the spines in this region are small in comparison with those in the ventral and ambital parts of Interambulacra 1, 2, 3 and 4; secondly, the main trend of ciliary activity, which must help the sand movements, is downwards and backwards (figure 7), and thirdly, a burrow of *E. cordatum* excavated after dropping red ballotini into the dorsal funnel showed that this, and presumably the sand also, was concentrated mainly in the bottom part of the burrow.

I have noticed, particularly in *S. purpureus*, that more material passes backwards down the periplastronal areas than either across the plastron itself or the more lateral regions of the body. In fact, in both forms these areas may well provide the main pathways for the transfer of material which is passing backwards, since no medium or large spines occur in them. It is interesting to note that Tornquist (1911) ascribed this function to the fascioles in *Brissus unicolor* (another spatangid), among which he included the periplastronal areas, remarking in support of this that the subanal fasciole of a specimen taken from the sand was always full of sand, a phenomenon also noticed by von Uexküll (1907) on *E. cordatum.* In *Brissus unicolor* the periplastronal areas are indeed very narrow and superficially like a fasciole, but without the characteristic spines, and sand probably does pass along them; but the collection of sand at the fascioles, which I also have observed in *E. cordatum* and *Brissopsis lyrifera*, is due to the fact that the fasciole spines (clavulae) do not plaster sand particles into the walls of the burrow, as the other spines do, yet their club-shaped ends contain mucus glands (Hamann 1887; Gandolfi-Hornyold 1910; confirmed by my own observations) and therefore some particles collect on them. However, it seems very probable that the function ascribed to the periplastronal areas by Tornquist was correct.

Many spines on the dorsal surface, and some of those at the anterior end, appear to have a protective function forming arches over the ambulacra (figure 26). The medium-sized spines bordering the anterior ambulacrum form the outer, single arch over the sensory tube-feet of this region (figure 4*a*, *b*, *d* and *e*), whilst other medium-sized spines arch over the respiratory parts of the other ambulacra. In the diagrams in figure 4 these have been shown only on *E. cordatum* (figure 4*d*) for clarity; a similar arrangement is found in *S. purpureus.* All the spatangids studied have this arrangement, but it is more pronounced in *B. lyrifera* than in any of the others, as shown partially in figure 5*d*, *e* and *f*. Here, even the sensory tube-feet on or near the ambitus are protected by an arcade of spines. This may reasonably be regarded as an extra precaution for a mud-dwelling form, whose ambulacra would otherwise become clogged while it was burrowing.

(*f*) *Division of labour in the tube-feet*

The activity and mode of operation of the burrow-building and feeding penicillate tube-feet have been discussed fully above, but one function of the tube-feet which has not been mentioned is that of sensation. All the tube-feet, with the possible exception of the respiratory organs, are sensory to some extent. It was shown on p. 374 that the oral tube-feet show one pattern of activity if they collect a particle or particles of the substratum during an extension, and another if they do not. This was not shown by the burrow-building tube-feet, which continue their activity irrespective of whether sand adheres to them or not, although extended burrow-building tube-feet of *E. cordatum* retracted rapidly when touched. Some tube-feet of every ambulacrum, however, are reduced and apparently act solely as sensory organs. These are found chiefly round the ambitus and within the periplastronal areas (figure 1), although in *S. purpureus* the dorsal part of the anterior ambulacrum is also sensory. I have noticed that a specimen of *S. purpureus* placed on the surface of the gravel will sometimes explore the surroundings with its ambital and periplastronal sensory tube-feet. These may be extended to 3 cm or more until a solid object is touched. Often the disk of a tube-foot would adhere to the object for a few seconds, presumably by a secretion of mucus from the disk, until the adhesive gave way when the tube-foot contracted. Ambital sensory tube-feet of all five ambulacra were often extended simultaneously during this exploration, or individual tube-feet were active for a short period (about 2 to 5 min) each. The sensory tube-feet of each ambulacrum, adjacent to the oral penicillate tube-feet, were always fairly active during feeding, extending to about 3 cm at times to explore the region round the mouth. This extension was not always at right angles to the test: sometimes the sensory tube-feet thrust between the bases of the spines moving parallel to the surface of the animal. I have even seen one of these captured by a pedicellaria, though it slipped quite easily from between its jaws.

(*g*) *Depth of the anterior groove*

It has already been mentioned (p. 387 above) that some urchins in both shell gravel and mud build double subanal tubes, and also (p. 380 and figure 21) that those shell gravel and mud forms with dorsal fascioles have a similar density of tube-feet working in conjunction with them. These facts strongly suggest a similarity between shell gravel and mud as building materials, and it has already been suggested that this may be due to the interlocking properties of the shell-gravel particles and the flocculation of the colloidal particles in the mud. This similarity is further emphasized by the depth of the anterior grooves. Both *E. cordatum* (figure 1*d*) and *S. raschi* (figure 2*a*), from sand or sandy mud, have deep anterior grooves, while the other urchins, from shell gravel and mud (*S. purpureus*, figure 1*a*; *E. pennatifidum*, figure 3*d*; *E. flavescens*, figure 3*a*; and *B. lyrifera*, figure 2*d*) have shallow grooves. Here again, therefore, it seems as though it is easier for the shell gravel and mud forms to maintain a tube from the dorsal surface round the anterior ambitus to the ventral surface than for the sand forms to do the same; presumably in sand it is necessary for the spines to arch over a groove and make a roof to it, rather than for the animal to rely on the spines bordering the anterior ambulacrum to make a tube between the front end of itself and the sand into which it is digging.

(*h*) *Arrangement of the respiratory organs*

As pointed out above, the respiratory ambulacra in *E. cordatum* are arranged in a funnel shape, whereas those of *S. purpureus* are petaloid. This has been related to the presence in the former of a dorsal fasciole to augment the normal body ciliation in drawing water down the respiratory funnel. It will now be shown that the arrangement of the actual respiratory tube-feet and their angle to the long axis of each ambulacrum also reflects this difference.

In figure 11 the respiratory currents down Amb. I and II of *E. cordatum* are shown in detail. It can be seen that the currents between the individual tube-feet are deflected sharply from the line of flow down the long axis, even, in many cases, at right angles to it. Only at the distal end of the ambulacrum, if at all, does the angle become obtuse. In *S. purpureus* (figure 12) the flow between the individual tube-feet is more gentle: towards the distal ends of the ambulacra the lines of pore-pairs converge more, and more of them are set at an obtuse angle to the main line of flow. This situation is clearly the most advantageous for an urchin relying on the ciliation of the body for its respiratory currents, since it brings the maximum number of respiratory surfaces into the stream of oxygenated water; most of the cilia providing these currents are located in the dorsal interambulacra and in those parts of the dorsal ambulacra between the respiratory organs and the ambitus, and the arrangement of the pore-pairs is exactly as would be expected, even to the extent of having quite a large number of small, and presumably non-functional, tube-feet adapically (see figure 1*a*), where there would be insufficient cilia adjacent to them to provide the necessary current.

The situation in *E. cordatum*, however, is more complicated. It is quite clear that a funnel arrangement is better where there is a dorsal fasciole, but why the angle of the pore-pairs is so sharp distally is not immediately evident. It seems most likely that two factors are important here: first, efficient burrowing requires a large surface area of spines near the ambitus for the movement of sand, and therefore space for the respiratory organs is restricted. The result is that the two columns of respiratory tube-feet occupy as little surface area as possible, and, while still maintaining the funnel near the apex, are brought close together distally. Secondly, were the angle of the pore-pairs to the long axis more obtuse, their columnar arrangement would mean that the passage between any two of the more distal tube-feet would be partially masked by the upper tube-foot; hence, they lie almost at right angles down their whole length. Evidence in support of these factors is provided by the posterior halves of Amb. I and V (see figure 11, which shows this only in Amb. I): because they lie adjacent to the anal region and are not limited by important spines nearby, the tube-feet in these halves are arranged in the least columnar manner of all, and the distal tube-feet are set at a more obtuse angle than any of the others. In the case of Amb. II and IV important spines lie on either side of them, and so this rather better arrangement is not possible.

The above remarks have dealt almost solely with the spatangoid sea-urchins. The tiny clypeastroid *Echinocyamus pusillus*, also studied, bears only minor resemblance in structure and mode of life to the spatangoids, as was pointed out in § 4 'Observations'. There are no fascioles, the larger spines are all similar in morphology and activity, except for a pair in each inter-ambulacrum round the mouth (figure 10*h*), and there is less division of labour among the tube-feet. There are, however, important points of similarity, the main ones being: (*a*) the presence of a modified apical eddy (see figure 10*d*), and (*b*) the arrangement of the respiratory organs.

In this urchin the apical eddy, as in spatangoids, appears to be present in order to ensure that the genital products are wafted away from the animal and do not get carried into the mouth. Although no currents were seen passing into the mouth (see also Gislén 1924), it is quite possible that particles falling on to the dorsal surface of the urchin, particularly the anterior part, are brought round to the ventral (oral) surface by ciliary action (figure 10*d* and *e*) and may be taken into the mouth in the same way as the fragments rasped off by the teeth. A histological study of this urchin (Nichols 1959*c*) has shown that the proximal part of the gut is heavily ciliated, and inward currents are likely to be produced on the inside of the teeth, to take up any fragments rasped off the particles of the substratum. This could be the fate of the genital products if they were to pass over the mouth also.

The remarks on spatangoids above (p. 392) concerning the arrangement of the columns of respiratory tube-feet on the dorsal surface also apply to this clypeastroid. Even those respiratory tube-feet close to the apex are inclined at a slightly obtuse angle (100 to 110°) to the long axis of the ambulacrum, and this angle increases to a maximum of about 135° at the distal end (figure 10*a*). From this point round the ambitus to the mouth each ambulacrum consists of many accessory tube-feet which have been shown (p. 374 above) to hold sand and small gravel particles on the animal for concealment. The importance of these tube-feet can be inferred by the number on each individual. Some may even be found on or between those ambulacral plates bearing respiratory tube-feet (figure 10*a*), so that even this region of the urchin can be concealed. A few only are necessary here, since a particle on top of the urchin can be kept in place by comparatively few tube-feet, but to pick up such a particle and pass it upwards and over the ambitus to the dorsal surface would not be so simple and would require a far greater density of tube-feet for the purpose. The occurrence of such accessory tube-feet between the two columns of respiratory ones possibly accounts for the fact that the petals are extremely broad and do not converge to any extent. Here again, it appears as though the expected balance has been set up between the number and arrangement of the solely respiratory tube-feet and the other needs of the animal.

6. COMPARISON OF RESULTS WITH THOSE OF PREVIOUS AUTHORS

One of the first descriptions of the initial burrowing of a spatangid is due to Osler (1826), who watched *Echinocardium cordatum* (which he called 'the Spatangus') burying itself in sand. Following a description of the arrangement and motility of the various spines (some of which is rather confused and difficult to reconcile with the present work), he explains how the plastron and lateral spines throw up the sand at the sides, until the animal has sunk low enough to allow this sand to flow back across it. He remarks that the long dorsal spines, arranged as a crescent-shaped tuft above the animal, prevent the sand from closing completely over, and 'preserve a small round hole, by which water is admitted to the animal, and which marks its situation'.

The first account of the use of tube-feet as burrow-building organs is that of Robertson (1871), who must have excavated the burrows of *E. cordatum* on the beach, since he describes the dorsal funnel rising vertically above the spines surrounding the dorsal impression. He also saw the tube-feet thrusting up through the sand, when he placed the urchin in a jar of sand, and describes them as 'searchingly wandering over the surface, then grasping particles of sandy matter in their tentacles, and finally dragging them rapidly down into their hole'. But he interpreted this as a feeding mechanism, and not as the desperate attempt of an urchin deprived of oxygen to make a respiratory funnel. However, he did see the oral feeding tube-feet in operation, but, contrary to my observations on more healthy urchins, noted that the feeding operation was seldom performed. Giard (1878) describes the burrow of *E. cordatum* as being in communication with the surface by two tubes, one of which opens above the apical disk, and the other at the anus. To this second 'anal' tube he ascribes the function of removing that sand, brought down by the dorsal tube-feet, which did not pass into the mouth. He interprets this as a by-pass, in fact. Giard noticed a current through the burrow and out of this tube (though how he detected it he does not explain), and attributed this to currents produced in the gut by the musculature of its wall. Although his descriptions are not very clear, it is highly probable that Giard had seen a situation similar to that illustrated in figure 17*f*, but either the urchin he was watching had built a second funnel abnormally while the first was still open, and the ciliary activity produced a current up the 'anal' limb, or the 'anal' limb was in fact blocked locally, and the current out of the top of it was produced by some other means (e.g. by pressure of his weight on the sand nearby). From his description it is clear, however, that Giard had seen only vertical tubes from the burrow to the surface; his 'anal tube' does not refer to a sanitary device originating at the subanal fasciole.

von Uexküll (1907) gives a diagram of *E. cordatum* in its burrow, and was the first to discover that the tube-feet of the anterior ambulacrum line the respiratory tube with mucus. He also first reports the horizontal tube originating at the subanal fasciole in *E. cordatum*, but its formation he thought to be brought about solely by the tuft of spines within the fasciole; he does not mention the tube-feet in this region. Gislén (1924) first ascribed a sanitary function to the horizontal tube and a pumping action associated with it to the subanal fasciole. He is the first to mention the presence of 'rosette feet' in this region for keeping open the tube and lining it with mucus. But, like Tornquist (1911) he ascribes the additional function of sand- or mud-collection to the fascioles, the clavulae of which he thought secreted mucus for this purpose, until the rosette feet removed the grains and the spines packed them into the walls of the burrow.

Among those who have examined the ciliary activity of the tests of these urchins Gislén (1924) and Kermack (1950, 1954) describe the course of the currents and give diagrams. As pointed out above, Gislén appears to have included local currents round the bases of tubercles in some of his diagrams (e.g. p. 249, figure 316) with confusing results. Kermack's diagrams give a more accurate general picture. One of his observations, however, differs from those made during the present work; in his diagram of the currents on the test of *E. cordatum* (Kermack 1950, but not published) he shows a centripetal current along the whole of the intra-fasciolar region of the dorsal part of the anterior ambulacrum. I have been unable to see a centripetal current in the anterior ambulacrum of any spatangid, except for $\frac{1}{2}$ cm or so anterior to the apical disk (part of the apical eddy). In his 1954 paper Kermack gives a diagram of currents on *S. purpureus* and no centripetal element is shown in the same region on this urchin.

Although I have found that *S. purpureus* can be kept alive in aquaria for longer periods than *E. cordatum* (as did Kermack 1950), it is difficult to obtain specimens in good enough condition to observe their burrowing. As far as I am aware, only Gislén (1924) has observed a specimen of *Spatangus* in its burrow. He reports that the dorsal surface was about 2 cm below the surface of the substratum. He mentions that no respiratory funnel was visible, but does not say whether he saw a horizontal tube or tubes originating at the subanal fasciole. The sanitary device of this form with its two tubes, therefore, does not seem to have been previously reported.

Again, only Gislén (1924) makes any mention of the burrowing habits of *B. lyrifera.* He comments that it does not burrow as deeply as *S. purpureus* (i.e. less than 2 cm), and he infers that the subanal tube-feet and the two tufts of spines within the fasciole serve to keep open and model the posterior sanitary tube, as far as this goes. He does not say whether the tube is single or double, and it is doubtful from his account whether he saw it at all.

Concerning the distribution of the urchins, Brady, as far back as 1872, noticed that specimens of *E. cordatum* offshore were under the normal size, and Robertson (1897) found only young specimens in deeper waters, but Moore (1936) was the first to suggest an inward migration of this urchin at sexual maturity. He also noticed that the average size of forms from southerly waters of the British Isles is larger than those from farther north. I have noticed this too, but have not collected sufficient of the southern forms to make a quantitative comparison. Brattström (1946) remarks that in the Gullmar Fjord specimens of *B. lyrifera* from deeper waters are generally larger than those from shallower waters. Allen & Todd (1900) noticed that, although specimens of *E. cordatum* are found between *Zostera* beds, the urchins seldom burrow among this marine grass, and this is to be expected, since the excavation of their burrows would be seriously hampered by its roots.

The succession of British irregular urchins with increasing depth and changing substratum is well shown in the manuscript of N. S. Jones's 'Records of the Offshore Fauna of the South of the Isle of Man', deposited in the library of the Marine Biological Station, Port Erin, and summarized in Jones (1951). These records, summarizing hauls made with a variety of gear, including dredges and a van Veen grab, show that the inshore *E. cordatum*, in sand, gives way either to *E. flavescens* in shell gravel or muddy sand up to about 30 fathoms, or to *S. purpureus*, in shell gravel, up to about 30 fathoms. Deeper still, in mud, *B. lyrifera* replaces all three. Ford (1923) also reports that *E. flavescens* replaces *E. cordatum* in deeper waters, and is associated more with *S. purpureus* in shell gravel. Allen (1896) reports finding a specimen of *E. pennatifidum* in shell gravel, and Pace, quoted in the *Plymouth Marine Fauna* (1957), remarks that this species is found in coarser grounds than *E. flavescens*. The occurrence of urchins dredged in the present work support these authors.

It would appear that *E. cordatum* is always found in sheltered sand banks such as sandy bays, and never in those banks which are subject to heavy wave or current action, as was pointed out by Wilson (1924). When wave action does become intense on a beach usually subject only to quite small ripples, many tests of dead *E. cordatum* are left behind by subsequent tides. It seems likely that this is the reason for the absence of *E. cordatum* in any numbers from beaches on the eastern side of Britain (Stephen 1934), which are subject to considerable buffeting and consequent instability. Stephen (1934) has shown that in the North Sea *E. cordatum* is spread over much of the area south of the 30 fathom line which runs north of the Dogger Bank, and this supports the earlier work of Davis (1923, 1925). I am grateful to Mr L. Burkett, of the Fisheries Laboratory, Lowestoft, for confirming that he too has found *E. cordatum* in the sand of the Dogger Bank, but has not come across many specimens inshore. Mr D. Kirby of Oxford tells me that they are found in a few sheltered sandy bays on the Northumberland coast.

III. THE MORPHOLOGY OF THE TUBE-FEET AND THE REGIONS OF THE TEST WHICH BEAR THEM

1. Introduction

Although Lovén (1883) describes the remains of tube-feet arising from the pore-pairs of the Ordovician *Bothriocidaris pahleni*, confirmed by Mortensen (1928), no trace of tube-foot remains has been reported in *Micraster*. At best, only the pores from which they arise may be studied in any detail, and therefore, for comparison, it is important to study the pores from which the tube-feet of living forms arise. In this section the morphology of the pores and surrounding regions from which the tube-feet of *Echinocardium cordatum* arise is described, together with comparative descriptions of the morphology of its tube-feet. Differences in the other spatangids studied are mentioned where they occur.

Differences in the ornamentation surrounding the pores show that those tube-feet which restrict their extensions to a direction at right angles to the test (the funnel-building and subanal tube-feet) do not require such broad bases to their stems as those which at times may extend parallel to the test (the feeding tube-feet). The most important differences in the tube-feet themselves concern the nature of the disks, and are shown to reflect the functions they serve.

2. The dorsal funnel-building tube-feet

In *E. cordatum* these tube-feet arise in that region of the anterior ambulacrum enclosed by the inner fasciole. As pointed out on p. 378, these fall into three regions from a functional point of view: apically there is a region of about forty-five very small and undeveloped tube-feet; these give way abruptly to much larger tube-feet (relaxed length about 4 mm) with considerable powers of extensibility; finally, there is a region of functional though smaller tube-feet (relaxed length about 1·5 to 2·0 mm) which have correspondingly less extended length, and to which on this account has been ascribed the function of building the first (lower) part of the respiratory funnel. In his description of the anterior ambulacrum of *E. cordatum* Hawkins (1913) recognizes three sections in the intra-fasciolar part differentiated on their pore configuration, and these correspond to the above functional divisions.

The podia in all three sections arise from a single pore, and figure 27 shows two such pores in biserial arrangement from approximately the centre of the region of largest tube-feet. At the surface the pore appears to be elongated, but the actual perforation of the plate, carrying the connexion from the tube-foot to its ampulla and to the tributary of the radial water-vascular canal, lies at the end nearest the mid-line of the ambulacrum (that is, nearest the radial canal) and a deep groove underlies the rest of the elongated 'pore'. Surrounding it is a low ridge; in sections the muscles of the stem of the podium can be seen to be attached to the top and inside edge of this ridge.

The disk bears finger-like processes or papillae confined to a fringe at the edge. Those functional tube-feet nearest the apical disk have a single row of processes, between sixteen and twenty in number, of about 1 mm in length. Occasionally, podia at this end of the region also bear one or two very small processes outside the main row. These processes increase in size and number towards the ambital end of the region, until, where the inner fasciole passes across the anterior ambulacrum, the total number of papillae on one tube-foot reaches thirty-five to forty in two rows and most of them are large (1 mm). Each process is supported internally by a rod of calcite, running from the edge of the disk for about two-thirds the length of the process; the unsupported third at the end may be narrower than the rest of it.

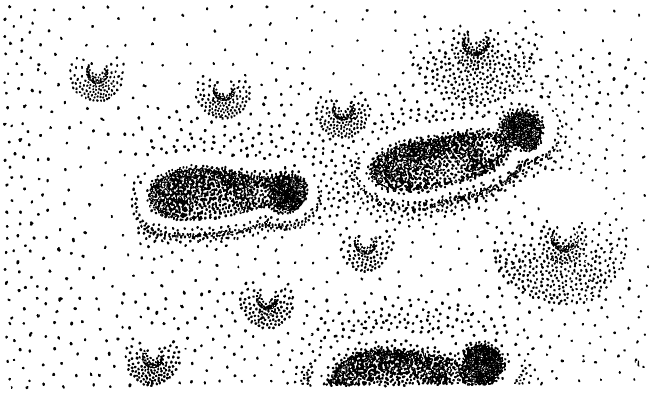


FIGURE 27. Drawing of two biserially arranged pores from the dorsal (intra-fasciolar) part of the anterior ambulacrum of *E. cordatum* from which two of the funnel-building tube-feet arise.

The other members of the genus *Echinocardium* (*E. flavescens* and *E. pennatifidum*) have very few dorsal funnel-building tube-feet (table 1) and the number of papillae is also reduced (between five and ten to each tube-foot, as compared with between twenty and forty for *E. cordatum*). In the case of *Brissopsis lyrifera* there is a single row of papillae round the edge of the disk, each one supported by a skeletal rod, but their separation into finger-like processes is not complete: the skeletal rods extend much further into the body of the disk than the divisions between the individual papillae, making the disk more extensive.

3. THE PERISTOMIAL FEEDING TUBE-FEET

These podia, up to forty in number, arise in the slightly expanded oral regions of all five ambulacra, the regions called phyllodes. The pores from which they arise are single, though there is one plate in each ambulacrum which bears two podia each from two distinct pores (on Lovén's (1874) scheme of orientation these are the end plates of columns I *a*, II *a*, III *b*, IV *a* and V *b*). The pores are circular or slightly oval (figure 28), except for a small irregularity which marks the end of a groove on the inside of the plate, bringing the tributary of the radial water-vascular canal to the podium. The pore itself is surrounded by a circular platform about 1 mm across; this may be set at an angle to the surface of the test around it, so that one part of it may be slightly depressed into the test while the part opposite to this is slightly elevated, in the way that foundations are excavated for a house built on the side of a hill. The elevated portion is generally bordered by a low ridge, which, together with the sides of the platform, are an attachment for the muscles of the tube-foot stem.

The stem of the tube-foot, when retracted, is about 1 mm long. At its distal end there is a slightly expanded and domed disk which bears up to 250 finger-like processes irregularly arranged over its entire surface. The stalks of these processes are about 50 μ thick. Those processes in the centre of the disk have very short stalks, but the length progressively increases towards the periphery, up to a maximum of about 1 mm.

Compared with the pores from which the funnel-building tube-feet arise, those bearing the feeding tube-feet are surrounded by ridges which enclose a much greater area, that is, the bases of the tube-foot stems are broader (compare figures 27 and 28). This is very likely correlated with a functional difference in the tube-feet. It was mentioned in § II (pp. 368 and 374) that whereas the funnel-building tube-feet extend perpendicular to the test, those for feeding habitually extend parallel to it, and it is not surprising that the bases of their stems need to be broader in consequence. Similarly, the purpose of their disks is to pick up sand particles for feeding, and a covering of papillae would seem to be more appropriate for this than a disk with only a fringe of papillae. Such a fringed arrangement, however, would be advantageous for the funnel-building tube-feet, since they can be folded over the disk during retraction of the tube-foot; a complete covering of papillae would prevent this. Histological differences between the feeding and the burrow-building tube-feet are dealt with elsewhere (Nichols 1959*b*).

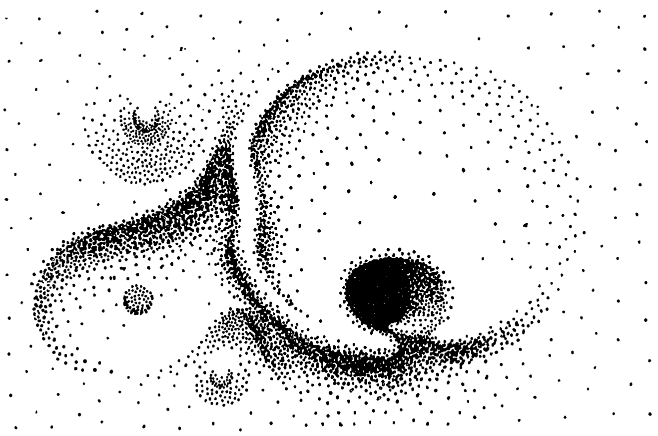


FIGURE 28. Drawing of a pore from the phyllode of *E. cordatum*, from which a feeding tube-foot arises. The pore is surrounded by a platform which is partly enclosed by a low wall. To the left of this a pit containing one of the sphaeridia (indicated by its stalk) is shown. The actual pore drawn (on Lovén's scheme of numbering) is that from the adoral plate of Amb. II, column *b*.

4. THE SUBANAL BURROW-BUILDING TUBE-FEET

In all the specimens I have examined each of these tube-feet has been borne by a pair of pores (unlike any of the others except the respiratory tube-feet), situated close to the inside edge of the subanal fasciole. The pores (figure 29), of which there are normally three pairs on each side, lie very close together in an irregular depression into which projects a strut for the attachment of muscles. The depression may be partly surrounded by a low ridge on the side opposite the strut, also for muscle attachment, though this is much lower than that surrounding the oral tube-feet.

The actual tube-foot is about 2 to 3 mm long when relaxed, and resembles the oral feeding tube-foot, except that the finger-like papillae are less numerous (up to about 100), those in the centre of the disk being appreciably shorter than those round the edge. Each process is supported by a slightly curved rod of calcite, and ends in a pigmented knob.

The fact that the central papillae are much shorter than those round the fringe seems to point to a compromise between the ability to fold the fringe of papillae over the disk during retraction (as in the funnel-building tube-feet) and an increase in surface area in the centre of the disk for a greater production of mucus (as in the feeding tube-feet). Other unknown factors clearly govern the disk pattern in the various tube-feet of this urchin, since it is difficult to explain why two patterns should be adopted in the two groups of burrow-building tube-feet.

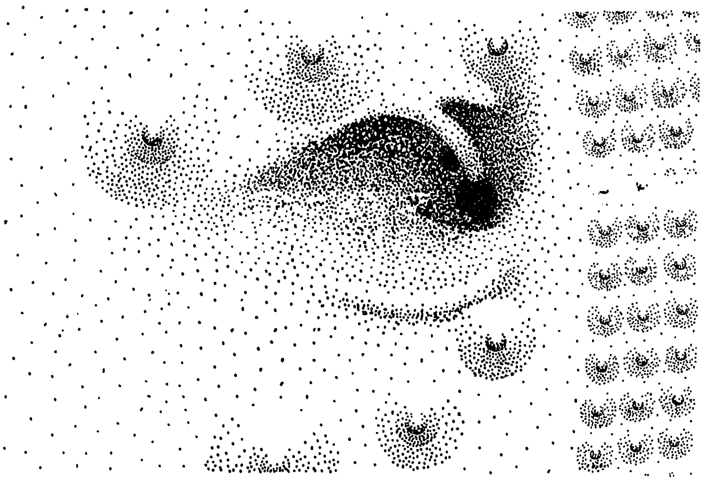


FIGURE 29. Drawing of a pore inside the subanal fasciole of *E. cordatum*. The actual pore, on Lovén's scheme, is from Amb. I, column *a*.

5. THE SENSORY TUBE-FEET

In *E. cordatum* sensory tube-feet occur in three regions of the body: (i) between the dorsal funnel building and the oral tube-feet of the anterior ambulacrum; (ii) between the respiratory and the oral tube-feet of the anterior paired ambulacra; (iii) between the respiratory and the oral tube-feet of the posterior paired ambulacra, except for an interruption in the subanal region of the posterior column of each ambulacrum, where about three tube-feet are modified for building the sanitary tube.

Each pore is set in an irregular depression (figure 30) which may be surrounded by a very slight wall, or this may be totally absent. The pores are not in pairs, though in some (e.g. the one drawn in figure 30) two projections can be seen traversing the pore from opposite sides, as though the cross-wall between what was originally a pore-pair has been incompletely broken down; I have never seen this projection completely divide the pore into two, even in very young specimens.

The relaxed length of the tube-feet is about 1 to 2 mm; they are by far the smallest fully developed tube-feet. They have no disk as such, and no papillae, but end bluntly. I have not seen them extend beyond about 3 mm in *E. cordatum*, though in *Spatangus purpureus*, as described on p. 391 above, they may extend to about 30 mm, their relaxed length in this urchin being 2 to 4 mm. There is another point of difference between the two species of *Spatangus* (*S. purpureus* and *S. raschi*) on the one hand and *E. cordatum* on the other: whereas the dorsal part of the anterior ambulacrum of *E. cordatum* contains funnel-building tube-feet, the entire anterior ambulacra of the two species of *Spatangus*, except for the feeding tube-feet orally, contain sensory tube-feet arising from reduced and relatively unornamented pores (figure 31).

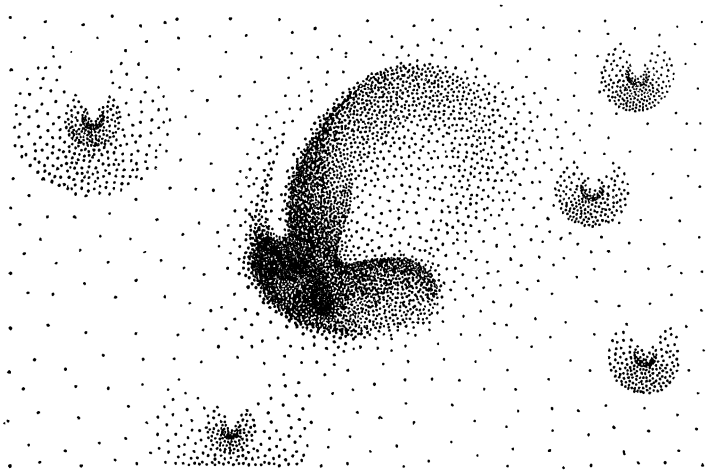


Figure 30. Drawing of a pore from the ambital part of the anterior ambulacrum of *E. cordatum* which bears a sensory tube-foot.

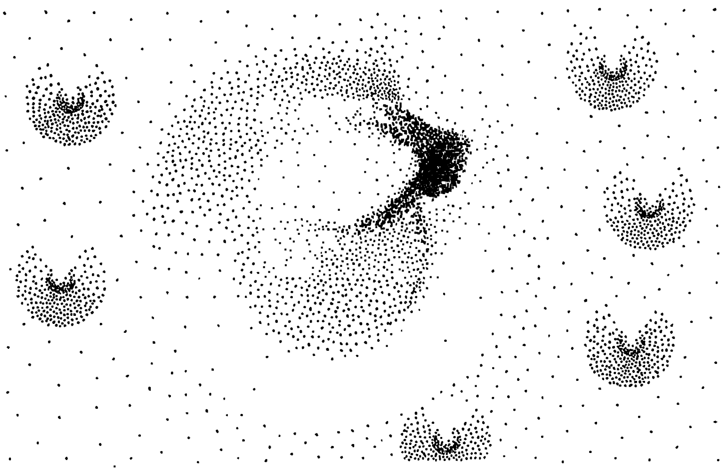


Figure 31. Drawing of a pore from the dorsal part of the anterior ambulacrum of *S. purpureus* from which a sensory tube-foot arises.

6. The respiratory tube-feet

The arrangement of these tube-feet has been described and discussed in detail in § II, p. 391. They are unique among the tube-feet in that each one is borne between a pair of pores set at anything up to 2 mm apart, the shape and configuration of which can be seen from figure 11. Each tube-foot is flattened along the plane joining the two pores and gradually tapers from the test to its apex. The tube-foot wall is heavily folded for greater surface area.

IV. THE *MICRASTER* GROUP OF FOSSILS

1. Introduction

The usual convenience afforded to stratigraphers by the imperfections and chronological breaks in the fossil record is denied those who study the Chalk fossils; whereas successful breaks in many sedimentary formations delineate ready made taxonomic pigeon-holes, very few discontinuities occurred during the formation of the Chalk. Consequently, the Chalk heart-urchin, *Micraster*, shows a continuously changing series in which all intermediates between any two easily distinguishable forms occur. This urchin was collected somewhat sporadically and haphazardly during the last half of the nineteenth century, and every form with a slight variation from the species already recognized was given a new varietal or even specific name, a practice to which continental workers were particularly prone (Rowe 1899, p. 495). The result was that the *Micraster* group became a target for what Cain (1954) aptly calls 'variety hunting', and the literature was swamped with a mass of meaningless names. Recent workers (e.g. Kermack 1954) have shown that it is sufficient to recognize only seven separately named parts of the series; in the latest review of the group Kermack (1954) has used the nomenclature of Lambert & Thiéry (1924), which will also be followed here.

2. General features of *Micraster*

On the aboral surface the paired ambulacra are petaloid, and the unpaired (anterior) ambulacra may become so as well. The ambulacra continue on from the ends of the petaloid portions towards the ambitus, but the pore-pairs are very much reduced in size and become widely spaced.

Between three and five pore-pairs on the posterior side of the body are enlarged and lie in two vertical lines on the outside edge of two slight protuberances from the test. Just before they meet the peristome on the oral side of the body the pore-pairs of all five ambulacra enlarge considerably to form phyllodes. The mouth itself is towards the anterior end of the body, and is partly covered (in most of the micrasters) by a forward projecting labrum.

A bi-lobed subanal fasciole may be present, surrounding the two slight prominences below the anus and the enlarged pore-pairs in that region.

3. The evolution of the group

The work of A. W. Rowe

Towards the end of the last century Rowe made the first extensive and accurately localized collection of *Micraster* with the help of quarrymen (who worked the Chalk by hand). By a painstaking analysis of various selected features of the test, he succeeded in producing a classic example of continuous and directional evolution (Rowe 1899), the main thesis of which has been reviewed elsewhere (Nichols 1956).

The more important changes which Rowe observed are as follows:

(*a*) In shape the test became relatively broader, the position of the broadest part moving progressively backwards. The tallest part of the test, originally at the apical disk, also moved posteriorly.

(*b*) The anterior groove became deeper and tiny swellings of the test appeared in it, becoming more frequent. The number of tubercles also increased. Rowe called both the tubercles and the swellings 'granules'.

(*c*) The mouth moved anteriorly, and the labrum became more pronounced, ultimately hiding the mouth when viewed from below. The granules around the peristome increased, including those on the labrum, while in some of the very high-zonal forms they extended on to the inside (upper) surface of the labrum.

(*d*) Those parts of the posterior paired ambulacra surrounding the plastron (the periplastronal areas) became progressively more granulated.

(*e*) The petaloid parts of the paired ambulacra became progressively shallower but longer, the posterior pair gradually straightened, and the area between the two columns of pore-pairs became increasingly ornamented, passing through stages called by Rowe 'smooth', 'sutured', 'inflated', 'subdivided' and 'divided' (see Rowe 1899, Plate XXXVI, figures 1–8). At the same time the tuberculated ridge between successive pore-pairs in each column became increasingly more marked, and the tubercles gradually extended towards the mid-line of the ambulacra, contributing ultimately to the conditions known as 'inflated', 'subdivided' and 'divided'. This progressive ornamentation of the ambulacra was stressed by Rowe as being of great importance as a zonal guide.

(*f*) The subanal fasciole became broader and the prominence in each lobe became more marked in the higher forms.

(*g*) In the low-zonal forms the oral tube-feet in the anterior paired phyllodes were situated in two pairs of grooves spreading out on either side of the peristome; these were not present in the high-zonal specimens.

As well as this continuous upward variation there is a range of variation existing at any one time. At some points in the Chalk forms assigned to one name may be distinct from forms assigned to another, though intermediate specimens exist. Rowe thought that this happened four times: the original stock in the *lata* (= *gracilis*) zone he called *Micraster corbovis*, and at the top of the zone *M. leskei* arose from this, itself giving rise at the bottom of the *planus* zone to two branches, '*M. praecursor*' and *M. cortestudinarium*. These persisted into the zone of *M. coranguinum* where they became respectively *M. coranguinum* and *M. coranguinum* var *latior*. The fourth form which Rowe recognized was that called by him '*Epiaster gibbus*'. This was the incorrect name which he gave to specimens of *M.* (*Isomicraster*) *senonensis*, and, as Kermack (1954) points out, from his paper it is clear that Rowe considered this to be closely related to *Micraster*, and, in fact, to be derived from it.

The work of Kermack

Using a large sample collected by Rowe from Northfleet, Kent, Kermack (1950, 1954) was able to show biometrically that, though some of Rowe's concepts were not justified, in the main his thesis could be upheld, and that in a population of *Micraster* the state of the characters in any one individual will average up to the level of evolution characteristic of its time, though it may be more advanced in some characters and lag behind in others. Concerning the evolution of the group, however, several of Rowe's concepts (e.g. his 'species' *M. praecursor* and his variety *M. coranguinum* var *latior*) become useless when growth ratios are taken into account.

As a result of this work Kermack considers that only two side-lines can be recognized with any certainty (Nichols 1956, figure 2), though in neither of these is the separation from the main stock complete. The first, in the *lata* and *planus* zones, and contemporaneous with *M. cortestudinarium* of the main phylum, is a series the extremes of which have been called *M. corbovis*. These differ from the members of the main stock in being markedly conservative in their features, the majority of characters still remaining low-zonal. Thus, the broadest part of the test is well towards the anterior end, it is longer than broad, the ambulacra lack any ornamentation in their interporiferous areas and between the pore-pairs of each column (the 'smooth' condition of Rowe), the mouth, with a poorly developed or absent labrum, is not very near the anterior end, and the phyllodes of the anterior paired ambulacra are grooved. Between these and the extreme forms of *M. cortestudinarium* every intermediate in character exists.

The second side-branch, in the zones of *cortestudinarium*, *coranguinium* and *testudinarius*, is that of *M.* (*I.*) *senonensis* which appears when the *corbovis* line dies out. The extremes of this branch differ from those of the main stock (Nichols 1956, figure 3) in having a taller test, a petaloid anterior ambulacrum and lacking a subanal fasciole. Kermack tested a large sample from the *coranguinum* zone which consisted of *M. coranguinum*, *M.* (*I.*) *senonensis* and specimens intermediate in character between them, and found that in six of the seven characters he chose there was an overlap between the named forms; the transitional forms, of course, fell between them. In fact, it is only in the one character 'lack of subanal fasciole' that the two named forms can be separated with any certainty. Nevertheless, though many intermediates occurred, probably representing a hybrid swarm, the broad differences between the two groups indicate a distinct difference in ecology, and therefore on this account they are good species.

Kermack attempted to explain these differences in terms of function, stating that the absence of a subanal fasciole in the *senonensis* group precludes its being a burrower. However, he does not discuss the presence in all micraster, including the isomicrasters, of enlarged pore-pairs in the subanal region closely similar to those present in this region in recent burrowers. Evidence is put forward later (p. 425) to show that Kermack's interpretation of the mode of life of *M.* (*I.*) *senonensis* at least as being a partial burrower was very likely correct, but that his evidence for it was inadequate.

Kermack's biometrical study of this group, in addition to bringing to light many unjustified conclusions made by Rowe, showed how the collecting had been biased in two ways: first, Rowe or his collectors had favoured large specimens, and secondly, they had tolerated a much greater degree of damage on the rarer specimens, such as those of *M.* (*I.*) *senonensis* and the passage forms between these and *M. coranguinum*, with the result that the relative abundance of the various forms is erroneously indicated by this collection. Besides its clarification of the situation in the micrasters, Kermack's work on the group has been of considerable value methodologically in showing how a collection of fossils may be, first, unrepresentative of the fossil population, and secondly, unrepresentative of the living population from which it was derived, both of which hold good in the case of the micrasters.

Concerning the other forms of *Micraster* occurring in Britain (the rare forms from what Wright (personal communication in Kermack (1954) calls the Northern Faunal Province)

Kermack is of the opinion that these very likely form a separate evolutionary series from the southern forms, terminating in the population from the *B. mucronata* zone of Norfolk consisting of *M. glyphus*, *M.* (*I.*) *stolleyi** and the still rarer 'aberrant forms of *M. coranguinum*', Kermack states (his p. 423) that no transitional forms occur between *glyphus* and *stolleyi* (though he quotes a good instance of hybridization on p. 421), and therefore complete separation can be considered to have taken place, probably outside the English area, to the advantage of both stocks (his p. 422). The situation in the Norfolk forms is discussed more fully later (p. 413).

4. Conditions in the Chalk sea

It has been emphasized elsewhere (Nichols 1956) that variations in the structure of the Chalk are less intense than is usual in sedimentary formations, reflecting the persistence of unusually stable conditions for the whole of the Chalk Stage, and those variations which do occur are apparently independent of evolutionary changes in *Micraster*. Even at great distance from the shore the depth of the sea is not considered to have exceeded much more than 150 to 200 fathoms, and at times was much less than this. It is interesting that one period of shallow water, the Chalk Rock of the *Holaster planus* zone, roughly corresponds to the failure of the shallow-burrowing form, *Micraster corbovis*, and its replacement by a close relative, *M.* (*Isomicraster*) *senonensis*, with a somewhat different mode of life (see p. 425 below). During the acme of *Micraster* a very pure white chalk was deposited in vast quantities in what has been interpreted as a tropical sea; Urey, Lowenstam, Epstein & McKinney (1951) have used the ratio of two radioactive isotopes of oxygen in belemnites to assess a temperature in the region of 23·8 °C for the *testudinarius* zone, though unfortunately they did not take a reading for the *Micraster* zones.

It is naturally quite impossible to assess completely the interrelations of animals of the Chalk sea and their effect on the micrasters, since only a mere fraction of these will be preserved, and only a few of those preserved will ever be found. In the words of T. H. Huxley: 'the whole geological record is only the skimmings of the pot of life'. Nevertheless, those which are found indicate that conditions in the Chalk sea are likely to have been as complex as those in present-day seas, with competition for food as the prime factor. Such interrelations are difficult enough to interpret in modern seas, but when only the 'skimmings' are collected any conclusions must be extremely tentative, though those forms which have left their mark as fossils of the Chalk give no reason for considering a comparison with present-day conditions unjustified.

As far as food is concerned, the chief competitors are likely to have been closely related echinoids. Unfortunately, most are not as abundant as *Micraster*, nor has as much carefully localized collecting been done on them, so again any conclusions must be tentative. Though some irregular echinoids which are likely to have been burrowers (e.g. *Hemiaster*, *Offaster* and the *Infulaster-Hagenowia* series (figure 44)) are fairly common in the lower zones and some again in the highest zones (Jukes-Brown & Hill 1904; Wright & Wright 1949), it is significant that they are not found in any numbers in those zones where *Micraster* is abundant. However, two important echinoids, *Echinocorys* and *Conulus*, persist throughout the Middle and Upper Chalk, becoming as abundant as *Micraster* in local pockets. Both

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* This appears to be the correct spelling; see the original description in Lambert (1901).

are conical forms and it is interesting that both show similar variations in shape at certain horizons. Neaverson (1955) has pointed out that species of *Conulus* attain their greatest height at those horizons which seem to mark the deepest conditions that obtained during the dominance of the Chalk sea over Britain, namely, the *M. coranguinum* and *Marsupites testudinarius* zones, and Brydone (1912) has shown that *Echinocorys* varies in the same way contemporaneously. Neither of these is considered (Hawkins 1912; Kongiel 1949) to have been a burrower, and I have compared them with *Micraster* and agree that in the shape of the test, nature of the petaloid ambulacra and position of the anus, etc., they were most likely surface dwellers and thus occupied a very different niche from *Micraster*. Nevertheless, since all of these fed on the detritus falling to the bottom, they must have competed for it.

As far as other groups are concerned, evidence of their presence is left behind by the following categories of animals:

(1) those which produce burrows and coverings from extraneous materials which are recognizable in the deposits,

(2) those with fossilizable hard-parts.

Among the first group, such soft-bodied animals as the polychaetes leave remains of their U-shaped burrows in the Chalk, or calcareous tubes on the tests and shells of other animals. It is unlikely that the burrowing inhabitants of the sea bottom affected the micrasters except as competitors for food, if, like their present-day counterparts, they were microphagous feeders and lacked hard jaws. The encrusting forms, such as *Serpula*, however, would be a source of continual danger to a surface-living or partially burrowing urchin, unless it had an effective defence against the settling larvae. In common with recent forms, the pedicellariae on the urchins very likely provided this, in conjunction with distasteful mucus, and therefore any encrustations which are found are likely to have occurred after the death of the urchin, when its test would be the only solid substratum for settling larvae.

Among the second group, remains have been found of ophiuroids, benthic and pelagic crinoids and asteroids, siliceous and calcareous sponges, actinozoans, bryozoans (on tests and shells), brachiopods, pelagic and benthic lamellibranchs, ammonites (including the uncoiling forms such as *Scaphites* and *Baculites*) and gastropods, many competing with the urchins for the rain of detrital matter. Active predation may well have occurred from such bottom-feeding elasmobranchs as *Ptychodus* and teleosts such as *Macropoma* and *Enchodus*, as is reported to occur from living elasmobranchs and teleosts (Mortensen 1951). Predation may have also occurred from brachyura such as *Enoploclytius*, in the same way that living crabs have been observed to nibble at the respiratory tube-feet of a specimen of *Spatangus purpureus* (see p. 415 below).

To summarize, therefore, the following points from the structure and palaeontology of the Chalk help to form a picture of conditions under which *Micraster* was living.

(1) The sea was very calm, and hence current action did not disturb the substratum to any extent, a condition which, by comparison with present-day seas (see p. 395 above), was decidedly advantageous to a burrower.

(2) The rain of detrital matter was vast, providing large quantities of food for microphagous feeders.

(3) Very few other burrowing urchins have been found in strata where *Micraster* is abundant, though non-burrowers have been collected in comparable numbers.

(4) Other animals were present in the Chalk sea which very likely preyed actively on burrowing and non-burrowing urchins, and also which molested them to a lesser extent by nibbling at their appendages.

V. A BIOMETRICAL STUDY OF THE PETALOID REGIONS OF THE PAIRED AMBULACRA IN *MICRASTER*

1. Introduction

One of the changes in the main *Micraster* line noted by Rowe (1899), as mentioned on p. 402 above, was the gradual increase in length of the paired ambulacra (i.e. the petaloid parts of them), though he makes no mention of an increase in number of pore-pairs in these regions. Similarly, though Kermack (1954) dealt statistically with seven shape characters of the test and the nature of the anterior ambulacra in an attempt to separate *M. coranguinum* from *M.* (*I.*) *senonensis*, he did not investigate the nature of the paired ambulacra in the two 'sub-genera', nor attempt to suggest a biological significance for the range of variation in the nature of the anterior ambulacra. The purpose of this section is to present the results of a biometrical study on the paired ambulacra, not only in the groups investigated in detail by Kermack, but on some of the other named forms of the *Micraster* complex. The results show that:

(1) there is intergrading between chronologically successive groups in this character;

(2) there is a modal shift in the mean for each named form investigated as the strata are ascended;

(3) there is no significant difference in this character between the micrasters and the isomicrasters of the Northern Province and those of the Southern.

The possible biological explanation of these trends and those of the anterior ambulacrum are discussed.

2. Material and methods

Samples of six of the named forms of the *Micraster* group and intermediates between two pairs of them were examined from four zones, as shown in the following scheme:

group	zone	no. in sample
(1) *M. corbovis*	*H. planus*	30
(2) *M. cortestudinarium*	*M. cortestudinarium*	30
(3) *M. coranguinum*	*M. coranguinum*	30
(4) *M.* (*I.*) *senonensis*	*M. coranguinum*	15
(5) Intermediates between 3 and 4	*M. coranguinum*	30
(6) *M. glyphus*	*B. mucronata* of Norfolk	24
(7) *M.* (*I.*) *stolleyi*	*B. mucronata* of Norfolk	25
(8) Intermediates between 6 and 7	*B. mucronata* of Norfolk	18

Material was drawn from the collections in the British Museum (Natural History), the Geological Survey Museum, the Norwich Castle Museum and from my own collection. The details of the individual specimens are given in the Appendix, tables 6 to 13.

It is impossible, in the Chalk micrasters, to obtain a series of exactly contemporaneous populations; some zonal spread, in some cases considerable, had to be tolerated, although the effect of evolution would tend to obscure the differences between successive stages. In two cases where contemporaneous spread occurs, and in which the extreme forms have been given separate names (in the *M. coranguinum* zone of the South of England and the *mucronata* zone of Norfolk), the population has been divided into three: the two extremes and the intermediates between them. The method of separating the intermediates in these two cases is dealt with under 'Results' on p. 411. Wherever possible specimens were selected on which three measurements (length, breadth and height) could be made and on which the pores in the petaloid paired ambulacra could be counted, except in small samples in which slightly damaged specimens had to be used; where a measurement could not be taken, an estimate was made by comparison with similar specimens of comparable size or, more often, the other side of the same urchin. These estimates are indicated by the letter **E** in the tables.

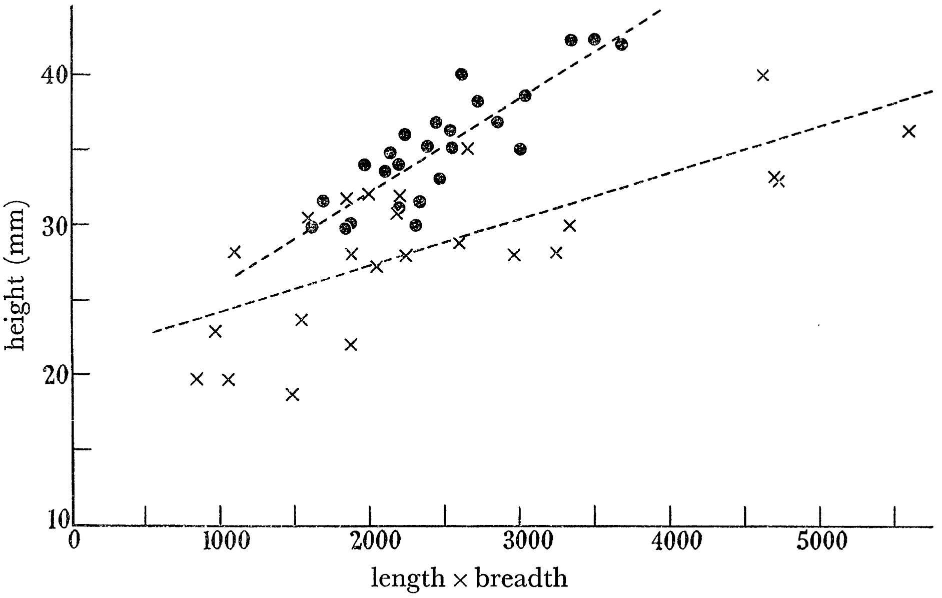

FIGURE 32. Graph showing the relationship between the height and a product of length and breadth in samples of *M. glyphus* (×) and *M.* (*Isomicraster*) *stolleyi* (●) from the *mucronata* zone of Norfolk. The calculated regression lines have been dotted in.

One variable in this study is the size of the specimens. It is convenient to use a size-number obtained by multiplying together several dimensions of the test. In § II length and breadth only were used, the height of all specimens used then being comparable; but in this case the tallness of the test, a diagnostic feature of the isomicrasters, is significantly different in the two groups ($P < 0{\cdot}01$). This was tested in the population from the *mucronata* zone of Norfolk, the first group examined, and the results are included in the Appendix, tables 11 and 12 and plotted in figure 32. Regressions were fitted to the two groups with the following results:

group	equation of regression line	$s(y.x)$	$s(b)$
M. glyphus	$Y = 21{\cdot}13 + 0{\cdot}003009x$	3·791	±0·000605
M. (*I.*) *stolleyi*	$Y = 19{\cdot}72 + 0{\cdot}006207x$	2·035	±0·000769

3. Results

The details of the results are given in the Appendix, tables 6 to 13. The number of tube-feet in the petaloid parts of the paired ambulacra have been plotted against a size-number obtained by multiplying length by breadth by height of the specimens (figures 33 to 38). Regression lines representing the dependence of the number of tube-feet in the petaloid paired ambulacra on the size-number were fitted to each group with the following results:

group	equation of regression line	$s(y.x)$	$s(b)$
(1) *M. corbovis* (figure 33)	$Y = 148·3 + 0·02680x$	19·66	$\pm 0·004433$
(2) *M. cortestudinarium* (figure 34)	$Y = 121·0 + 0·07267x$	15·237	$\pm 0·009006$
(3) *M. coranguinum* (figure 35)	$Y = 135·8 + 0·07221x$	13·538	$\pm 0·007562$
(4) *M.* (*I.*) *senonensis* (figure 35)	$Y = 180·8 + 0·06555x$	18·564	$\pm 0·01410$
(5) Intermediates between 3 and 4 (figure 36)	$Y = 199·6 + 0·03714x$	13·563	$\pm 0·008810$
(6) *M. glyphus* (figure 37)	$Y = 148·1 + 0·05133x$	22·50	$\pm 0·009123$
(7) *M.* (*I.*) *stolleyi* (figure 37)	$Y = 211·2 + 0·03889x$	20·20	$\pm 0·014272$
(8) Intermediates between 6 and 7 (figure 38)	$Y = 140·6 + 0·11560x$	19·472	$\pm 0·01725$

The results are summarized in figure 39, in which the calculated regression lines for each group are plotted on the same graph.

In the case of adjacent groups the regression lines were tested against each other with the following results:

group	$\dfrac{\text{mean diff.}}{\text{S.E.}} = $ 't'	D.F.	probability
(1) *M. corbovis* and *M. cortestudinarium*	4·568	56	$<0·001$
(2) *M. coranguinum* and *M.* (*I.*) *senonensis*	0·4163	41	$>0·6$
(3) Intermediates and mean of *coranguinum* and *senonensis*	2·2733	49	$<0·05$
(4) *M. glyphus* and *M.* (*I.*) *stolleyi*	0·7344	45	$>0·4$
(5) Intermediates and mean of *glyphus* and *stolleyi*	3·594	40	$<0·001$
(6) *M. coranguinum* and *M. glyphus*	1·762	50	$>0·1$
(7) *M.* (*I.*) *senonensis* and *M.* (*I.*) *stolleyi*	1·329	36	$>0·1$

Similarly, the variance between adjacent groups was analyzed as follows:

group	variance ratio (F)	D.F.	probability
(1) *M. corbovis* and *M. cortestudinarium*	0·4167	30; 30	$<0·01$
(2) *M. cortestudinarium* and *M. coranguinum*	15·23	30; 30	$\leqslant 0·001$
(3) *M.* (*I.*) *senonensis* and *M.* (*I.*) *stolleyi*	0·0229	15; 30	$<0·2$
(4) *M. glyphus* and *M.* (*I.*) *stolleyi*	72·799	24; 25	$\leqslant 0·001$

The scatters of *M. coranguinum* and *M. glyphus* are sufficiently like those of *M.* (*I.*) *senonensis* and *M.* (*I.*) *stolleyi* for one to assume that they too are significantly different at around the 0·2 level of probability.

The relative body sizes of the three Norfolk groups were tested, and it was found that, though there is no significant difference between the *glyphus* and *stolleyi* groups ($P > 0·2$), the intermediates between them are significantly smaller than both of these ($P < 0·05$; $P < 0·001$, respectively).

As Rowe pointed out (1899, p. 519), *M. corbovis* attains a larger size than any other *Micraster* in the English Chalk, although the very large forms are comparatively rare: though no other micrasters in the samples exceeded a size-number of 1800, seven of this sample did so. It may appear from the graph (figure 33) that the presence of these larger

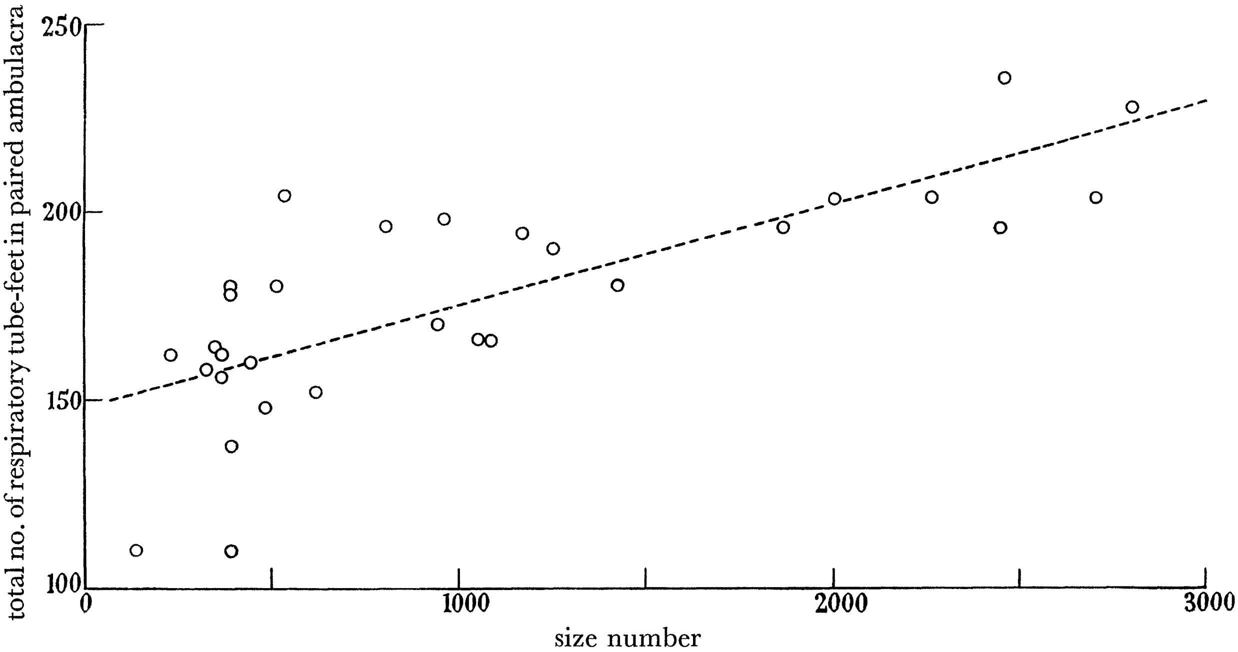

FIGURE 33. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra of *M. corbovis* from the *planus* zone and the size (length by breadth by height). The calculated regression line has been dotted in.

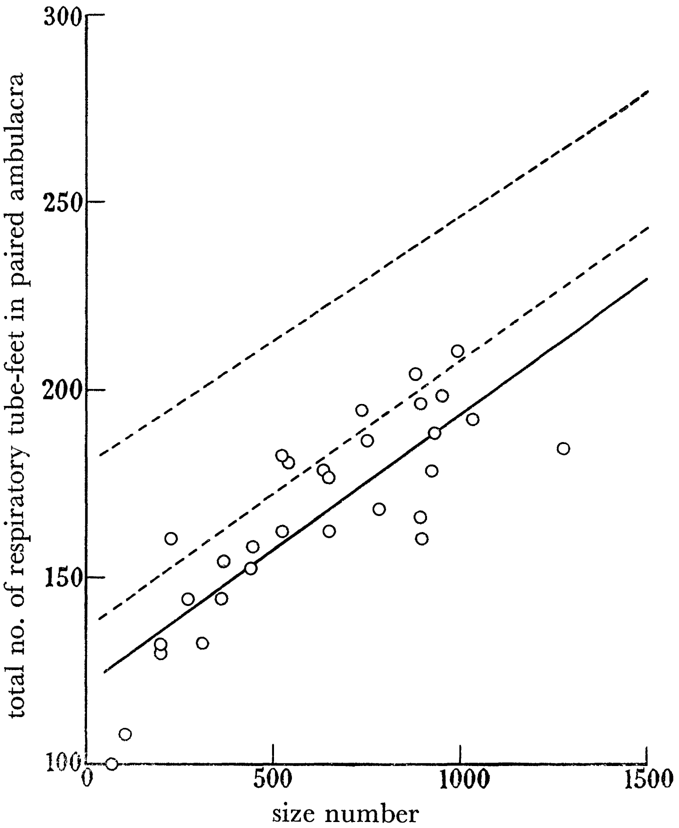

FIGURE 34. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra of *M. cortestudinarium* from the zone of *M. cortestudinarium* and the size (length by breadth by height). The calculated regression line has been drawn in, and those of *M. coranguinum* and *M.* (*I.*) *senonensis* (figure 35) dotted in for comparison.

specimens has influenced the regression line by including effects of allometric growth most visible on large specimens, and that the true situation is being masked by the inclusion of these forms, a comparison with the other micrasters being possible only when considering forms of comparable size. To test this, the sample of *corbovis* was considered in two separate groups, those below a size-number of 1800 (selected arbitrarily as above the size of any other forms) and those above, regression lines being fitted to each with the following results:

group	equation of regression line	$s(y.x)$	$s(b)$
below 1800	$Y = 143{\cdot}0 + 0{\cdot}03621x$	21·8	0·01233
above 1800	$Y = 153{\cdot}5 + 0{\cdot}02372x$	14·83	0·01758

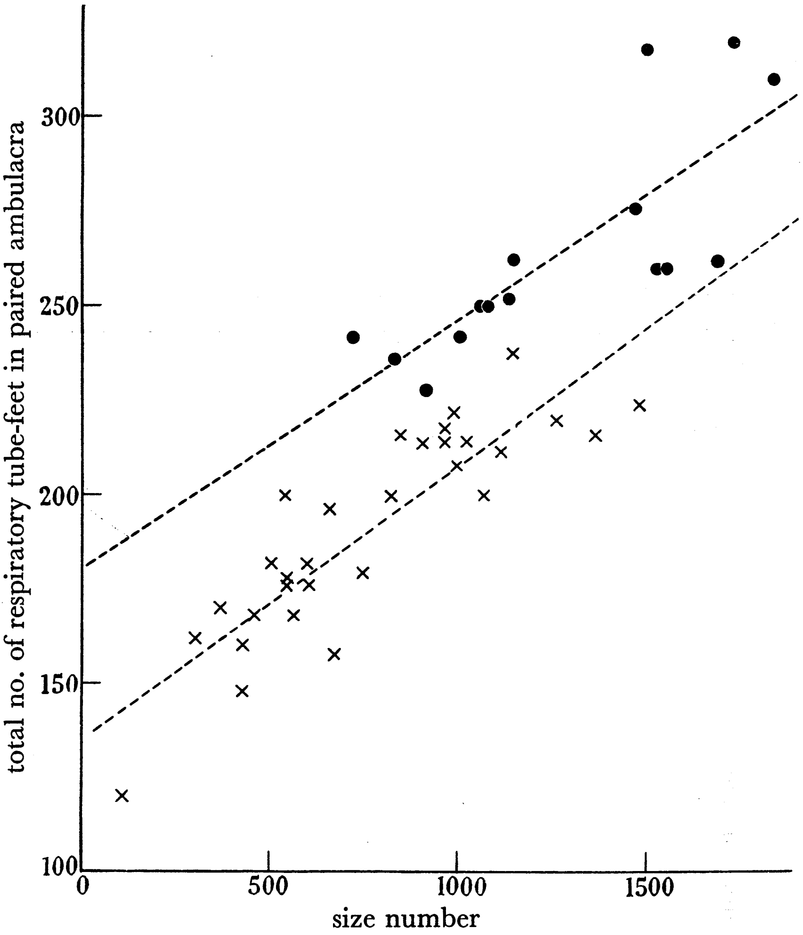

FIGURE 35. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra and the size (length by breadth by height) of *M. coranguinum* (×) and its contemporaneous *M.* (*I.*) *senonensis* (●) from the zone of *M. coranguinum*. The calculated regression lines have been dotted in.

The regression coefficients (coefficients of x in the equations) were tested ($t = 0{\cdot}5817$) and were not significantly different ($P > 0{\cdot}5$). Also, the coefficient of that part of the sample below a size-number of 1800 was tested against the coefficient for the full sample (equation no. 1, p. 408) and was not significantly different ($P > 0{\cdot}5$), so it is unlikely that the presence of larger forms in this sample from the *planus* zone has affected the overall picture.

The sample from the next zone was a collection of the name-fossil, *M. cortestudinarium* (figure 34). The regression line for this group was significantly different from that of *corbovis*, a fact which might be interpreted as meaning that there was some difference in ecology between these two adjacent named forms (see § VI).

Three samples were tested from the next zone (of *M. coranguinum*): the name-fossil, *M.* (*I.*) *senonensis*, and the intermediates between them (figures 35 and 36). The main differences between typical examples of the named forms from this single zone have been oulined in Kermack (1954), and Nichols (1959*a*), figure 2. Any specimen with most of its

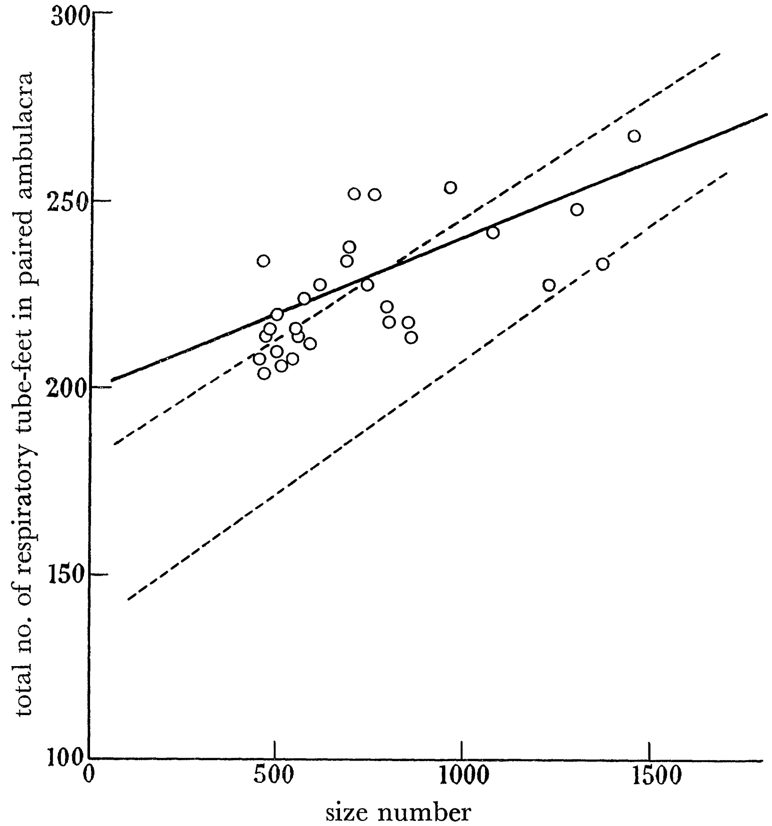

FIGURE 36. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra and the size (length by breadth by height) in the intermediates between the contemporaneous named forms *M. coranguinum* (lower dotted line) and *M.* (*I.*) *senonensis* (upper dotted line). The calculated regression line for the intermediates has been drawn in as a full line.

characters appropriate to one-named form, but with any of the following characters appropriate to the other, or intermediate in nature, has been included among the 'Intermediates':

(1) nature of the subanal fasciole,
(2) nature of the anterior ambulacrum,
(3) general shape of the test.

The regression line of the intermediates between *M. coranguinum* and *M.* (*I.*) *senonensis* is significantly different from the mean of the two-named forms, the smaller ones tending towards the *senonensis* condition in their paired ambulacra, while the larger ones tend more towards the *coranguinum* condition. A similar, though by no means identical situation

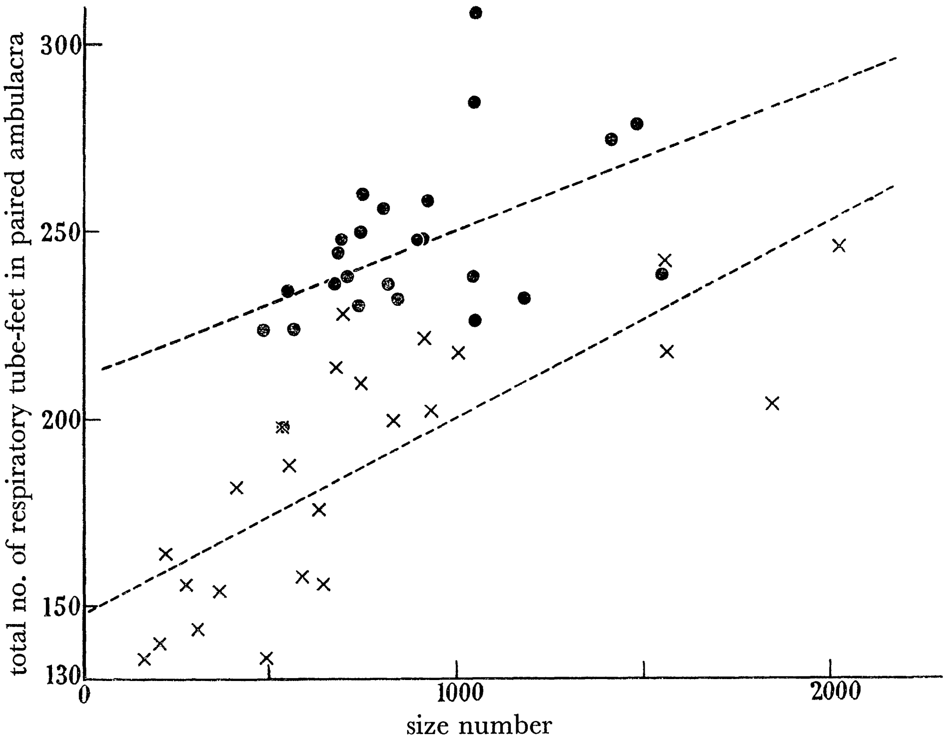

FIGURE 37. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra and the size (length by breadth by height) in *M. glyphus* (×) and its contemporaneous *M.* (*I.*) *stolleyi* (●) from the *mucronata* zone of Norfolk. The calculated regression lines have been dotted in.

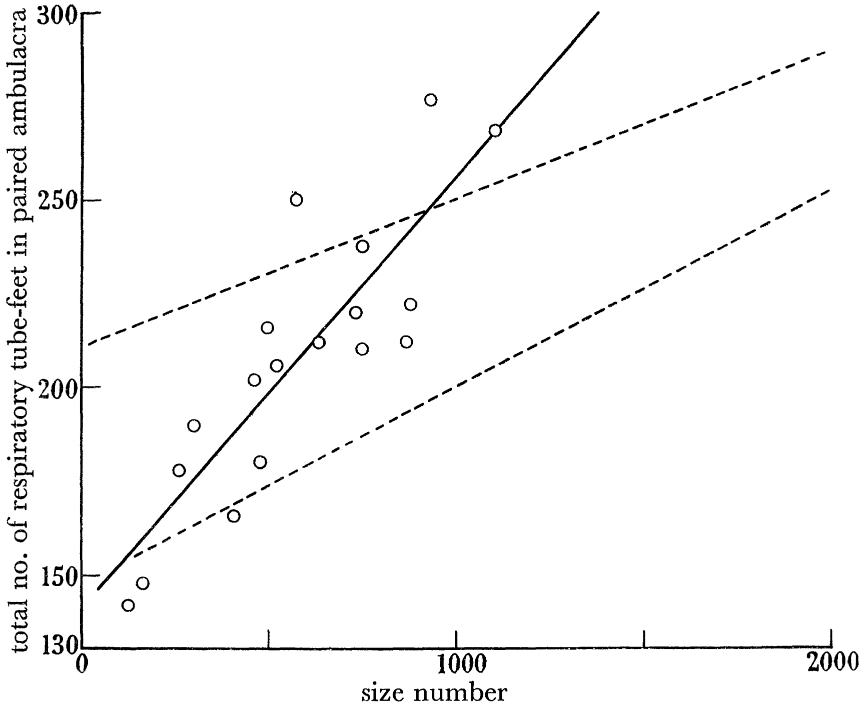

FIGURE 38. Graph showing the relationship between the total number of tube-feet in the petaloid parts of the paired ambulacra and the size (length by breadth by height) in the intermediates between the contemporaneous named forms *M. glyphus* (lower dotted line) and *M.* (*I.*) *stolleyi* (upper dotted line). The calculated regression line for the intermediates has been drawn in as a full line.

occurs in the intermediates, selected on the same characters, between the Norfolk *M. glyphus* and *M.* (*I.*) *stolleyi* populations (figure 38), and so the significance of these intermediates can be considered together (see Discussion).

4. Discussion

Although Kermack (1954) states that he recognizes three distinct forms from the Norfolk *mucronata* zone (p. 404 above), I have been unable to find any accurately localized specimens 'resembling in some ways *M. coranguinum*' (his p. 423). He also states, also on p. 423, that the other two forms, the flatter one identical with *M. glyphus* described from the German Chalk by Schlüter (1869), and the tall, almost pyramidal form called by him *Isomicraster stolleyi* (see Schlüter's figures, Plate 1, figures 2, 2*a* and *b*; Plate 2, figures 1, 1*a*, *b* and *c*), have no transitional forms; there is thus an advantageous absence in the two forms which replace the southern *coranguinum* and *senonensis*, between which there *are* intermediates. He does not say whether he regards *glyphus* or 'aberrant *coranguinum*' as the end-product of the *Micraster* phylum in the North; but from what he does say (see particularly his p. 422) it is probable that he considers both *glyphus* and *stolleyi* to be immigrants, returning to the Northern Faunal Province of England after becoming distinct from each other and from aberrant *coranguinum* outside it. All three he therefore considers good species.

I have examined a larger sample than was available to Kermack, and find that transitional forms do indeed exist: of the sixty-seven specimens studied by me I have classed eighteen as intermediates (see Appendix, table 13). Of these fourteen had the general appearance of *M. glyphus* and possessed a subanal fasciole, yet had anterior ambulacral pores either like those of *stolleyi* or intermediate between these and the normal *glyphus* pores (e.g. B.M. (N.H.) specimen E. 19755). Conversely, one specimen was found in the collections (B.M. (N.H.) specimen E. 10544) which on its shape and absence of a subanal fasciole would be called *stolleyi*, but which had anterior ambulacral pores closely similar to those generally associated with *glyphus*.

Again, three specimens occurred (Geol. Survey Museum specimen HBW 372; Norwich Castle Museum specimen 75.937 (19); B.M. (N.H.) specimen E. 10765) which had the general shape and anterior ambulacral pores of the *stolleyi* type, yet they possessed a well-marked subanal fasciole. I have not seen a single specimen from this material which resembles the micrasters in shape and anterior ambulacral pore configuration, yet has no subanal fasciole; this absence, which also holds good for the Southern forms, is discussed later (p. 416).

The situation in the Norfolk forms (figures 37 and 38) thus parallels that in the *coranguinum* zone population from the South of England in the presence of intermediates. It is doubtful, however, whether a comparison may be made regarding the proportions of intermediates in the two zones, since specimens have been drawn from many collections whose sampling bias will differ. From an overall picture of the collections, however, it appears that there are fewer intermediates in the *mucronata* group than there are in the *coranguinum* group, a fact which, if it could be proved, would indicate a greater degree of ecological and genetic separation of the micrasters and isomicrasters in the higher zones of the Northern Province than in the lower zones of the south.

The statistical analysis of the two series of fossils from the *coranguinum* and *mucronata* zones supports the assumption that two very closely related species or subspecies (divided by earlier palaeontologists into separate genera) lived in the Chalk seas in these times, and that quite a considerable amount of interbreeding and hybridization occurred between them. The regressions of the micrasters and isomicrasters may be considered coincident (figure 39) though the respective intermediates are markedly different. These intermediates, with the one notable exception to be discussed later, appear to have had a life-span almost as long as typical members of the named forms in the case of the southern (*coranguinum*) zone forms, but never as long as the extremes in the case of the Norfolk forms. This supports the suggestion that the south of England micrasters and isomicrasters were genetically (and possibly ecologically) more alike than the Norfolk ones, producing secondary hybrids roughly intermediate in all characters between the two 'parent' groups. In the Norfolk forms, however, though separation of micrasters and isomicrasters never became absolute, they tended to be genetically (and ecologically) more distinct, and as a consequence to produce fewer hybrids, those which were produced being less able to take a middle course between two well-adapted modes of life.

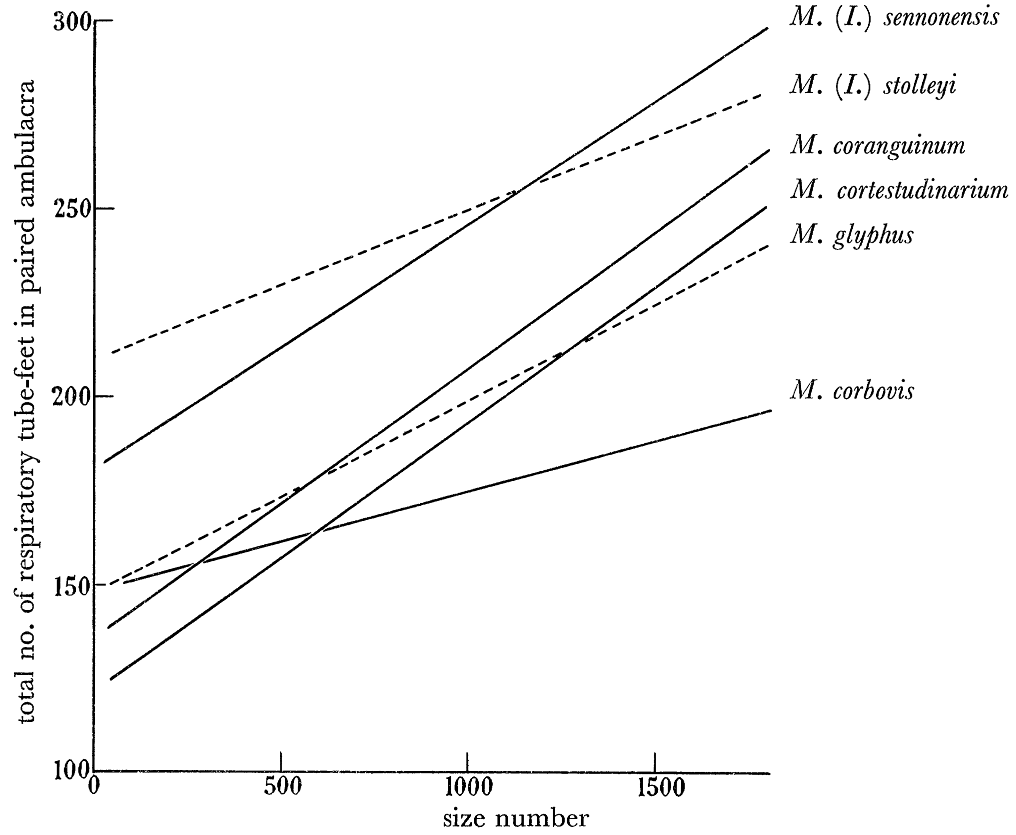

FIGURE 39. Summary graph in which the regression lines representing the dependence on size of the number of tube-feet in the petaloid paired ambulacra of the named forms of the *Micraster* and *Isomicraster* series of fossils have been plotted on the same axes. The regressions of the southern forms are drawn in as full lines while those of the Norfolk forms are dotted.

By comparison with all living spatangids one can see that the tube-feet in the petaloid regions of the paired ambulacra were respiratory in function in all the micrasters and isomicrasters, and in addition it seems likely that those of the petaloid part of the anterior ambulacrum in the isomicrasters were also respiratory, or at least partly so. The results show, however, that even if this possible fifth respiratory ambulacrum is ignored, the isomicrasters had more pores for respiratory tube-feet than did the micrasters; the difference, however, is one of degree, the two 'subgenera' intergrading to a varying extent.

Since the tube-feet themselves are not preserved, we do not know whether the total area of the respiratory surfaces was greater, but a comparison with living forms seems to indicate that it was not. The two living spatangids whose morphology and behaviour throws most light on the interpretation of the results are *S. purpureus* and *S. raschi*. *S. purpureus* obtains water for respiratory purposes by drawing it through the interstices of the gravel particles in which it burrows by means of the cilia over the body surface. This water, after flowing between the respiratory tube-feet, is wafted to the posterior side of the animal, and thence down the subanal sanitary tubes, to filter away between the gravel particles again. The current down these backward prolongations of the burrow is augmented by the cilia on the clavulae of the subanal fasciole (a structure which is also present in the micrasters but lacking in the true isomicrasters). The tubes are made and maintained by three or so pairs of special tube-feet with great powers of extensibility, situated within the fasciole (these are present in both the micrasters and the isomicrasters).

In the case of *S. raschi*, the animal does not burrow beneath the mud in which it is found, but ploughs through it with most of its corona exposed above the surface, so that its respiratory tube-feet are bathed in the currents over the sea bottom. Consequently, although it does build a subanal sanitary device, this is a single tube, and a very small one at that, down which a current is maintained by a greatly reduced subanal fasciole. The individual respiratory tube-feet, also, are very much smaller than those of a similar sized specimen of the burrower, *S. purpureus*, and the pore-pairs which give rise to them are much smaller and closer together. The number of these tube-feet is not increased in the case of *raschi* compared with *purpureus*, neither is there any move towards the anterior ambulacrum becoming respiratory in *raschi*. It must be concluded, therefore, that because the current of oxygenated water across the respiratory surfaces in a partly burrowing form like *raschi* is greater than that in the burrow of a form like *purpureus*, smaller tube-feet can be tolerated in *raschi* without any detriment to its physiology. Correspondingly, larger tube-feet would be detrimental to a partial burrower like *raschi*, since it would then be prone to molestation from bottom-feeding animals. I have observed crabs nibbling at the respiratory tube-feet of a living specimen of the normally burrowing form *S. purpureus* in an aquarium in which there was insufficient gravel for it to burrow. Naturally, it is quite impossible to test this hypothesis when applied to the micrasters and isomicrasters, since there is no sure way of comparing the relative sizes of their respiratory tube-feet. Although no exact measurements have been made, the individual pores of a pair which gave rise to the respiratory tube-feet in life are approximately the same distance apart in individuals of about the same size. But this does not preclude the possibility of the tube-feet being reduced in height—indeed, this is what would be necessary, while still keeping the tube-feet as wide as possible and as far apart as necessary to obtain currents between them.

The conspicuous absence in the sample of any specimen having all characters of a *Micraster* but lacking a subanal fasciole, mentioned previously, lends support to the hypothesis that the micrasters were burrowers. The isomicrasters could exist perfectly well without such a sanitary apparatus, because their respiratory tube-feet were exposed to the currents above the surface of the substratum, and therefore they needed very little extra flow within their burrows. The micrasters, on the other hand, could not respire efficiently unless this apparatus was present to help the circulation of water round the animal. Nevertheless, subanal burrow-building tube-feet were present in both forms, and the degree of development of ornamentation round the pores for muscle attachment seems to indicate that they were both equally extensile. This may well have been the case, since the absence of a subanal fasciole does not necessarily mean the absence of a subanal sanitary tube. The fasciole was, as now, a device for ensuring a fast flow down the tube for getting rid of respiratory waste; but the normal body ciliation (which is assumed to have been present, as it is on all living urchins) could have maintained a *slow* current down such a tube for the purpose of ridding the animal of faecal matter and other non-respiratory waste only.

The conclusion that may be drawn regarding the respiration of the isomicrasters, the partial burrows, seems to be that a reduction in the size of the individual tube-feet was desirable as a counter-measure to the nibbling of bottom feeding animals, and this was brought about by a flattening of the normal *Micraster*-type respiratory tube-feet, and a consequent increase in number both in the paired ambulacra and by conversion of the anterior ambulacrum to a respiratory function.

It seem most likely that the significant increase in the number of respiratory tube-feet from the low-zonal forms, such as *corbovis*, through their chronological successors, *cortestudinarium*, to the high-zonal *coranguinum* (summarized in figure 39) can be attributed to an increase in respiratory efficiency, with the consequent potentiality to burrow deeper in the Chalk silt as the trend progressed. Many other progressive transformations of the test of the micrasters, first pointed out in any detail by Rowe (1899), can best be explained as adaptations towards the same end, as will be shown in § VI.

VI. POSSIBLE FUNCTIONAL SIGNIFICANCE OF SERIAL CHANGES IN *MICRASTER*

1. Introduction

Those evolutionary changes in *Micraster* which have been described chiefly by Rowe and Kermack (§ IV), and the others described for the first time in § V occur irrespective of changes in those environmental conditions which have left their mark in the Chalk, and are therefore likely to represent either a change in niche or an improvement of the animal in an effectively unchanged habitat. It is shown in this section that the changes in the main *Micraster* phylum from *M. leskei* through *M. cortestudinarium* to *M. coranguinum* very likely represent a gradual and progressive change in niche, while the replacement of *M. corbovis* by *M.* (*I.*) *senonensis* and the appearance in the Northern Province of *M.* (*I.*) *stolleyi* probably represent the immigration of better-adapted forms.

2. Changes in the main phylum

The trends may best be dealt with according to function.

Burrowing and locomotion

Since there is very little difference in the arrangement of tubercles of *Micraster* from that of *E. cordatum* and indeed the recent spatangids generally, it may be assumed that the arrangement of spines was similar to that illustrated in figure 26, and that the micrasters dealt with the substratum in much the same way. Then the spines at the anterior end of the body scraped the front wall of the burrow, whilst those at the sides passed the material backwards. The initial burrowing, in which mounds of material are thrown up at the sides and front of living urchins (figure 15), later to join across their dorsal surface as they sink down, may also be considered to have taken place in a similar way. Although some of the scraping and silt-moving spines are occasionally preserved on the tests (though not *in situ*), as in my specimen J. 5, and four specimens in the collection at the British Museum (Natural History), I am not aware of any spatulate spines having been found. Nevertheless, by comparison with recent forms it is most probable that those of the plastron were markedly flattened, as they are in *Brissopsis*, *Spatangus raschi* and *Echinocardium cordatum*, all of which normally inhabit substrata of small particle size, and also in *E. pennatifidum* and *E. flavescens*, which have sometimes been found in such substrata.

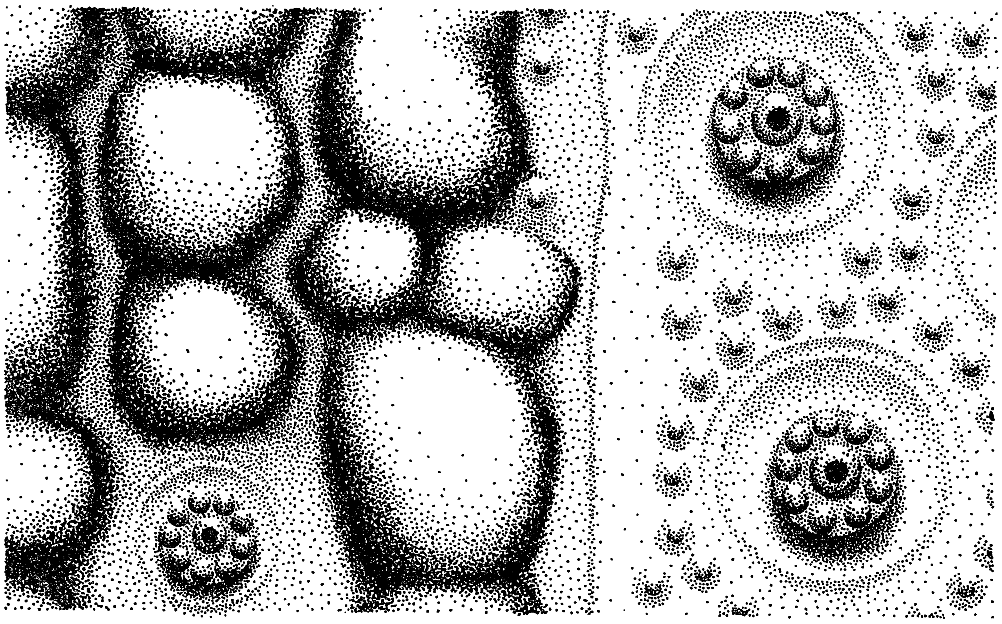

Figure 40. Drawing of part of the oral surface of *M. coranguinum*, showing, on the right, two tubercles of the plastron (part of Interamb. 5), and on the left part of the periplastronal area of Amb. I. Norwich Castle Museum specimen 247.956 (3).

A very important feature of locomotion during burrowing is the transport backwards of silt. It was pointed out on p. 390 that the periplastronal areas of living forms provide the main pathways along which the material of the substratum passes. One important feature of the evolution of the main *Micraster* line is that these areas become increasingly granular, finally attaining the degree illustrated in figure 40. This drawing shows two of the large plastron tubercles with their ornamentation for muscle attachment surrounding the mamelon in the centre; within the periplastronal area on the left some small tubercles may be scattered (upper centre), and also some fairly large ones (one of which is drawn), but the majority of the area consists of ridges and bumps in lines running roughly antero-posteriorly. Some tubercles may also arise on the tops of the ridges, though this has not been drawn. It seems likely that this increase in ornamentation is due to a need for increasing the transport of silt backwards during locomotion. The particle-size of the Chalk silt was small—most like the *Brissopsis* mud of the recent substrata studied—and in consequence much could be passed back by ciliary action assuming the pattern to be similar to the activity shown by living forms. I consider, therefore, that the increase in granulation represents an improvement in function and a greater reliance on ciliary activity instead of activity of large moveable appendages, in this case the silt-moving spines.

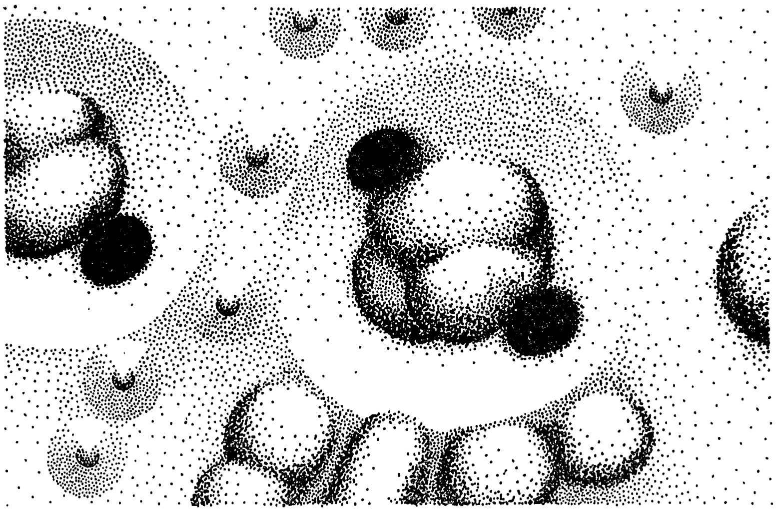

FIGURE 41. Drawing of a pore and part of another from the phyllode of Amb. II of *M. coranguinum.* In the lower centre of the picture and on the right some of the bumps on the test, similar to those of the periplastronal areas, can be seen. Norwich Castle Museum specimen 247.956 (3).

Feeding

The mouth moved from a fairly subcentral position in the early micrasters to a more anterior position, the labrum became more pronounced and its tuberculation and granulation increased. Figure 41 shows one of the pore-pairs and a portion of another which occupy a similar position to the pores bearing feeding tube-feet in living urchins. Whereas the living ones have a wall of calcite round the pores for muscle-attachment, those of *Micraster* have both a slight depression in the test and a few closely packed bumps between the individual pores, most likely for the same purpose. The number of spines in the area increased, even to the extent of covering the inside of the lip. Living forms use spines in this area as a grating on which to scrape the disks and papillae of their tube-feet to dislodge particles of the substratum, with their covering of organic matter, so that the material passes into the gut (pp. 374, 376), and it seems reasonable to assume that all the micrasters did the same. An increase in the size of the labrum would thus mean that fewer particles fell out again, and the appearance of spines inside the mouth on the upper surface of the labrum would provide an even greater array of scrapers, and these in a much better position for the function which they perform, especially for dealing with a finely comminuted substratum.

The fact that the mouth moved forwards with time is functionally correlated, it seems most likely, with the increase in depth of the anterior groove. It is probable that there was a ciliary mode of feeding in the fossils just as there is in the living forms (p. 388), and that they relied to quite a considerable extent on the method of wafting food from the dorsal surface where it had settled, down the anterior groove and into the mouth. This could not happen efficiently in the low-zonal forms such as *M. leskei* and *M. corbovis*, since the mouth was too far back and the labrum too small, so that many of the minute particles obtained via the anterior groove would have dropped to the floor of the burrow. The anterior groove, also, was probably too shallow to keep a permanently free passage round the front end of the animal as it pushed through the substratum. But the food which did drop down in this way would not be wasted: the facts suggest that these early forms relied to a large extent on their tube-feet for feeding. I have examined many hundreds of specimens of *Micraster* and it is quite evident that the low-zonal forms, principally *M. corbovis*, have pore-pairs for their oral tube-feet set deeper in the test and with more pronounced granulation between the individual pores than the high-zonal forms. Ornamentation round the pore-pairs in living forms is for muscle attachment (see, for example, p. 397), and therefore it seems likely that the early micrasters possessed more muscular tube-feet, and thus may have relied more on their use than on the ciliary currents, while in the later forms the reverse was true. Rowe (1899) noticed a feature in connexion with this (my p. 402), and pointed out that the pores of the feeding tube-feet in the low-zonal forms generally lie in a groove, whereas this is but slightly indicated in the higher zonal series.

In the depth of their anterior grooves the later micrasters are paralleled by such living forms as *E. cordatum* and *S. raschi*, inhabiting the very unmouldable sand, with which the depth seems to be functionally related (p. 391). It is almost certain that the silt at the bottom of the Chalk sea was equally disagreeable as a burrowing medium, if not more so, one feature of its constitution being the absence of large particles, as in shell gravel, and of clay, as in mud, and it is to be expected that the micrasters would parallel the sand-living forms in features which reflect the type of substratum.

It is, of course, quite impossible to say whether an apical eddy of currents, present in all the spatangoids studied (pp. 359 and 388) and found in a modified form in a clypeastroid as well (p. 362), was present in *Micraster*, but, assuming that feeding currents passed down the anterior groove, such a ciliary pattern on the dorsal surface may well have been present to protect the genital products when extruded.

As far as the histology of the feeding tube-feet of *Micraster* may be inferred, the differences between the pore configuration of the living forms and that of the fossils suggests that the majority of muscle fibres were attached to the walls and floor of the depression which surrounds the pores, but for greater mechanical leverage, especially when the tube-foot was extended parallel to the test, some of the fibres were attached to the bumps between the pores. These bulges, common to all the *Micraster* pores from which prehensile tube-feet are thought to have arisen, are not present in any of the living forms and therefore any discussions as to their function is purely hypothetical.

Respiration

As pointed out in § IV (p. 401) the dorsal parts of the paired ambulacra of *Micraster* are petaloid, and the configuration of the pore-pairs within these regions (figure 42) gives adequate grounds for concluding that the tube-feet which arose from them, like those in similar positions in living urchins, were respiratory in function. The problem of maintaining a current of oxygenated water over these surfaces appears to have been solved in much the same way as in living burrowers, with minor modifications; although there is good evidence (see next paragraph) for concluding that the micrasters of the main phylum built respiratory funnels to the surface of the substratum, the problem of drawing sufficient water down the deeper funnels was solved in a different way.

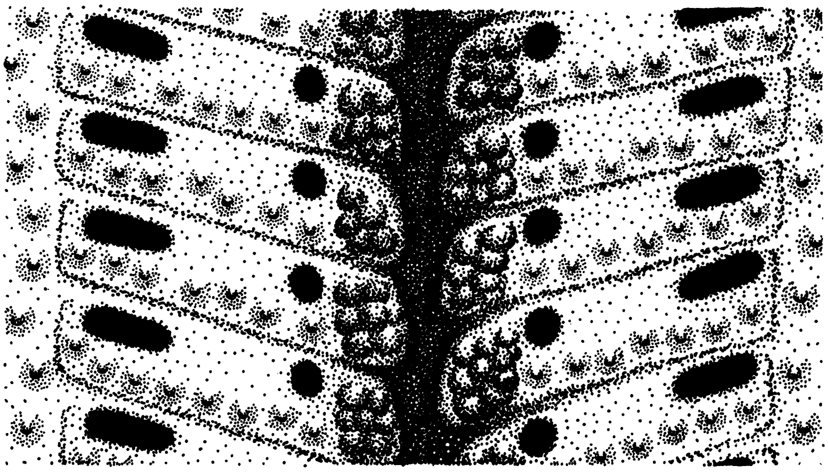

FIGURE 42. Drawing of part of a petaloid paired ambulacrum of *M. coranguinum* in which the ornamentation has attained the 'divided' condition. Norwich Castle Museum specimen 247.956 (3).

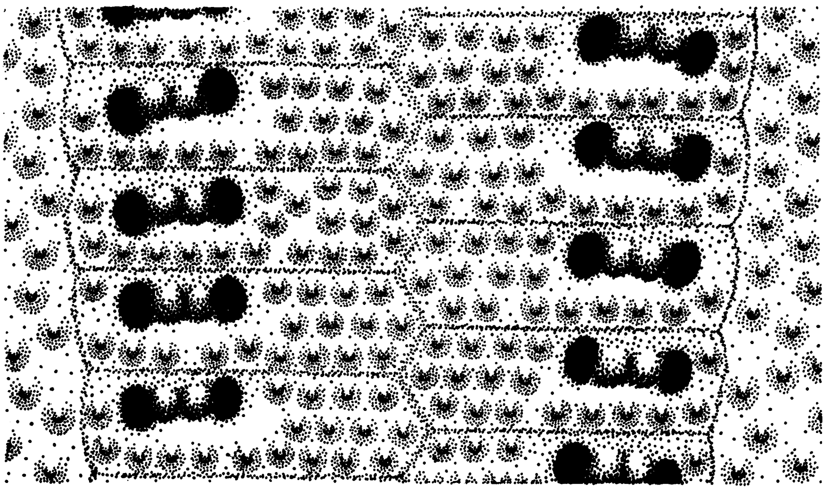

FIGURE 43. Drawing of part of the anterior ambulacrum of *M. coranguinum*. While most of each plate is covered with small tubercles, there is a narrow non-tuberculate area surrounding each pore-pair.

In the dorsal part of the anterior ambulacrum (figure 43) of all the micrasters in the main phylum (and in the *corbovis* group as well) the individual pores of each pair are fairly close together compared with the respiratory pores and have two (sometimes more) bulges of calcite between them. Surrounding each pore-pair there is a non-tuberculated region, sometimes slightly sunken in the test. From what has been said concerning the feeding tube-feet of *Micraster* (p. 418 above) it is likely that these dorsal pore-pairs also gave rise to prehensile tube-feet, both the non-tuberculated area surrounding them and the bulges between the individual pores being for muscle attachment. In some forms, particularly *M. cortestudinarium* and *M. coranguinum*, the adapical part of the anterior ambulacrum may be almost horizontal, then turn abruptly downwards towards the ambitus some 20 to 25 plates from the apical disk. At this point, too, the arrangement and shape of the pores usually changes abruptly: the pore-pairs become more widely separate, the two (or more) interpore bulges are replaced by one and the pores become crescentic in shape and nearly completely surround the central bulge. There does not appear to be a depression surrounding the pore-pairs here, and the interpore bulge is much lower than in the adapical section. These facts may be interpreted as meaning that the tube-feet which arose from the adambital pores were not as extensile as the adapical ones—in other words, that they parallel those living forms which build respiratory funnels. The tube-feet near the apical disk were therefore very likely for building a funnel to the surface of the Chalk silt, while those nearer the ambitus were mainly sensory in function, as is the case in such present-day forms as *E. cordatum* and *B. lyrifera*, in which there is a marked difference between the adapical funnel-building tube-feet and the sensory ones nearer the ambitus.

Without any indication of the size of the funnel-building tube-feet or their extensibility, it is difficult to assess the probable depth of burrowing in *Micraster*, and the configuration of the funnel-building pore-pairs gives no help in this direction. However, by comparison with the living forms it is possible to say that the depth of burrowing changed with time. One of the factors influencing the depth of burrowing in living forms (p. 377) is the degree of development of heavily ciliated regions, in their case the dorsal fascioles. No similar fasciole occurs in *Micraster*, but it seems likely that its function was performed by the petaloid parts of the paired ambulacra. It was pointed out above (p. 402) that these regions, like others on the test, become progressively more ornamented with time; in the earliest forms the interporiferous areas and the areas between the successive pore-pairs in each column are smooth, but become increasingly more 'granular', ultimately reaching the condition which Rowe called 'divided' (figure 42). In this condition the sutures between the plates are deep, particularly the perradial suture between the two columns of one ambulacrum; the regions between successive pore-pairs become heavily tuberculated; finally, and most important of all, those parts of each plate bordering the perradial suture develop numerous bulges, some of which may have tubercles on them. The most likely explanation of this increase in ornamentation is as a device for increasing the surface area of the test. There is no reason to doubt that the epidermis of *Micraster*, as in all the living urchins, was heavily ciliated, and thus whereas the low-zonal forms with 'smooth' ambulacra relied on the normal ciliation of the body, the high-zonal ones increased the number of cilia in just that region of the test where they were most needed to maintain a respiratory current. The perpendicular grooves leading from the deep central groove out alongside the tube-feet would direct these currents across the respiratory surfaces. If this view is correct, then one must conclude that the low-zonal forms required less ciliation in this region for some reason, and in view of the fact that the coherence of the substratum apparently remained unaltered the most likely reason is that the low-zonal forms burrowed less deeply than the high-zonal series, and in consequence required less motive power to pass the same quantity of water over the respiratory surfaces. This view is supported to a considerable extent by the probable mode of feeding of the micrasters: it has been stated (p. 419 above) that the low-zonal forms very likely relied to a large extent on their oral feeding tube-feet, whereas the high-zonal ones probably used a ciliary mode to a large extent. This would be much easier if a strong current were being drawn down the funnel for respiratory purposes, presumably bringing with it quantities of detritus. Thus, although it is not possible to make an estimate as to the actual depth of burrowing, it is possible to say that the low-zonal series were fairly shallow burrowers compared with the high-zonal forms.

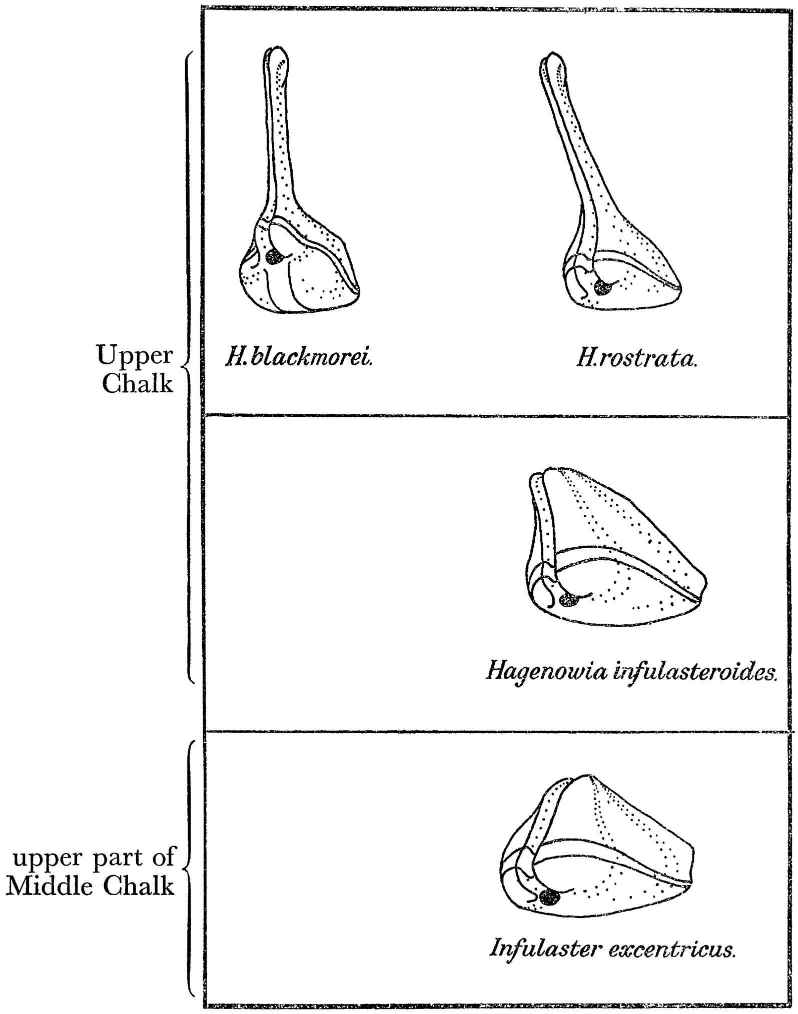

Figure 44. Diagram to show the changes in shape which occur in the *Infulaster–Hagenowia* series from the Middle and Upper Chalk of England. The main trends are a decrease in body volume and a lengthening of the rostrum, which projects forwards in *H. rostrata* but vertically in its contemporary *H. blackmorei*. A lateral fasciole is present.

As regards the probable morphology of the funnel-building tube-feet it has been shown (p. 397) that the funnel-building tube-feet of *Brissopsis* are unique among the urchins studied in that their disks are much more extensive and their papillae less finger-like than any others. This strongly suggests that building a respiratory funnel in mud, regardless of its cohesive properties (p. 380 and figure 21), requires a flatter instrument to work it than other substrata (a trowel rather than a glue-brush). This must be purely due to particle size, and therefore it is not unreasonable to suggest that the funnel-building tube-feet of *Micraster* could well have been of a similar pattern for building a funnel in the Chalk silt of similar particle size.

The possible increase in the depth of burrowing as the *Micraster* series progressed is paralleled by the *Infulaster–Hagenowia* group (figure 44). I have examined the pore-pairs of specimens of all stages in this series (except *H. infulasteroides*, which is known only from a flint cast); those in the apical region resemble the apical pores of *S. purpureus* (figure 31) more than those of such funnel-building urchins as *E. cordatum* (figure 27), and I therefore conclude that, like *Spatangus*, the pore-pairs gave rise to tube-feet which were wholly sensory. In consequence, deeper burrowing has been achieved by the development in *Hagenowia* of a rostrum, quite small at first in *H. infulasteroides*, but ultimately, in *H. rostrata* and *H. blackmorei*, attaining considerable length and projecting diagonally forwards in *rostrata* and vertically in *blackmorei*. On the tip of this are the genital openings and the madreporite, and on its anterior surface is a deep groove, in which are found the pore-pairs for the tube-feet mentioned above. It is likely that all members of this series progressed with the apical disk exposed above the surface of the substratum and fed mainly by wafting food particles down the anterior groove to the mouth. For respiration the urchins must have relied to a large extent on the ciliary currents produced by the epithelium of the rostrum, though a wide lateral fasciole is present in the main body region, presumably both to augment the rostrum currents and to assist in the removal of respiratory and other waste. It is significant that this fasciole widens out in two places: first, where it passes across the anterior ambulacrum (and it is likely, therefore, to have augmented the feeding currents as well), and secondly, where it passes beneath the anus (possibly to assist in the removal of faecal matter).

Sanitation

The fact emerges from the study of living urchins that some sort of drain-away for the waste-products of respiration, defaecation, etc., is essential and that the best way to do it would seem to be to build a tube or tubes in the substratum as it falls in behind the animal while burrowing. It is fairly certain that the micrasters, like the living forms, built such a device, because they are provided with the same combination of characters in the posterior region which are concerned with its building and maintenance in living forms (subanal fasciole, special large spines and burrow-building tube-feet). The pore-pairs belonging to the burrow-building tube-feet in this area (figure 45), like the oral pore-pairs, are set in a slightly sunken bowl, and between the individual pores are several bulges, both features most likely for muscle attachment. Moreover, the subanal fasciole is bi-lobed, the tubercles which bore the special large spines are in two groups, one in each lobe, and each group is borne on a slight protuberance of the test. This arrangement strongly suggests that the sanitary device had two tubes, as has been directly observed in *S. purpureus* (p. 367) and inferred in *Brissopsis* (p. 387) The most likely factor affecting the number of tubes has been shown (p. 387) to be the coherence of the substratum, the forms which build two tubes and can hence attain a greater maximum size being found in those substrata more readily moulded. But it has already been pointed out (p. 419 above) that the Chalk silt cannot be considered an easily mouldable substratum, and this being so it is interesting to find that in *Micraster* there are about twice as many burrow-building tube-feet in the subanal region as there are in any of the living urchins studied (5 or 6 as opposed to 2 or 3). One can assume that this increase in the number of mucus-producing organs enabled *Micraster* to build two subanal sanitary tubes in a situation in which it would be otherwise impossible to do so. This has enabled it to attain a fairly large size, the average size-number compared with that of *E. cordatum* from an equally difficult burrowing medium (thirty specimens of each) being 2327 and 1337, respectively.

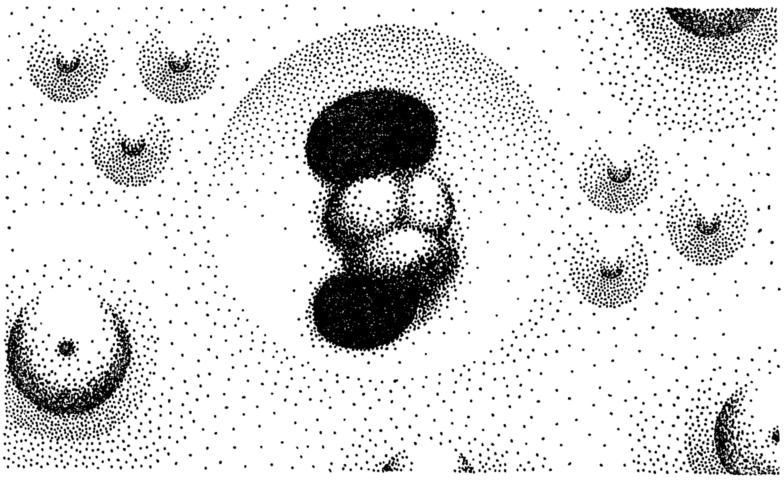

FIGURE 45. Drawing of a pore from Amb. I from within the subanal fasciole of *M. coranguinum*. Six small tubercles and parts of several large tubercles are shown in the vicinity of the pore-pair. Norwich Castle Museum specimen 247.957 (3).

Some direct evidence of a double sanitary tube has been obtained from the Chalk in which *Micraster* burrowed. One remarkable feature of the Chalk as a sedimentary rock is that it is almost unaltered since its deposition, except for compression, and may be returned to its original condition as a silt by shaking with water. This being so, it seemed likely that remains of the burrows might remain in it. To examine this possibility, some large blocks of chalk were removed from the *M. cortestudinarium* and *M. coranguinum* zones of Dorset (White Nothe) and ground flat along the bedding-plane. In one case out of about twenty-five two parallel grey lines, about 6 in. long and 5 mm apart, were visible on the fresh surface closely resembling a fallen-in sanitary tube of a living urchin in an aquarium when viewed from below (see figure 49, extreme left, plate 9). The two tubes were much closer together (5 mm) than the lobes of the fasciole (centre to centre, about 13 mm) but this could be the result of lateral compression. These grey lines, therefore, may well be the remains of the double sanitary tube of *Micraster*.

In support of my hypothesis (p. 422 above) that the high-zonal members of the main phylum burrowed deeper than their forbears is the fact that the subanal fasciole becomes broader (p. 402). In the light of observations on the fascioles of living forms (p. 361), this strongly suggests that the fascioles of the high-zonal series produced stronger currents. The body-size of the animals, however, did not increase; in fact, *corbovis*, markedly low-zonal in all its features, was the largest of the micrasters (p. 408). In view of this, one may conclude from this character also that there was an increase in the ciliary currents permitting a greater depth of burrowing in the high-zonal forms.

Sensation

In every ambulacrum of *Micraster* in the region of the ambitus about twenty pore-pairs are very much reduced as are those in similar positions in living urchins. The same is true of about eight pore-pairs in each periplastronal area. Pores in these regions in the living forms give rise to tube-feet whose function appears to be wholly sensory (p. 399), and which have been observed in some forms (p. 391) to explore the substratum in which the animal is burrowing. The position of these tube-feet is such as to give them contact with the substratum on all sides of the test; only the apex of the test is not provided with reduced pore-pairs, but this region is not in contact with the substratum, since it is likely to underlie a respiratory funnel.

3. The isomicrasters

The main features in which this group differs from the main phylum are in the more pyramidal shape of the test, the petaloid shape of the anterior ambulacrum and the absence of a subanal fasciole. However, it should be noted that enlarged pore-pairs do occur in the subanal region, just as they do in members of the main phylum. The absence of any pore-pairs in the dorsal region, which are likely to have borne prehensile tube-feet, suggests at once that the isomicrasters were not burrowers. Further, when compared with a living non-burrower such as *S. raschi* (pp. 355 and 415) they have marked similarities in general shape and in the reduction of the subanal fasciole. The reason for this has been suggested (p. 415) to be due to the fact that the respiratory tube-feet were exposed above the surface of the substratum to be bathed in the currents there, and hence the need to remove waste respiratory currents from the vicinity of the animal is eliminated. Kermack (1954) has pointed out that a tall test is of advantage to a non-burrower, since particles of settling sediment will be easier to remove down a steep slope. It has been shown above (§ V) that the number of respiratory tube-feet in the paired ambulacra (disregarding the respiratory function taken on by the anterior ambulacrum) is markedly higher in the isomicrasters compared with all the members of the main phylum (figure 39) and I interpret this (p. 415) as being due to a reduction in size of the respiratory tube-feet in free water, and also as a countermeasure to predation. Further, the paired ambulacra (figure 46) are ornamented only by numerous small tubercles and do not have either the very deep perradial suture of their contemporaries or the numerous bumps of calcite on either side of it (compare figure 42).

These facts suggest that the isomicrasters were not total burrowers, though they proceeded with the lower parts of the body submerged beneath the surface of the substratum. They probably built a subanal sanitary tube, however, for removal of faecal products, etc., but probably it was sufficient for these to dribble into the tube and be buried as the animal progressed, thus eliminating the need for a current down the tube produced by a subanal fasciole. It is interesting to observe that the anus in all the isomicrasters is set much lower down on the posterior surface compared with the micrasters, and the reason for this is likely to be that only if they were extruded low down could the faeces be buried as the animal progressed, thus reducing the chances of self-fouling.

Although the *corbovis* series may have lived completely submerged beneath the substratum, they were much shallower burrowers than *coranguinum* and consequently the isomicrasters more closely resembled them in habit than any other member of the series. It is quite possible, therefore, that only when the *corbovis* series died out (for an unknown reason) could the *senonensis* series re-invade the English area.

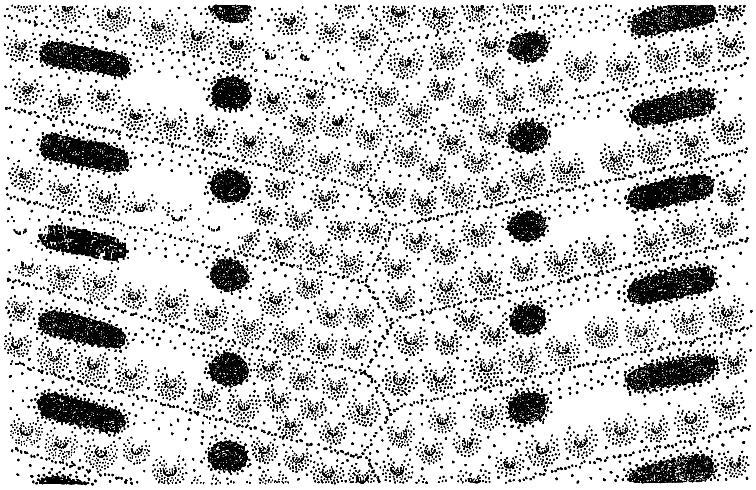

FIGURE 46. Drawing of part of the dorsal region of an ambulacrum of *M.* (*I.*) *senonensis* from the *M. coranguinum* zone. The paired ambulacra and the anterior ambulacrum are almost identical in the isomicrasters. British Museum (Natural History) specimen no. E. 35555.

4. TAXONOMIC CONCLUSIONS

The main taxonomic conclusions which may be drawn from the *Micraster* group from Southern England only in the light of this work have been dealt with fully elsewhere (Nichols 1959*a*). These may be summarized as follows:

From its appearance in the *cuvieri* zone the *Micraster* series became progressively more variable, and I have interpreted this variability as manifesting itself in the depth to which the urchins could burrow. Thus, the rare *M. leskei* was most likely a shallow-burrowing form, and the features it possessed were retained by part of the later series (in the *lata* and *planus* zones), called *M. corbovis*, while other features appeared contemporaneously in increasing abundance to suggest deeper burrowing (*M. cortestudinarium*). Both Rowe (1899) and Kermack (1954) point out that these two forms intergrade in all characters, and it is probable that the intermediates could burrow to an intermediate depth. At the top of the planus zone the shallow burrowers died out, but the deeper burrowers continued into the next two zones, where they are name-fossils (*M. cortestudinarium* and *M. coranguinum*). In these zones the high-zonal features, in addition to becoming more common, became more pronounced suggesting even deeper burrowing. Meanwhile, following the failure of *corbovis*, a new form appeared in the English area which was closely related to the micrasters but differed from them in features which suggest that its burrowing was even shallower than *corbovis*, in fact, that most of its corona was exposed above the surface of the silt. This is the form called by Lambert & Thiéry (1924) *M.* (*Isomicraster*) *senonensis*, and interbreeding occurred between it and the main *Micraster* line. This partial burrower is not found higher than the *testudinarius* zone, but *coranguinum* continues sporadically to the top of the Chalk.

The work in the present paper on the micrasters and isomicrasters from the North of England suggests that a similar situation exists. The *mucronata* zone of Norfolk is considered (p. 404) to have been part of the Northern Faunal Province, separated from the southern region of the Chalk sea by a barrier. Kermack recognizes three forms from here: *M. glyphus*, *M.* (*I.*) *stolleyi* and 'aberrant forms resembling in some ways *M. coranguinum*'. These three he regards as the end-products of an evolutionary series following similar though by no means identical trends to those described by Rowe (1899) for the southern forms and specifically distinct from them. Kermack suggests (his pp. 442, 423) that *glyphus* and *stolleyi* in the north replace *coranguinum* and *senonensis* in the south, with the advantageous absence in the northern forms of intermediates. He does not say whether he regards *glyphus* or aberrant *coranguinum* as the end product of the *Micraster* phylum in the north; but from what he does say (see, particularly, his p. 422) it is probable that he considers both *glyphus* and *stolleyi* to be immigrants returning to the Northern Faunal Province of England after becoming distinct from each other and from aberrant *coranguinum* outside it. All three he therefore considers good species.

I have examined a larger sample of the Northern forms than was available to Kermack, and I find (§ V) that transitional forms do exist between *glyphus* and *stolleyi*, though the sample available to me was also too small to decide whether the situation parallels the southern forms. From what I have examined, however, it appears that the number of intermediates between the northern micrasters and isomicrasters is smaller than between the southern, and therefore that a greater degree of separation has probably occurred. I cannot agree with Kermack, however, that they are good species. Also, I have been unable to find any accurately localized specimens resembling *coranguinum* in the collections from the *mucronata* zone, and therefore cannot comment on his third form. I agree with Kermack that the facts regarding the *mucronata* forms suggest that they are specifically distinct from the southern forms, being the end-products of a northern phylum all stages of which were almost certainly also specifically distinct from contemporaneous members of the southern phylum. The facts suggest that a non-burrower, *stolleyi*, like *senonensis*, re-invaded an area already occupied by a burrower. Whether 'aberrant forms resembling *coranguinum*' were this burrower, and *glyphus* an immigrant with *stolleyi* I will not attempt to say, but it seems surprising that two burrowers, inhabiting presumably almost identical niches, should coexist in the *mucronata* Chalk.

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LIST OF THE ABBREVIATIONS USED IN THE FIGURES

a.fasc.	anal fasciole
a.tf.	sensory tube-feet of the anterior ambulacrum
ac.tf.	accessory tube-feet
al.tf.	anterior lateral sensory tube-feet
an.	anus
fb.tf.	funnel-building tube-feet of the anterior ambulacrum
fun.b.s.	funnel-building tuft of spines
f.s.	feeding spines as a grill round the peristome
g.p.	genital pores
in.fasc.	inner fasciole
loco.s.	locomotory spines of the plastron
m.	mouth
mad.	madreporite
o.tf.	oral feeding tube-feet
p.fasc.	peripetalous fasciole
plas.	plastron
pl.s.	plastering spines of sides of test
pl.tf.	posterior lateral sensory tube-feet
pp.tf.	periplastronal sensory tube-feet
p.p.	peristomial plates
pro.s.	protective spines covering ambulacra
pr.p	periproctal plates
r.tf.	respiratory tube-feet
sa.fasc.	subanal fasciole
sa.tf.	subanal burrow-building tube-feet
scra.s.	scraping spines of anterior end
s.m.s.	sand-moving spines of lower part of test
s.t.b.s.	sanitary tube-building spines

APPENDIX

TABLE 2. SELECTION FOR PARTICLE WEIGHT DURING FEEDING OF *SPATANGUS PURPUREUS*

The weights are shown of the twelve heaviest particles from the gut of two specimens of approximately the same size which had been kept in aquaria containing different kinds of gravel.

	dimensions (mm)			twelve heaviest particles lifted (mg)	
	length	breadth	size no.		
animals kept in natural shell gravel	76·1	73·2	5570	1. 82·5	7. 44·3
				2. 62·0	8. 37·0
				3. 60·0	9. 35·5
				4. 53·5	10. 34·0
				5. 52·5	11. 32·0
				6. 47·0	12. 28·0
				average 47·4	
animals kept in chicken-grit shell gravel	87·3	85·3	7447	1. 95·0	7. 58·0
				2. 82·5	8. 51·5
				3. 65·5	9. 48·2
				4. 64·0	10. 47·2
				5. 60·0	11. 46·0
				6. 58·0	12. 39·0
				average 59·6	

Table 3. Selection for particle weight during feeding of thirty specimens of *Spatangus purpureus*

The results are plotted in figure 20 and the equation for the regression line is given on p. 375.

no. of sample	mean of heaviest six particles (mg)	$\log_{\text{mean}}$	size no.
1	70·83	1·8502	7447
2	59·58	1·7751	5570
3	47·30	1·6749	4792
4	33·73	1·5280	4609
5	37·20	1·5705	4571
6	26·45	1·4224	4319
7	44·90	1·6522	4120
8	47·15	1·6735	4119
9	35·70	1·5527	3943
10	28·63	1·4567	3830
11	45·90	1·6618	3760
12	42·83	1·6317	3635
13	28·85	1·4602	3226
14	17·02	1·2309	3225
15	15·00	1·1761	3125
16	11·58	1·0637	2904
17	15·15	1·1804	2620
18	8·28	0·9180	2529
19	24·30	1·3856	2318
20	12·97	1·1130	2235
21	24·23	1·3843	1900
22	11·25	1·0511	1772
23	8·07	0·9069	1760
24	17·48	1·2425	1712
25	14·32	1·1559	1656
26	3·27	0·5145	1513
27	3·13	0·4955	1342
28	18·10	1·2577	1278
29	1·88	0·2742	789
30	2·47	0·3927	685

Table 4. Selection for particle weight during feeding of *Echinocardium pennatifidum* and *E. flavescens*

(See p. 376)

	dimensions (mm)			twelve heaviest particles lifted (mg)	
	length	breadth	size no.		
E. pennatifidum	41·8	39·6	1655	1. 30·0	7. 17·6
				2. 28·1	8. 17·5
				3. 22·2	9. 13·8
				4. 19·3	10. 13·7
				5. 18·0	11. 13·6
				6. 17·8	12. 11·0
				average 22·6	
E. flavescens	41·8	40·5	1693	1. 34·1	7. 21·9
				2. 26·2	8. 21·5
				3. 24·6	9. 20·9
				4. 24·0	10. 20·9
				5. 23·6	11. 19·9
				6. 22·4	12. 19·4
				average 25·8	

Table 5. Table of the size, area of dorsal fasciole and number of tube-feet in the anterior ambulacrum in those spatangids which build respiratory funnels

(See pp. 379 and 384)

		size no. (length × breadth)	area of fasciole (cm^2)	number of funnel-building tube-feet	number of funnel-building tube-feet per cm^2 of fasciole	number of undeveloped tube-feet in anterior ambulacrum	total number of tube-feet in anterior ambulacrum
group	no.	*a*	*b*	*c*	*d*	*e*	*f*
E. cordatum	1	2303	0·730	103	141·0	50	153
	2	2090	0·698	96	137·6	43	139
	3	1841	0·698	83	118·9	57	140
	4	1722	0·698	90	128·8	44	134
	5	1603	0·572	79	138·2	43	122
	6	1596	0·572	79	138·2	51	130
	7	1494	0·508	72	141·8	53	125
	8	1433	0·572	80	140·0	48	128
	9	1373	0·572	88	154·0	39	127
	10	1250	0·508	84	165·4	37	121
	11	1242	0·540	76	140·8	45	121
	12	823	0·413	68	164·7	53	121
	13	818	0·413	64	155·1	52	116
	14	753	0·381	56	147·1	45	101
B. lyrifera	1	3272	1·047	32	30·5	11	43
	2	3010	0·952	32	33·6	12	44
	3	2310	0·984	26	26·4	10	36
	4	2160	0·667	30	45·0	15	45
	5	2102	0·571	28	49·0	12	40
	6	2010	0·698	28	40·1	15	43
	7	2006	0·794	30	37·8	16	46
	8	1865	0·698	26	37·2	12	38
	9	1598	0·508	22	43·3	16	38
	10	1556	0·540	24	44·4	14	38
	11	1528	0·490	26	53·1	13	39
	12	1228	0·539	23	42·6	18	41
	13	1081	0·222	17	76·5	18	35
	14	1075	0·349	20	57·3	14	34
E. pennatifidum	1	2542	0·540	6	11·1	—	—
	2	2180	0·254	6	23·6	—	—
	3	1676	0·286	5	17·5	—	—
	4	1588	0·381	5	13·1	—	—
	5	1482	0·317	5	15·7	—	—
	6	1439	0·254	5	19·7	—	—
	7	1327	0·190	5	26·2	—	—
	8	1095	0·190	5	26·2	—	—
	9	1046	0·222	5	22·5	—	—
E. flavescens		846	0·143	5	35·0	—	—

Tables 6 to 13 show the collection details, size and number of tube-feet in the petaloid parts of the paired ambulacra in the micrasters used for the biometrical study in § V, as follows.

Table 6. *Micraster corbovis*, south of England, *planus* zone

		dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
collection	registered no.	length	breadth	height	$L \times B$	$\frac{L \times B \times H}{100}$	
B.M. (N.H.) (various collections, mainly Rowe)	4638	71·5	68·4	46·4	4891	2269	204
	48766	42·8	38·1	24·3	1631	396	138
	E. 8789	67·2	63·0	44·2	4234	1871	196
	E. 9405	73·3	71·5	47·0	5241	2463	236
	E. 9832	53·7	52·8	34·0	2835	964	198
	E. 9833	56·5 (E)	56·7	33·0 (E)	3204	1057	166
	E. 9835	56·3	55·8	34·7	3141	1090	166
	E. 9895	41·1	37·7	24·0	1549	372	156
	E. 9896	42·2	37·4	23·5	1578	371	162
	E. 9920	27·9	26·4	19·2	737	141	110
	E. 16775	60·0	58·2	36·0	3492	1257	190
	E. 16776	72·8	68·8	49·0	5009	2454	196
	E. 16777	66·8	64·0	47·0	4275	2009	204
	E. 18867	55·7	54·2	39·0	3019	1177	194
	E. 18868	34·5	32·8	20·8	1132	235	162
	E. 37682	75·7	77·0	48·2	5829	2809	228
	E. 37684	76·5	71·5 (E)	49·5	5470	2707	204
	E. 37706	48·3	42·5	30·3	2053	622	152
	E. 37709	49·0	50·1	33·0	2455	810	196
	E. 38383	54·5 (E)	50·9	34·2	2774	949	170
	E. 38751	45·0	45·0	26·8	2025	543	204
	E. 38753	42·1	41·5	28·0	1747	489	148
	E. 38772	41·7	38·1	25·0	1589	397	178
	E. 38773	43·8	42·3	28·0	1853	519	180
	E. 38774	41·8 (E)	38·2	25·0	1597	399	180
	E. 38777	41·3	37·0	26·0	1528	397	110
	E. 40960	40·4	37·5	23·0	1515	357	164
	E. 41268	43·6	40·2	25·7	1753	450	160
	E. 41656	37·7	36·1	24·3	1361	331	158
	E. 41657	58·5	58·2	42·0	3405	1430	180

Table 7. *Micraster cortestudinarium*, south of England, *cortestudinarium* zone

		dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
collection	registered no.	length	breadth	height	$L \times B$	$\frac{L \times B \times H}{100}$	
D.N. collection	C. 1	51·8	52·5	32·3	2720	879	204
	C. 2	48·0	52·2	31·3	2506	784	168
	C. 3	57·5	58·0	38·2	3335	1274	184
	C. 4	50·3	52·9	38·9	2661	1035	192
	C. 5	45·0	45·0	26·8	2025	543	180
	C. 6	46·3	46·2	30·0	2139	648	176
	C. 7	52·0	52·5	34·1	2730	931	188
	C. 8	37·4	36·0	23·5	1346	316	132
	C. 9	52·3	50·6	34·0	2646	900	160
	C. 10	39·5	40·5	27·7	1600	443	152
	C. 11	40·3	39·3	23·7	1584	375	154
	C. 12	34·0	32·3	21·1	1098	232	160
	C. 13	34·6	33·9	23·6	1173	277	144
	C. 14	31·1	32·7	20·4	1017	207	130
	C. 15	32·6	31·6	20·0	1030	206	132
	C. 16	26·0	24·0	17·5	624	109	108
	C. 17	45·7	47·5	29·3	2171	636	178
	C. 18	54·2	57·2	32·0	3100	992	210
	C. 19	38·6	38·3	25·0	1478	369	144
	C. 20	43·9	42·3	28·4	1857	527	182
	C. 21	49·1	49·0	31·2	2406	751	186
	C. 22	47·1	47·6	32·9	2242	738	194
	C. 23	47·0	46·1	30·0	2167	650	162
	C. 24	43·0	43·6	28·0	1875	525	162
	C. 25	40·4	40·7	27·4	1644	450	158
	C. 26	49·8	50·1	36·0	2495	898	196
	C. 27	50·3	52·7	33·7	2651	893	166
	C. 28	23·8	21·1	14·8	502	74	100
	C. 29	50·1	54·4	33·9	2725	924	178
	C. 30	54·6	52·0	33·5	2839	951	198

TABLE 8. *MICRASTER CORANGUINUM*, SOUTH OF ENGLAND, *CORANGUINUM* ZONE

		dimensions (mm)			size no.		
collection	registered no.	length	breadth	height	$L \times B$	$\frac{L \times B \times H}{100}$	no. of tube-feet in petaloid part of paired ambs.
B.M. (N.H.)	E. 32760	49·1	55·0	35·7	2700	964	214
(Rowe collection)	E. 32763	42·4	44·9	28·8	1904	548	176
	E. 23767	41·4	43·7	29·8	1809	539	200
	E. 32772	56·8	59·5	40·4	3380	1365	216
	E. 32774	40·1	42·8	25·0	1716	429	160
	E. 32789	39·8	41·3	41·2	1644	677	158
	E. 32790	54·8	58·7	34·7	3217	1116	212
	E. 32791	55·5	61·6	36·9	3419	1261	220
	E. 32792	60·0	65·2	37·8	3912	1479	224
	E. 32795	46·4	48·9	44·0	2269	749	180
	E. 32796	52·6	56·5	33·1	2972	984	222
	E. 32799	23·7	26·8	17·2	635	109	120
	E. 32818	53·0	56·4	34·3	2989	1025	214
	E. 32819	39·7	43·8	31·5	1739	548	178
	E. 32821	40·8	44·4	31·0	1811	562	168
	E. 32822	53·5	59·1	33·8	3162	1069	200
	E. 32823	47·2	50·6	27·7	2388	662	196
	E. 32824	38·9	42·1	28·1	1638	460	168
	E. 32826	35·1	37·8	27·9	1327	370	170
	E. 32827	36·7	39·0	29·8	1431	426	148
	E. 32828	33·7	34·7	26·1	1169	305	162
	E. 32829	48·5	52·3	32·4	2537	822	200
	E. 32832	53·1	56·0	32·4	2974	963	218
	E. 32835	40·8	43·4	28·4	1771	503	182
	E. 32836	50·9	55·9	35·3	2845	1004	208
	E. 32859	49·7	53·4	34·2	2654	908	214
	E. 32860	54·8	59·0	35·5	3233	1148	238
	E. 32861	43·3	47·1	29·5	2039	602	182
	E. 32862	41·6	45·8	31·7	1905	604	176
	E. 32863	49·9	52·4	32·5	2615	850	216

Table 9. *Micraster* (*Isomicraster*) *senonensis*, south of England, *coranguinum* zone

collection	registered no.	dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
		length	breadth	height	$L\times B$	$\frac{L\times B\times H}{100}$	
B.M. (N.H.)	E. 32513	62·4	65·0	41·5	4056	1683	262
(Rowe collection)	E. 32519	48·3	46·0	37·4	2222	831	236
	E. 32520	52·3	57·9	37·5	3028	1136	252
	E. 32521	59·0	64·5	40·0	3805	1522	260
	E. 32526	65·4	66·8	42·0	4369	1835	310
	E. 32527	59·2	60·5	43·2	3582	1547	260
	E. 32528	53·0	55·8	35·7	2957	1056	250
	E. 32530	47·4	49·2	30·9	2332	721	242
	E. 32531	58·2	62·6	41·1	3643	1497	318
	E. 32533	54·5	60·0	35·1	3270	1148	262
	E. 32534	58·3	63·4	39·7	3696	1467	276
	E. 32535	50·1	54·4	33·6	2725	916	228
	E. 32536	52·7	52·5	38·8	2767	1073	250
	E. 32537	63·0	67·3	40·7	4240	1726	320
	E. 32538	52·0	53·7	36·0	2792	1005	242

Table 10. Intermediates between *coranguinum* and *senonensis*

collection	registered no.	dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
		length	breadth	height	$L\times B$	$\frac{L\times B\times H}{100}$	
B.M. (N.H.)	E. 32463	61·0	60·9	39·0	3715	1449	268
(Rowe collection)	E. 32464	48·6	47·3	37·4	2299	860	214
	E. 32465	50·0	58·1	42·3	2905	1229	228
	E. 32466	56·0	56·9	43·0	3186	1370	234
	E. 32467	45·2	50·4	37·5	2278	854	218
	E. 32468	47·0	48·9	34·6	2298	795	222
	E. 32469	42·3	42·5	28·6	1798	514	206
	E. 32470	40·9	40·2	28·4	1644	467	204
	E. 32473	45·2	45·5	33·7	2057	693	238
	E. 32474	40·0	40·3	31·1	1612	501	220
	E. 32475	46·7	47·7	34·0	2228	757	252
	E. 32476	38·9	39·1	30·3	1521	461	234
	E. 32477	41·3	43·8	30·0	1809	543	208
	E. 32478	45·6	45·5	33·1	2075	687	252
	E. 32479	43·6	41·4	31·9	1805	576	224
	E. 32480	42·8	42·0	26·7	1798	480	216
	E. 32481	41·9	42·4	31·1	1777	552	216
	E. 32482	39·1	39·8	29·3	1556	456	208
	E. 32483	43·1	44·2	29·3	1905	558	214
	E. 32484	40·1	41·1	28·5	1648	470	214
	E. 32485	48·9	51·5	31·8	2518	801	218
	E. 32486	51·2	52·9	35·5	2708	961	254
	E. 32488	46·4	48·4	33·0	2246	741	228
	E. 32489	43·9	44·8	30·1	1967	592	212
	E. 32490	45·8	46·1	33·4	2111	705	252
	E. 32495	40·8	40·8	30·1	1665	501	210
	E. 32503	54·6	55·7	42·8	3041	1302	248
	E. 32505	46·1	46·1	29·0	2125	616	228
	E. 32506	45·9	48·8	30·6	2240	685	234
	E. 32511	53·2	54·7	37·0	2910	1077	242

TABLE 11. *MICRASTER GLYPHUS*, NORFOLK, *MUCRONATA* ZONE

collection	registered no.	dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
		length	breadth	height	$L \times B$	$\frac{L \times B \times H}{100}$	
Norwich Castle Museum (Brydone collection)	76·937 (10)	57·5	58·3	30·0 (E)	3352	1006	218
	76·937 (11)	67·5	70·2	33·0 (E)	4738	1563	242
	76·937 (13)	55·0	59·1	28·2	3250	916	222
	76·937 (14)	47·4	47·8	28·0	2266	634	176
	76·937 (15)	48·5	53·7	28·8	2604	750	210
Geol. Surv. Museum (Woodward collection)	H.B.W. 427	68·8	68·5	33·2	4713	1565	218
	H.B.W. 556	44·3	45·5	32·2	2016	649	156
	H.B.W. 560	37·8	42·5	30·6	1606	491	136
	H.B.W. 561	32·0	34·3	28·3	1098	311	144
	R. 250	51·9	51·3	35·0	2662	932	202
B.M. (N.H.) (Savin and Rowe collections)	E. 10541	56·2	53·0	28·1	2979	837	200
	E. 19732	44·9	48·8	32·0	2191	701	228
	E. 19733	41·5	45·5	28·1	1888	530	198
	E. 19734	45·1	48·6	31·2	2192	684	214
	E. 19736	30·5	31·8	23·0	970	223	164
	E. 19772	70·0	66·0	40·0 (E)	4620	1848	204
	E. 19773	41·8	44·5	31·8	1860	591	158
	E. 19774	72·0 (E)	77·9	36·2	5609	2030	246
	E. 19775	39·0	38·2	18·7	1490	279	156
	E. 19740	44·7	46·0	27·3	2056	561	188
	E. 19741	43·0	43·7	22·1	1879	415	182
	E. 19742	40·3	38·5 (E)	23·7	1552	368	154
	E. 19743	30·8	27·7	19·8	853	169	136
	E. 19745	31·2	34·2	19·7	1067	210	140

TABLE 12. *MICRASTER* (*I.*) *STOLLEYI*, NORFOLK, *MUCRONATA* ZONE

collection	registered no.	dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
		length	breadth	height	$L \times B$	$\frac{L \times B \times H}{100}$	
Norwich Castle Museum (Rose and Brydone collections)	15·72	50·2	52·4	40·0	2630	1052	284
	76·937 (2)	58·5	60·0	42·3	3510	1485	278
	76·937 (3)	42·8	43·5	29·7	1862	553	234
	76·937 (5)	46·1	47·9	31·1	2208	687	244
	76·937 (6)	41·7	45·1	30·0 (E)	1881	564	224
	76·937 (7)	46·1	48·7	36·0	2245	808	256
	76·937 (8)	50·5	50·7	35·2	2560	901	248
	76·937 (9)	41·2	41·3	31·6	1702	538	198
	76·937 (16)	43·5	45·5	34·0	1979	673	236
	76·937 (17)	56·0	59·8	42·3	3349	1417	274
	76·937 (18)	49·2	50·0	36·8	2460	905	248
	76·937 (20)	48·2	48·8	31·5	2352	741	230
	76·937 (21)	54·0 (E)	56·0	35·0	3024	1058	308
Geol. Surv. Museum (Woodward collection)	H.B.W. 306	47·1	51·0	35·2	2402	845	232
	H.B.W. 370	47·9	51·8	33·0	2481	819	236
	H.B.W. 371	49·0	51·9	36·3	2543	923	258
B.M. (N.H.) (Savin and Rowe collections)	24890	51·3	53·3	38·2	2734	1044	238
	E. 2104	54·7	55·9	38·6	3058	1180	232
	E. 10545	39·0	41·7	29·9	1626	486	224
	E. 19763	45·1	48·8	34·0	2201	748	260
	E. 19764	46·9	49·5	29·9	2322	694	248
	E. 19766	59·8	61·8	42·0 (E)	3696	1552	238
	E. 19767	44·0 (E)	48·0	33·5	2112	707	238
	E. 19768	52·5	54·6	36·7	2866	1052	226
	E. 34721	46·5	46·0	34·8	2139	744	250

TABLE 13. INTERMEDIATES BETWEEN *GLYPHUS* AND *STOLLEYI*

collection	registered no.	dimensions (mm)			size no.		no. of tube-feet in petaloid part of paired ambs.
		length	breadth	height	$L\times B$	$\frac{L\times B\times H}{100}$	
Norwich Museum	76·937 (12)	56·9 (**E**)	63·6	30·5	3619	1104	268
	76·937 (19)	47·0	53·0	35·2	2491	877	222
Geol. Surv.	H.B.W. 372	47·4	49·9	31·8	2365	752	210
B.M. (N.H.) (Rowe collection)	E. 10544	41·0	41·6	27·0	1706	461	202
	E. 19735	40·6	43·1	28·4	1750	497	216
	E. 19737	43·2	47·7	30·6	2061	631	212
	E. 19738	46·8	50·0	31·3	2340	732	220
	E. 19744	38·1	38·6	27·6	1471	406	166
	E. 19746	41·9	46·8	29·0	1961	570	250
	E. 19755	49·0	54·7	32·4	2680	868	212
	E. 19756	48·8	51·9	36·7	2533	930	276
	E. 19757	45·0	51·2	32·4	2304	746	238
	E. 19758	41·2	43·8	29·1	1805	525	206
	E. 19759	34·0	35·6	25·0	1210	302	190
	E. 19760	32·6	34·5	23·2	1125	261	178
	E. 19761	28·1	27·9	20·9	784	164	148
	E. 19762	25·6	26·5	18·6	678	126	142
	E. 19765	39·7	41·6	29·0	1651	479	180

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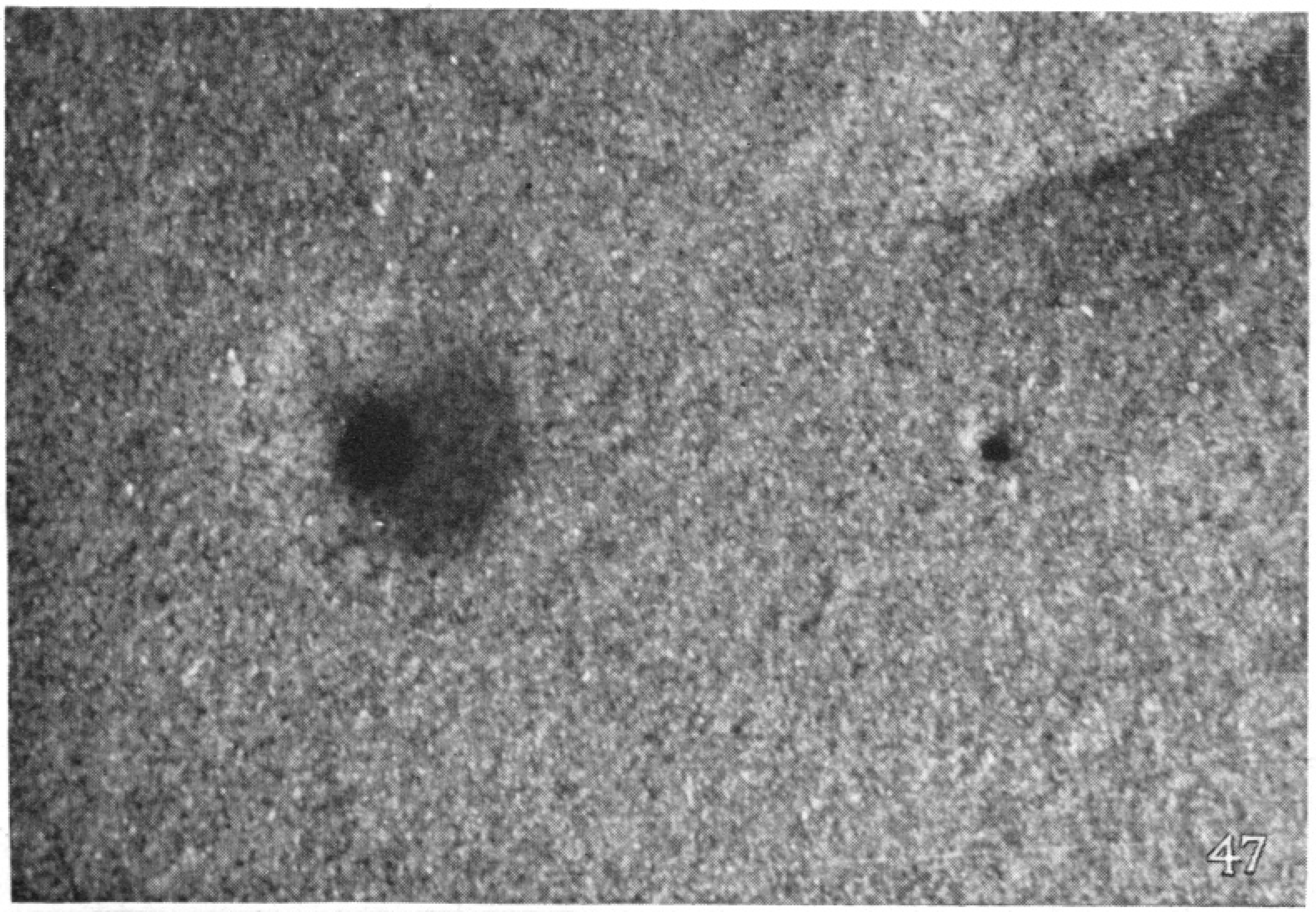

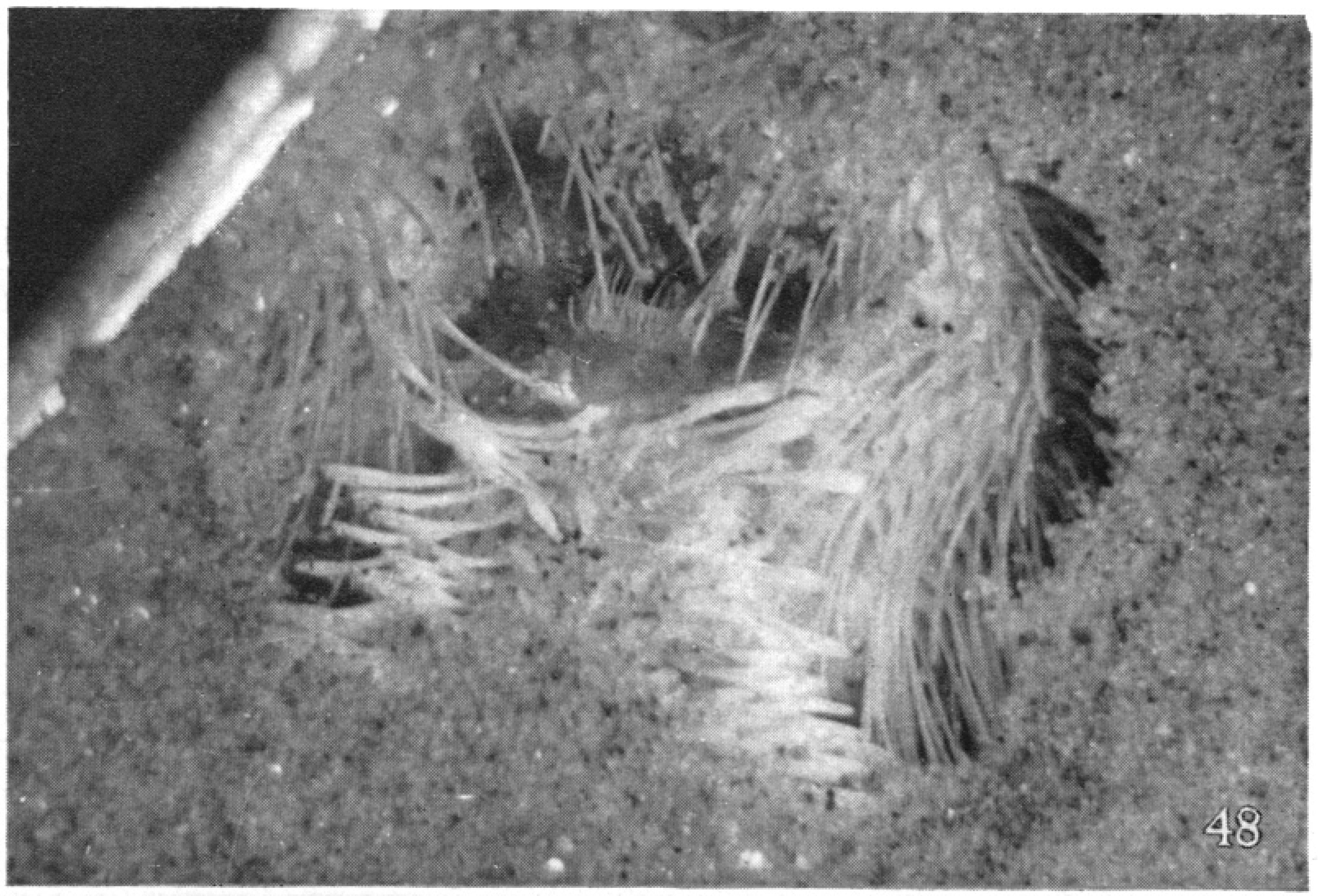

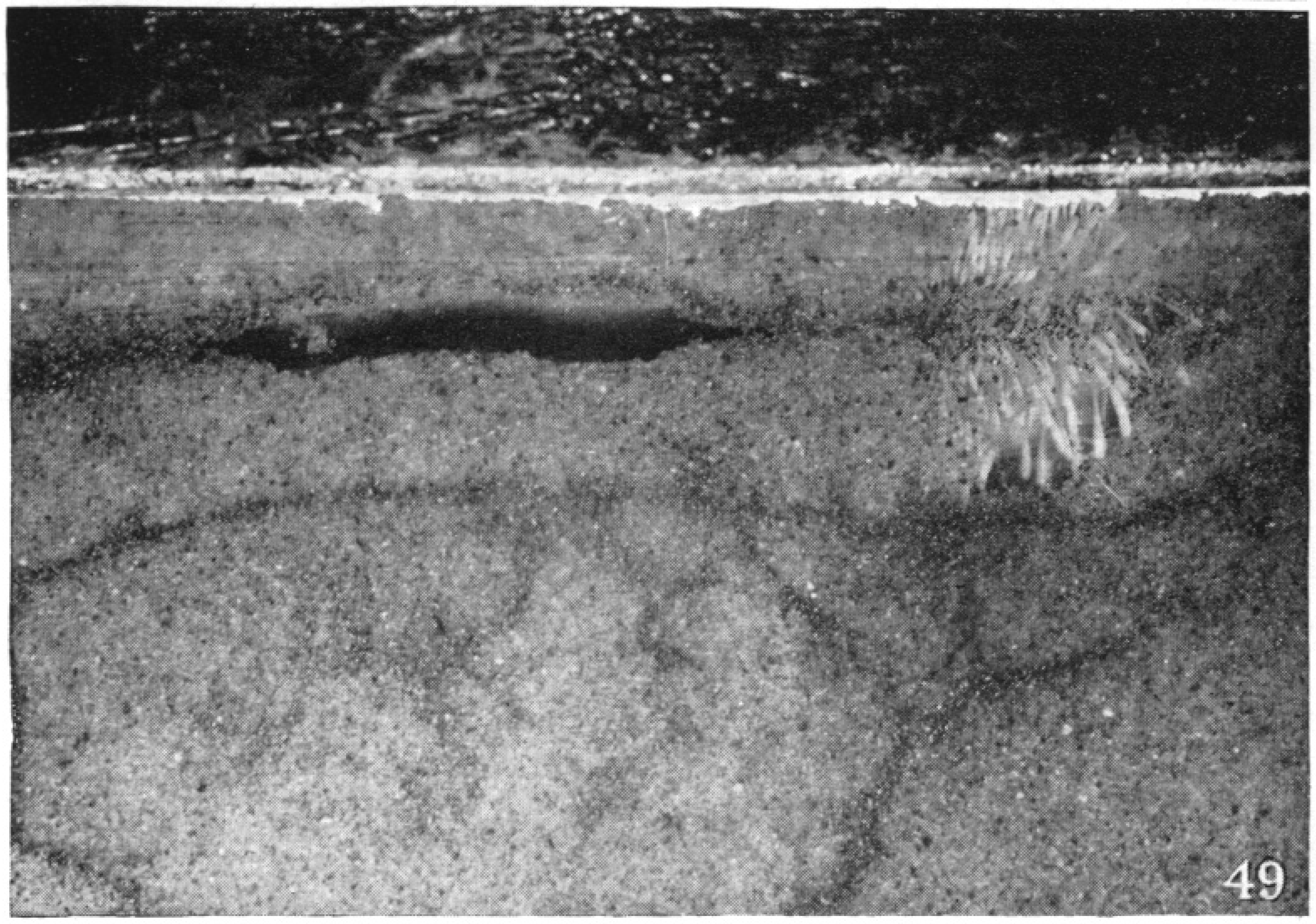

FIGURE 47. Surface view of the openings of two successive funnels built by a burrowing *E. cordatum* in sand in an aquarium. The pit on the left is the remains of the first-formed funnel, which has filled in and been discarded; the small hole on the right has just been opened by the urchin, and the tube-feet of the dorsal anterior ambulacrum will now be maintaining it. The distance between the two pits in this case is about 4 cm.

FIGURE 48. Ventral view, looking upwards at the bottom of an aquarium, of a burrowing *E. cordatum* which has just appeared, and is about to move along the side of the tank. The long scraping spines of Interambs. 1 and 4 have cleared two areas on either side of the plastron, of which some of the paddle-shaped spines can be seen. The urchin is feeding, and the oral tube-feet are blurred in consequence; however, the disk of one, pressed to the glass bottom of the tank, can be seen posterior to the mouth.

FIGURE 49. Ventral view, looking upwards at the bottom of an aquarium, of a burrowing *E. cordatum* moving along the side of the tank, and of which only the plastron spines are visible, showing the single sanitary tube extending from the posterior side of the animal for a distance of about 8 cm. An explanation is given in the text, p. 368.

FIGURE 50. Photograph of a spadeful of sand which has been dug up on the beach. The sand has cleaved across the burrow of an *E. cordatum* and the urchin can be seen in its burrow 10 to 12 cm below the surface of the sand. The respiratory funnel to the surface is also visible, with the dorsal tuft of spines extending up it for about 1 cm. The anterior side of the urchin is to the right: the subanal tube is not visible.