THE STRUCTURE, FUNCTION, AND EVOLUTION OF TUBE FEET AND AMBULACRAL PORES IN IRREGULAR ECHINOIDS

by ANDREW B. SMITH

ABSTRACT. The variation in the tube foot morphology of twenty species of Recent irregular echinoids, with representatives from all four principle groups, is described and correlated with the structure of the associated ambulacral pores. Tube feet are often highly modified and sensory, respiratory, suckered, feeding, and funnel-building tube feet are all described. Three types of pore are recognized—isopores, anisopores, and unipores—and these are further subdivided on the basis of pore size and shape, size and position of the neural canal, development of an attachment area, and the extent of the periporal area.

Tube foot morphology is interpreted in functional terms and related to the animal's mode of life. Functionally significant features of pores include their shape and size, the number of pores, their divergence, and the attachment and periporal areas. The structure and arrangement of pores can often be used to identify the morphology and function of the associated tube foot.

The evolution and diversification of irregular echinoids is seen as a direct consequence of changes in feeding method. Primitive irregulars had abandoned grazing or scavenging for selective particle ingestion and rapidly diversified as bulk sediment swallowers in less organic-rich substrates. Like Recent holectypoids and cassiduloids, the early groups appear to have used suckered tube feet for feeding and were thus restricted to coarse sediments. By the Cretaceous, mucous adhesive tube feet had developed in the disasteroids enabling them to feed on finer substrates and spatangoids and holasteroids probably evolved from an ancestor with penicillate tube feet. Clypeasteroids evolved from cassiduloids initially to gain access to finer sediments. Pourtalesiids have evolved a feeding mechanism that does not involve tube feet.

TUBE feet are undoubtedly organs of great importance to the echinoderms. These external extensions of the water vascular system are found in all extant classes of the phylum Echinodermata, but the variation in tube foot structure and function that occurs in irregular echinoids surpasses that found in any other group of echinoderms. In irregular echinoids the adoption of a buried mode of life has been accompanied by a marked specialization and diversification of the tube feet. As well as sensory and suckered tube feet, which also occur in regular echinoids, irregular echinoids may possess tube feet especially modified for mucus secretion, gaseous exchange, feeding, and funnel-building. Accompanying this diversification in tube foot structure and function there is a corresponding change in the pore, or pores, through which each tube foot connects with its internal ampulla.

Although the morphology of the tube feet of irregular echinoids is relatively well known, from external descriptions and histological studies by such workers as Lovén (1883), Hamann (1887), Nichols (1959*a*, *c*), and Fenner (1973), the corresponding variation in pore morphology has been largely ignored from a functional point of view. Only Lovén (1883) has described and illustrated a variety of tube feet and their associated ambulacral pores, though he made no attempt to correlate pore morphology with tube foot structure, and gave no functional interpretations. Nichols (1959*a*, *b*) has described the tube feet and ambulacral pores in the spatangoid *Echinocardium cordatum* and suggested that pore morphology could be used to help reconstruct the tube feet of fossil echinoids. Analysis of the functional morphology of the coronal pores of regular echinoids (Smith, 1978*b*) has shown that pore morphology and tube foot morphology are closely linked.

[Palaeontology, Vol. 23, Part 1, 1980, pp. 39–83, pls. 1–6.]

With the exception of the elongate pores making up the petals, which are generally known to bear specialized respiratory tube feet, the functional significance of the different pore morphologies is poorly understood. This paper sets out to describe the variation in ambulacral pores of irregular echinoids and to correlate this with the variation in tube foot morphology. Once the functional significance of the pore morphology in Recent species is better understood it should be possible to reconstruct the tube feet of fossil species with more certainty. A knowledge of the probable tube foot morphology in fossil species can be extremely helpful in palaeobiological studies as has been shown by Nichols (1959*b*) and Smith (1978*a*).

MATERIALS AND METHODS

A histological study of the tube feet of a variety of irregular echinoids, listed in Table 1, was carried out using the method outlined in Smith (1978*b*). Each species was examined under a light microscope to identify areas bearing different tube feet and a number of tube feet from each area were sectioned. The pore morphology associated with each type of tube foot was studied by placing cleaned and gold-coated pieces of test under a scanning electron microscope (SEM). Stereo electron micrographs were taken by rotating the stage through 7½ degrees and re-centring. In addition the morphology of the tube feet and pores was examined in a number of other Recent species by means of a binocular microscope. Ambulacral pores of a number of fossil species have also been examined using the SEM.

TABLE 1. Recent species in which the tube feet were examined histologically

HOLECTYPOIDA

Echinoneus cyclostomus Leske

CASSIDULOIDA

Apatopygus recens (Milne-Edwards)
Cassidulus cariboearum Lamarck
Echinolampas crassa (Bell)

CLYPEASTEROIDA

Clypeaster rarispina de Meijere
C. rosaceus (Linnaeus)
Dendraster excentricus (Eschscholtz)
Echinocyamus pusillus (Müller)
Echinodiscus bisperforatus Leske
Mellita quinquiesperforata (Leske)

HOLASTEROIDA

Pourtalesia miranda Agassiz
Urechinus wyvilli (Agassiz)

SPATANGOIDA

Aeropsis rostrata (Wyville Thomson)
Brissopsis lyrifera (Forbes)
Echinocardium cordatum (Pennant)
E. pennatifidum Norman
Hemiaster expurgitus Lovén
Metalia sternalis (Lamarck)
Palaeostoma mirabile (Gray)
Spatangus raschi Lovén

NOMENCLATURE

The area of the test, to which each tube foot attaches, is perforated by a single or double pore, and the plate surface surrounding the pore or pores is typically modified to accommodate the base of the tube foot. Where this area contains two more or less equally sized pores, then it is described as an *isopore*. Where the two pores differ markedly in size it is termed an *anisopore*. Where only a single pore is present then the area is described as a *unipore*. Much of the terminology applied to ambulacral pores has been given in Smith (1978*b*) and it is only necessary to mention briefly a number of those terms that are to be used throughout this paper. The *attachment area* is defined as that area of the plate surface into which the connective tissue fibres of the tube foot insert. The stereom of the attachment area is modified for fibre insertion. Where there are very few connective tissue fibres to accommodate, as in some respiratory tube feet, no stereom modification occurs and the attachment area is said to be absent. If the stereom is not well preserved the attachment area can often be recognized by the fact that it usually forms an elevated rim around the pore or pores. The area which lies within the attachment area and which surrounds the pore or pores is termed the *periporal area*. This is covered in life with squamous epithelium and is best developed in certain unipores. In isopores and anisopores the pore lying nearer to the perradial suture is the *perradial pore*. This pore accommodates a branch of the radial nerve which, when well developed, lies in a groove—the *neural canal*. The other pore, lying nearer the adradial suture, is termed the *adradial pore*. In some cases the two pores may lie in an adoral/adapical orientation so that the perradial pore takes up an adoral position relative to the adradial pore. The area which lies directly in between the two pores is the *interporal partition*.

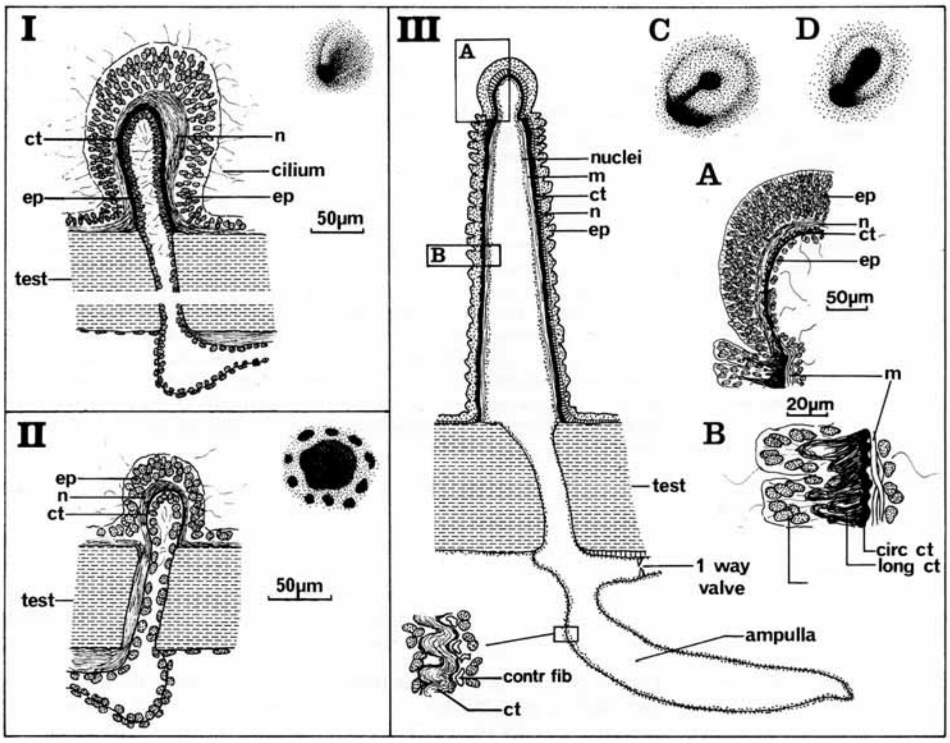
TUBE FOOT MORPHOLOGY

Before discussing the functional morphology of ambulacral pores, it is necessary to outline the morphology of the tube feet of irregular echinoids. These tube feet show considerable morphological variation and can be arranged into the following functional groups.

Sensory tube feet (text-fig. 1). The simplest of tube feet are those found ambitally in the lateral and posterior ambulacra of some spatangoids, as in *Echinocardium cordatum* (text-fig. 1ɪɪ). Above each unipore there is a small mound of sensory epithelium. The lumen is small and extends only slightly above the level of the test. A thin connective tissue layer separates the ectodermal cells from the endothelial cells, both of which are densely ciliated. Muscle fibres are absent and there is no ampulla, thus these tube feet are apparently non-extensible. Much of the pore space through the test is taken up with nervous tissue and there is a thick nerve plexus which underlies the epithelial cells of the tube foot. This tube foot is similar in construction to the terminal tube foot of ocular plates. These tube feet are presumably chemo-sensory in function.

A similar type of tube foot is found at the apex of the anterior ambulacrum of *Brissopsis lyrifera* (text-fig. 1ɪ). Here the ten or twelve most adapical tube feet are squat and bulbous and are richly endowed with nerve fibres and cilia. Stem muscle fibres and an ampulla are again absent indicating that these tube feet are also non-extensible. These tube feet, as well as being important chemo-sensory receptors, are also likely to enhance cilia-induced water movement down the anterior ambulacrum.

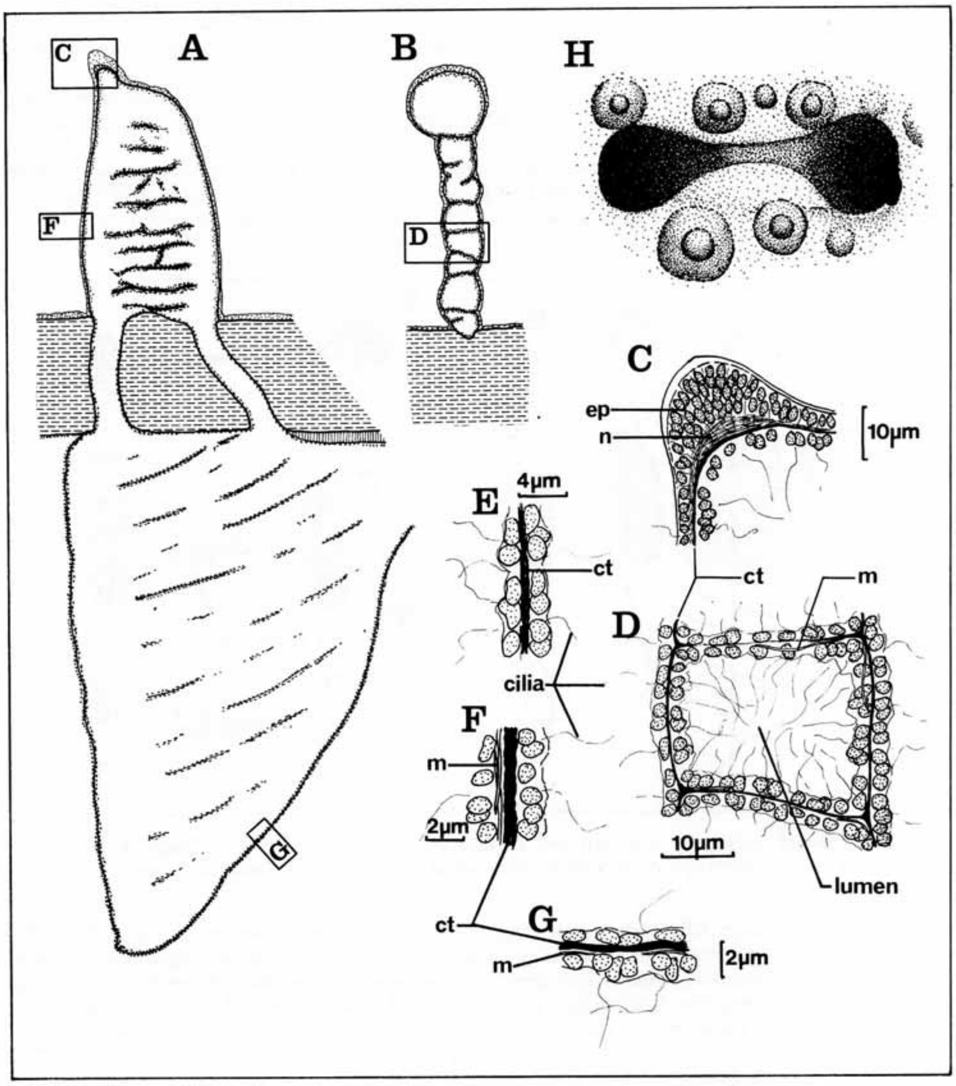
In the majority of spatangoids, the sensory tube feet that occur between the petals and the phyllodes are long and extensible. The stem, which has a few muscle fibres as well as circular and longitudinal connective tissue fibres, terminates in a cap of dense epithelial cells underlain by a thickened nerve plexus (text-fig. 1ɪɪɪ). The connective tissue layer of the tip commonly incorporates spicules or, occasionally, sheet-like elements, composed of a single layer of trabeculae (see Lovén 1883, pl. X). The associated ampulla is small and cylindrical. There are obvious bands of contractile fibres which branch and interconnect with one another as illustrated by Nichols (1959*c*, fig. 5) for the cylindrical ampullae of a clypeasteroid. The lumen of the ampulla is not crossed by septa. These tube feet are extensible and probe the surrounding substrate. In spatangoids, all ambital tube feet in ambulacrum III have this structure. In addition, the aboral tube feet in ambulacrum III of certain species are also sensory. Finally, in the holasteroids *Urechinus naresianus* and *Pourtalesia*



TEXT-FIG. 1. Sensory tube feet. I, longitudinal section through an apical tube foot in ambulacrum III of *Brissopsis lyrifera* and the associated unipore. II, longitudinal section through an ambital ambulacrum IV tube foot of *Echinocardium cordatum* and the associated simple unipore. III, longitudinal section through an ambital ambulacrum I tube foot and ampulla of *Spatangus raschi*: A and B, detailed structure of terminal pad and stem as indicated: C, ambital ambulacrum III unipore of *S. raschi*: D, aboral ambulacrum III unipore of *Pourtalesia miranda*. Abbreviations used in text-figs.: circ ct = circular connective tissue; contr fib = contractile fibre; ct = connective tissue; cyt septum = cytoplasmic septum; ep = epithelium; long ct = longitudinal connective tissue; m = muscle; muc cells = mucus cells; n = nerve.

miranda aboral respiratory tube feet are lacking and in their place are found simple sensory tube feet borne upon unipores. In *Pourtalesia* these are no more than minute, non-extensible sensory mounds but in *Urechinus* they are slightly larger.

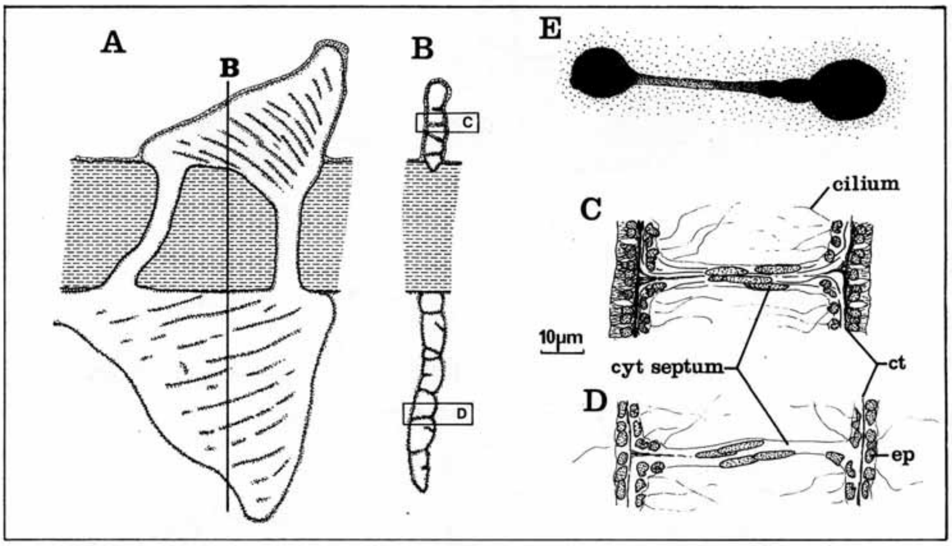
Respiratory tube feet (text-figs. 2-5). Tube feet that are specialized for gaseous exchange are always associated with isopores or anisopores. The lumen of such tube feet is divided into two large tubular channels separated by a thin-walled central area. This central region is crossed by epithelial septa, each with a thin core of connective tissue, which effectively partitions the lumen into narrow, parallel passageways connecting the two major channels (text-fig. 2). In its simplest form this central region is planar with the parallel passageways stacked one above the other (text-figs. 2, 3). This is the case in tube feet of cassiduloids, most clypeasteroids, and a few spatangoids. The tube foot may either be tall and approaching bilateral symmetry (text-fig. 2), as found in the respiratory tube feet of arbacioids (Fenner 1973; Smith 1978*b*), or may be strongly skewed towards the adradial pore



TEXT-FIG. 2. Aboral respiratory tube foot and ampulla of *Apatopygus recens*. A, longitudinal section; B, sagittal section; C, D, F, G, details of structure as indicated; E, longitudinal section through part of the stem of a respiratory tube foot of *Cassidulus cariboearum*; H, aboral conjugate isopore of *A. recens*.

where the tip may be developed into a sensory pad (text-fig. 3). In *Clypeaster rarispina* and *B. lyrifera* lobes extend from the central region of respiratory tube feet increasing the surface area (text-fig. 4). Larger lobes are septate.

The petal tube feet in spatangoids such as *E. cordatum* and *Spatangus raschi* are exceedingly convolute making the reconstruction of the precise three-dimensional appearance of these tube feet extremely difficult. Longitudinal, sagittal, and transverse sections through respiratory tube feet of *Spatangus* are given in text-fig. 4. From these it appears as though the central region of the tube foot gives off prominent branched and lobed outpouchings which are partitioned by septa. In some instances these outpouchings appear to be better developed on one side of the tube foot.

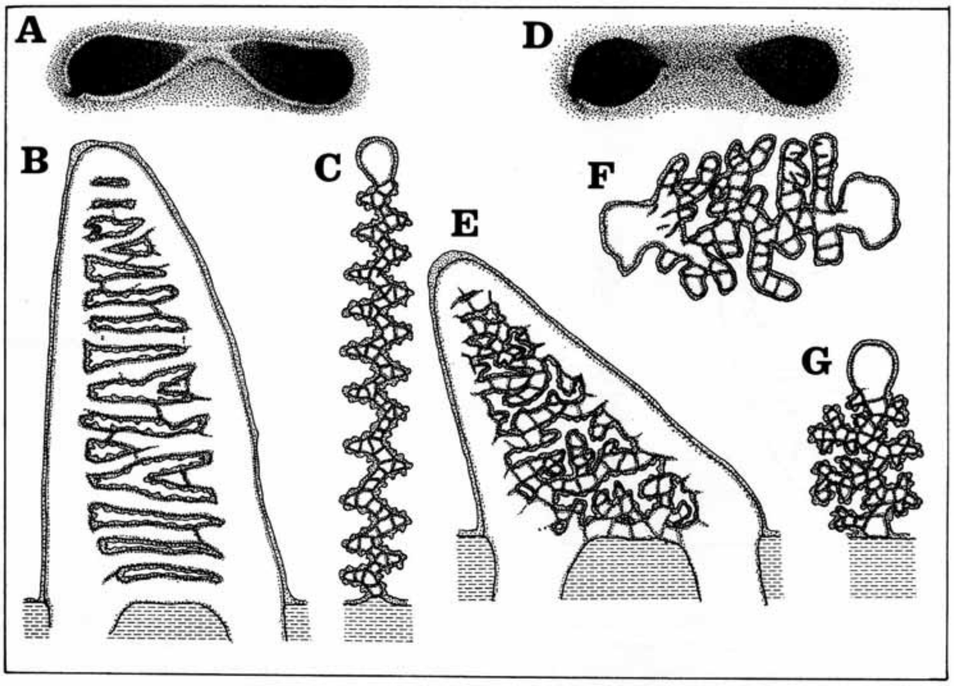


TEXT-FIG. 3. Aboral respiratory tube foot and ampulla of *Echinolampas crassa*. A, longitudinal section; B, sagittal section; C, D, detailed morphology as indicated; E, associated anisopore.

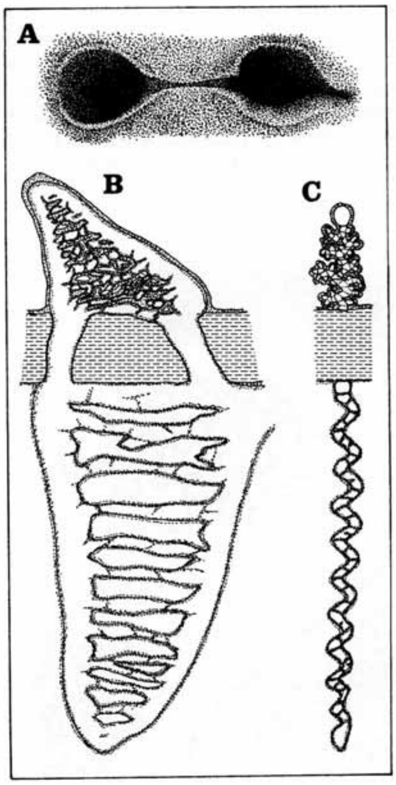
In all these respiratory tube feet a single layer of fine muscle fibres is present in the walls of the two main channels and fine contractile fibres are also sparsely distributed throughout the central region. A circular connective tissue layer is present but is usually thin so that the combined thickness of the muscle and connective tissue layers is never more than a few μm. The epithelial layers are usually just one cell thick and in the ectoderm it is typical to find groups of nuclei clustered together. The endothelial cells, lining the passageways of the central area, are heavily ciliated. The ectoderm is also well ciliated.

The associated ampulla is extremely broad and flat. The walls of the ampulla have no more than a thin membrane of connective tissue and few, if any, contractile fibres. The narrow lumen of the ampulla is crossed by epithelial septa with elongate nuclei, partitioning the lumen into a large number of passageways, much as in the respiratory tube feet (text-fig. 2). These ampullae may be linked with one another by thin, connective-tissue strands which originate from the inner edge of the ampullae. In *E. cordatum* and *S. raschi*, the ampullae were found to have a broad, central, corrugated area, crossed by septa and linking the two major channels which run the length of each ampulla (text-fig. 5).

Suckered tube feet (text-figs. 6–8). Suckered tube feet which resemble those of regular echinoids were found only in the holectypoid *Echinoneus cyclostomus*. This species has both oral and aboral suckered tube feet (text-fig. 6). The stem of the tube foot has both circular and longitudinal connective tissue fibres and there is also a layer of stem retractor muscle fibres. A short septum extends for about a quarter of the length of the lumen from the interporal partition. The sucking disc is composed of an outer ring of dense epithelial cells, forming a sensory pad, and a central region with muscle fibres running from the cuticle to the connective tissue layer. There are clumps of cells, found largely beneath the rosette, giving rise to ducts which can be traced to the disc surface. These are presumably secretory in function. Levator muscle fibres run from the centre of the disc to the rosette. The rosette and frame in a tube foot of *Echinoneus* have been illustrated by Lovén (1883). Oral and aboral tube feet of *Echinoneus* are similar in structure but differ in size, the diameter of the disc in oral tube feet being around 150 μm compared with 120 μm for aboral tube feet. In some aboral tube feet the skeletal framework of the disc may be so reduced as to be almost lost. These tube feet still retain their suction power since the disc and levator muscle fibres are just as well developed as they are in oral tube feet.



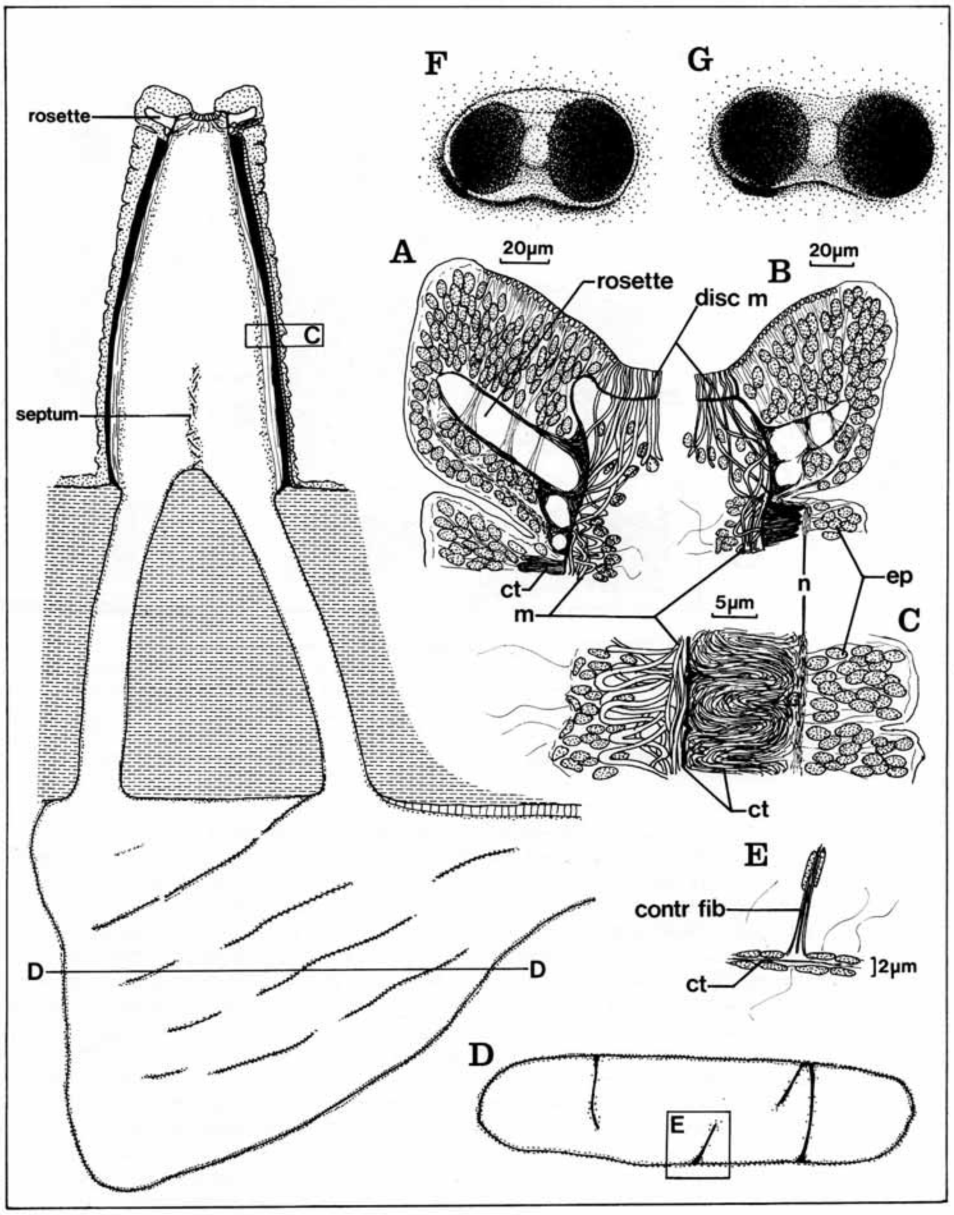
TEXT-FIG. 4. A–C, aboral respiratory tube foot and isopore of *Brissopsis lyrifera*: A, associated isopore; B, longitudinal section; C, sagittal section. D–G, aboral respiratory tube foot and isopore of *Spatangus raschi*: D, associated isopore; E, longitudinal section; F, transverse section through tube foot; G, sagittal section through tube foot.



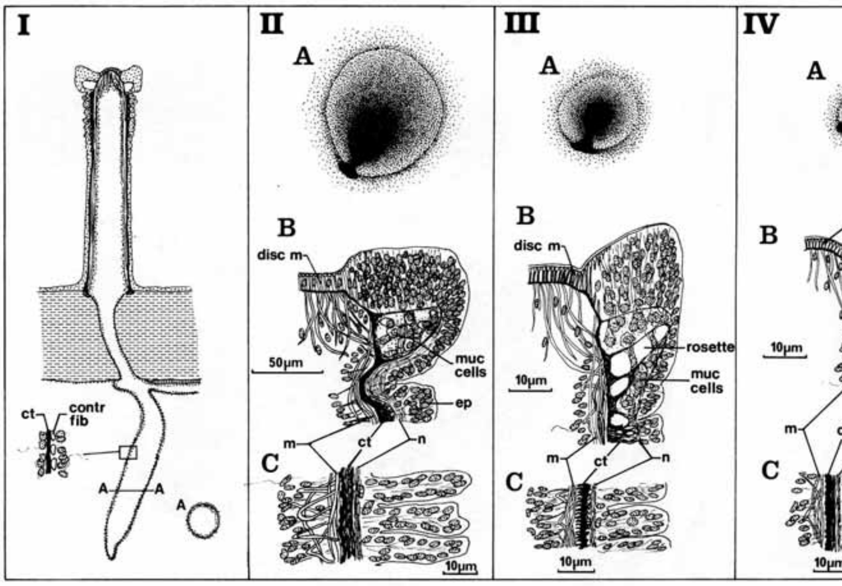
TEXT-FIG. 5. Aboral respiratory tube foot and ampulla of *Echinocardium cordatum*. A, internal plate surface showing the conjugate furrow between pores; B, longitudinal section; C, sagittal section.

The sucking disc in *Echinoneus* is intermediate in character between the discs of regular echinoids and the sucking discs of cassiduloids and clypeasteroids. On the one hand the disc has many of the features, including a frame and rosette, that are found in the discs of regular echinoids. Yet, as in cassiduloids and clypeasteroids there are disc muscles lying outside the connective tissue layer, a condition only met with in certain cidaroids amongst regular echinoids (Nichols 1961; Smith 1978*b*). The ampullae of *Echinoneus* are also intermediate in their characteristics. They are rather squat and relatively broad and the lumen is crossed by only three or four septa. Contractile fibres are associated with the septa and they are also present in the walls of the ampulla.

In other groups of irregulars, suckered tube feet tend to be much smaller and possess less well-developed rosettes. In the cassiduloids that were examined the oral tube feet were all found to have a terminal sucking disc (text-fig. 7). The stem follows the normal pattern found in echinoid tube feet, with both circular and longitudinal connective tissue fibres as well as muscle fibres. In the disc there is a small rosette but no frame. Both levator and disc muscle fibres are present and there is an outer ring of dense epithelial cells which form a sensory pad. Between the sensory pad and the disc muscle fibres there is a loose mesh of cells amongst which ducts can be seen running to the surface of the disc. The ampulla is always elongate and cylindrical. The lumen of the ampulla is not crossed by septa. Contractile fibres are readily apparent in the walls of the ampulla and these run circularly and branch to interconnect with one another.



TEXT-FIG. 6. Tube foot and ampulla of *Echinoneus cyclostomus*. A, longitudinal half-section of the sucking disc of an oral tube foot; B, longitudinal half-section of the sucking disc of an aboral tube foot; C, longitudinal section of part of the stem of an oral tube foot; D, E, structure of the ampulla, as illustrated; F, partitioned isopore of the oral surface; G, partitioned isopore of the aboral surface.

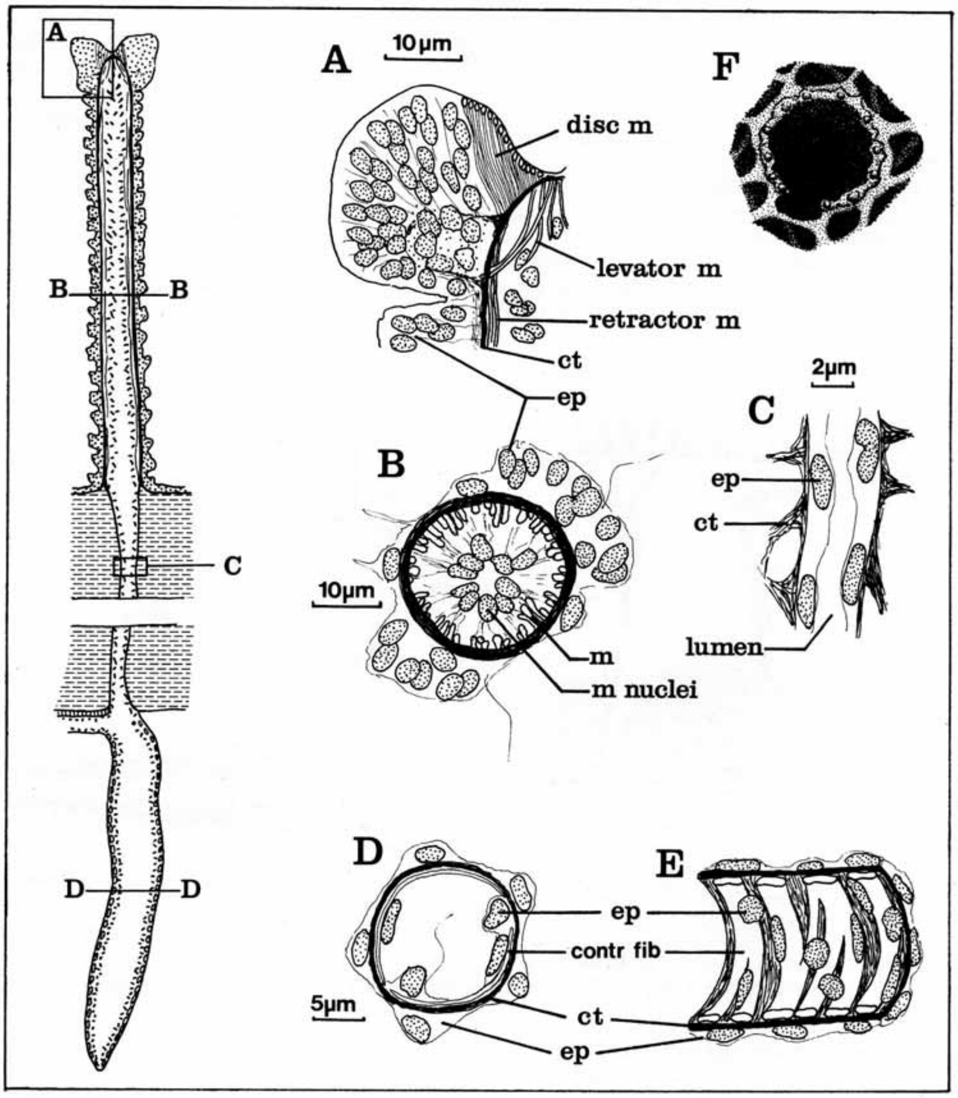


TEXT-FIG. 7. Suckered tube feet of cassiduloids. I, general longitudinal section. II, phyllode tube foot of *Echinolampas crassa*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. III, phyllode tube foot of *Cassidulus cariboearum*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. IV, ambital tube foot of *Apatopygus recens*: A, associated unipore; B, longitudinal half-section of the disc; C, longitudinal section of part of the stem. The difference in disc shape is due to the state of contraction of the levator and disc muscles.

The ambital tube feet of cassiduloids are relatively smaller but are similar in structure (text-fig. 7). The disc muscle fibres are well developed and the rosette is commonly reduced to a circle of spicules. The ampullae are again cylindrical and have prominent contractile fibres.

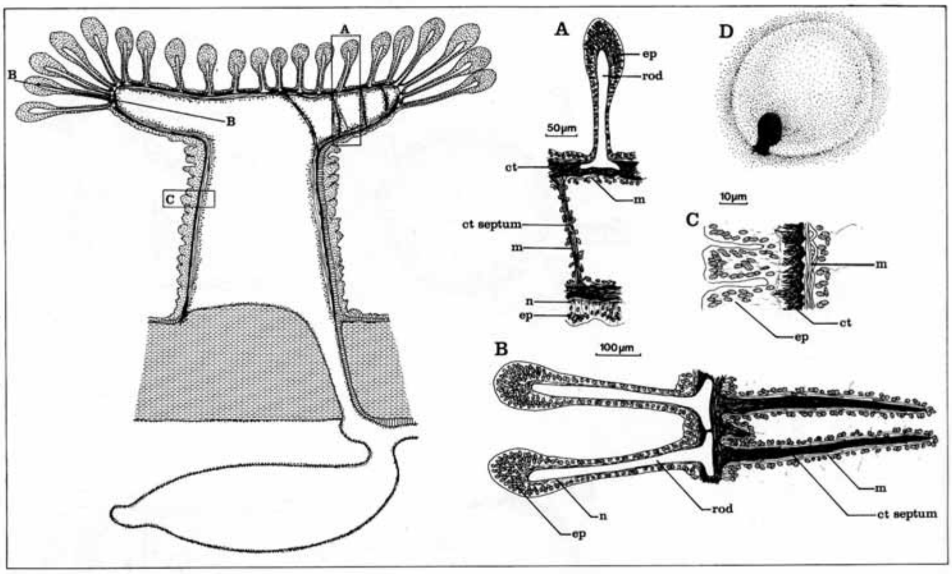
The smallest suckered tube feet that were found in this survey are the so-called 'accessory' tube feet of clypeasteroids. These are very similar to the ambital tube feet of cassiduloids. The detailed histology of these tube feet in *Echinocyamus* has been provided by Nichols (1959*c*) and other suckered tube feet of clypeasteroids were found to differ little in their structure. The morphology of the suckered tube feet of *Echinodiscus bisperforatus* is given in text-fig. 8. The terminal disc has well-developed, disc muscle fibres and levator muscles. The rosette, in *Clypeaster*, is reduced to a small circular element and in sand dollars there is only a ring of spicules (Durham 1955). The ampulla is simple and cylindrical with prominent contractile elements which run circularly around the walls. In the clypeasteroids which have a system of food grooves, it is common to find that those tube feet lying in, or adjacent to, a food groove are squat with large heads and fewer disc and stem muscle fibres. These tube feet possess a thickened nerve plexus and epithelial pad which includes mucous-secretory cells, according to Chia (1969). These tube feet are likely to be much less active than the more slender and elongate tube feet of the rest of the ambulacral surface. The variation in size of these suckered tube feet has recently been pointed out by Phelan (1977).

There are a number of published accounts concerning the activity of suckered tube feet and it appears that they are primarily used in feeding and burial activities. Rose (1978) reports that, in *Echinoneus*, oral tube feet collect grains of substrate and pass them towards the peristome and into



TEXT-FIG. 8. Suckered tube foot of *Echinodiscus bisperforatus*. A–D, detailed morphology as indicated; E, diagrammatic cut-out section of the wall of the ampulla to show the interbranching of the circular contractile fibres; F, associated micro-unipore.

the mouth. Oral tube feet are also used to adhere to rocks and large coral fragments, possibly for stability. Tube feet are also involved in passing grains aborally during burial where the aboral tube feet hold them in position. The life styles of three species of cassiduloid have recently been published (Higgins 1974; Thum and Allen 1976; Gladfelter 1978) and it is known that oral tube feet selectively collect and transfer sediment grains to the peristome. It is likely that ambital tube feet may help to pass sediment grains aborally during burial but this has not been reported. In the clypeasteroid *Echinocyamus* tube feet again assist in burial by passing grains aborally and holding them there (Nichols 1959*c*) but apparently take little part in feeding activities. However, in sand dollars, such as *Leodia* (Goodbody 1960), *Mellita* (Bell and Frey 1969), and *Dendraster* (Chia 1969; Timko 1976) tube feet appear to be primarily concerned with the capture of particles and their transference to the mucous-rope which lies in the food groove. The large and squat tube feet of the floor of the food grooves are sites of mucus production and their activity moves the mucous-rope towards the peristome. These tube feet also play an active role in the selection and rejection of particles at the Y junctions of food grooves (Timko 1976).



TEXT-FIG. 9. Phyllode tube foot of *Spatangus raschi*. A–C, detailed morphology as indicated; B, part of a transverse section across half of the disc in the plane BB; D, the associated unipore.

Buccal and phyllode tube feet (text-fig. 9). In the cassiduloids, tube feet of the oral surface are all suckered and have more or less the same structure, described above. In a number of clypeasteroids, however, ten large tube feet are found surrounding the peristome and these are known as buccal tube feet. The histology of buccal tube feet of *Echinocyamus* has been detailed by Nichols (1959*c*). The buccal tube feet of sand dollars appear to be similar in structure to those of *Echinocyamus* but much difficulty was encountered in serial sectioning these tube feet due to the large number of adhering sand grains. In *Echinocyamus* buccal tube feet are largely sensory in function and actively probe the substrate (Nichols 1959*c*). In *Dendraster*, however, these tube feet transfer the mucous feeding-rope into the peristome (Chia 1969).

It is in the holasteroids and spatangoids that highly modified phyllode tube feet are found. The structure of these tube feet is remarkably uniform so that tube feet from the phyllode of the holasteroid *Urechinus naresianus* are more or less identical to those of spatangoids such as *S. raschi* (text-fig. 9) or *Echinocardium cordatum* (Nichols 1959*a*). These tube feet, when contracted, are very squat and possess a broad disc which is covered in papillae. The stem has the typical morphology found in most tube feet (text-fig. 9C) with only a thin layer of retractor muscle fibres. These muscle fibres attach to the periphery of the isopore or unipore leaving a large periporal area, which is covered by a single layer of squamous epithelial cells which are sparsely ciliated. The lumen of the tube foot extends well into the disc but it is here partitioned by a large number of septa, composed of connective tissue fibres, which connect the upper and lower surfaces of the disc. These septa radiate out to the margin of the disc lumen from a central position. A skeletal rod forms the core to each papilla and each has its base embedded within the connective tissue layer of the disc. The stem of each papilla has a single layer of epithelial cells which, on the underside of the skeletal rod, is underlain by nervous tissue. The tip of the papilla is swollen and is composed of a densely nucleated pad of epithelium in which Nichols (1959*a*) found abundant mucous glands. The papillae, which occur over the whole surface of the disc, are largest at the periphery and decrease in size towards the centre of the disc. There is no apparent correlation between the positioning of the radial septa of the lumen and the positioning of the papillae.

Although levator muscle fibres are wanting there are numerous muscle fibres in the lumen of the disc. Stem retractor muscle fibres appear to continue into the disc, running along the lower floor of the lumen to the periphery. Muscle fibres also run obliquely up the radial septa connecting the lower and upper surfaces of the lumen. There are also muscle fibres that run radially across the upper surface of the lumen.

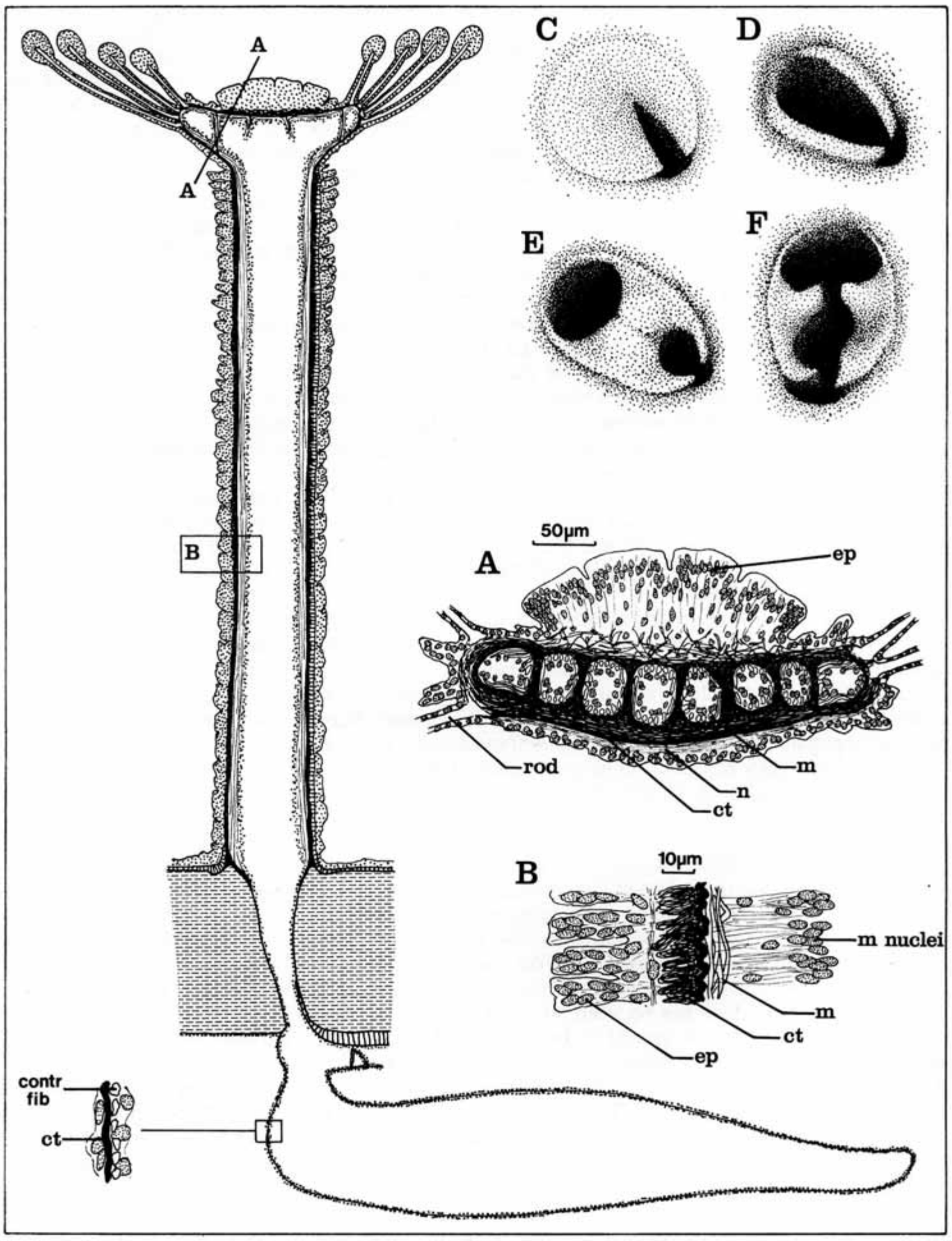
The ampulla is a large bulbous tube lacking septa. Both the connective tissue layer and the contractile fibre layer are well developed, their combined thickness being about 2 to 5 μm. As in other cylindrical ampullae, these contractile fibres run circularly and interconnect with one another.

Lovén (1883) found only three spatangoids in which the phyllode tube feet differed in appearance from that described here. In all three (*Aceste*, *Palaeostoma*, *Palaeotropus*) the tube feet differed in possessing papillae only around the margins of the disc, an arrangement typical of sub-anal tube feet.

The phyllode tube feet of a number of species have been shown to function primarily in the gathering and transference of quantities of substrate into the peristome (Nichols 1959*b*; Chesher 1963, 1968, 1969).

Funnel building tube feet: sub-anal tube feet (text-fig. 10). In spatangoids, the tube feet which originate from within the sub-anal fasciole are highly specialized. These tube feet have a long and slender stem which terminates in a disc bearing papillae (text-fig. 10). In *Brissopsis lyrifera*, *S. raschi*, *Metalia sternalis*, and *E. pennatifidum* the disc has a broad, central pad of epithelial tissue, and papillae are found only around the rim of the disc. The papillae are arranged into from two to four irregular rows, with the largest papillae being situated furthest from the centre. Depending upon the size of the disc, there are between 50 and 120 or so papillae to each tube foot. The skeletal rods of the papillae do not appear to be bound into the connective tissue layers of the disc but simply rest in the overlying epithelium, as noted by Nichols (1959*a*). The lumen extends into the disc and radial septa are present. The muscle and septal arrangement is similar to that described previously for phyllode tube feet. The central pad appears to be well endowed with mucous glands and the underlying connective tissue is loosely packed and either contains spicules or small plates (illustrated by Lovén 1883). The tube foot stem and its ampulla (text-fig. 10) are standard in their morphology.

The sub-anal tube feet of *E. cordatum* differ from those of other spatangoids in that the disc has papillae which cover the whole of the surface of the disc. This disc is, however, very much smaller than the disc of phyllode tube feet. Nichols (1959*a*) reports finding one tube foot within the sub-anal fasciole which corresponds with the more typical structure, described above, but this is an unusual occurrence.



TEXT-FIG. 10. Sub-anal tube foot of *Brissopsis lyrifera*. A, section across the disc in the plane AA; B, longitudinal section of part of the stem; C, the associated unipore; D, sub-anal unipore of *Echinocardium cordatum*; E, sub-anal isopore of *Metalia dichrana*; F, sub-anal constricted unipore in *Protenaster australis*.

The sub-anal tube feet have been shown to construct and maintain a sanitary drain in the sediment (Nichols 1959*b*; Chesher 1968). These tube feet excavate particles from the back wall and drop them by the sub-anal tuft of spines which then incorporates them into the burrow wall. They also plaster mucus along the walls of the tunnel.

Funnel-building tube feet: aboral ambulacrum III tube feet (text-fig. 11). The least specialized dorsal, funnel-building tube feet were found in *B. lyrifera* and *Hemiaster expurgitus* (text-fig. 11I). These possess a broad, circular disc which, in *Brissopsis*, is scalloped at the margins. The disc is supported upon a short and relatively squat stem of standard morphology. The disc incorporates a ring of flattened rods which form a rosette. There are ten or eleven such rods in *Hemiaster* and fifteen to eighteen rods in *Brissopsis*. These rods do not continue to the centre but leave an uncalcified circle at the centre of the disc. (Lovén (1883) reported finding a single specimen of *B. lyrifera* in which there was a thin central plate.) In the inner part of the rosette the rods abut on one another but towards the distal end each becomes separate (text-fig. 11I). The nerve ring, which lies beneath the rosette at the top of the stem, gives off tracts of fibres which pass to the upper surface of the disc at the point where adjacent rods diverge. The surface of the disc has a broad pad of epithelial tissue with what appear to be numerous mucous glands. Towards the tip of each rod the epithelial layer swells slightly and, in *Brissopsis*, the margin is indented between each rod. The densely nucleated, epithelial pad at the tip of each rod bears some similarity to the epithelial pad at the tip of the papillae. Levator muscle fibres are present and these run from the connective tissue at the centre of the disc to the rosette. The associated ampulla is cylindrical with prominent contractile fibres and no septa. Lovén (1883) found a rather similar skeletal arrangement in the dorsal, funnel-building tube feet of a number of other species. In some the disc is circular, in others it is deeply indented but all have a similar rosette. This appears to be the most common type of dorsal, funnel-building tube foot in the spatangoids.

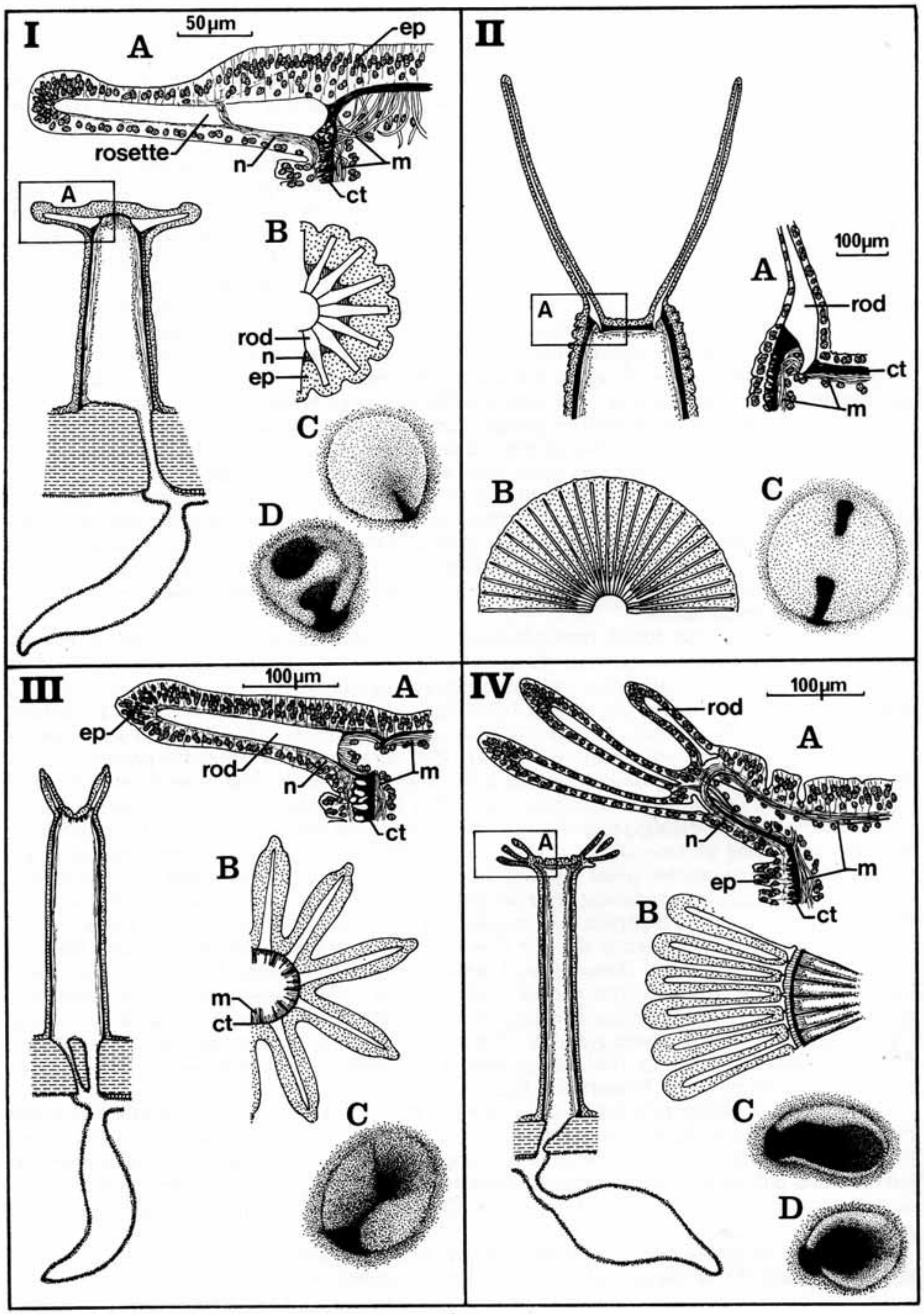
In *Aeropsis rostrata* the dorsal, funnel-building tube feet are very large and the rods of the disc are very long and thin (text-fig. 11II). Each rod enlarges and becomes keeled proximally, where it comes to abut on to neighbouring rods. Along the rest of their length the rods are connected by a connective tissue sheet to produce a webbed disc. The surface of the disc is covered with a thin layer of epithelial cells. Muscle fibres run between rods, across the centre of the disc, and also from the hooked proximal end of each rod to the stem. The disc can therefore be opened to present a broad, circular surface or can be closed to produce a flat, fan-shaped array. The arrangement of rods is only superficially similar to the arrangement found in the 'umbrella' tube feet of *Micropyga*.

In the dorsal, funnel-building tube feet of *E. pennatifidum* the disc morphology is rather different. The disc has a ring of nine or ten acicular rods which are independent of one another. Each terminates in the connective tissue layer of the disc (text-fig. 11III). The lumen of the tube foot enters the disc, and short radiating septa of connective tissue cross the lumen of the disc. Each element forms the core to a papilla. The papillae are composed of dense epithelial tissue. Muscle fibre arrangement in the lumen of the disc is similar to that described for phyllode tube feet.

The most highly modified dorsal, funnel-building tube feet are found in *E. cordatum* (text-fig. 11IV). The disc has a central pad of epithelial cells and mucous glands surrounded by a marginally situated ring of papillae, irregularly arranged into three or four rows. The detailed histology of these tube feet has been given by Nichols (1959*a*). They are very similar to the sub-anal tube feet of other spatangoids, described previously, but differ in commonly possessing a massive, bipolar spicule immediately beneath the disc.

Dorsal, funnel-building tube feet function in much the same way as do sub-anal tube feet in that they excavate sediment from an apical funnel and they plaster mucus on to the walls of this funnel. In addition the tube feet of *E. cordatum* are known to rake particles from the sediment/water interface and pull them down the funnel (Robertson 1871; Buchanan 1966). Similar activity has never been observed in *B. alta* or *B. atlantica* (Chesher 1968). The function of the tube feet of *Aeropsis*, with their webbed disc, is unknown.

In a number of spatangoids, the dorsal tube feet of ambulacrum III are discless and terminate in a sensory pad. These sensory tube feet have been described above.


I
A
50µm
ep
rosette
n
m
ct
A
B
rod
n
ep
C
D
II
A
100µm
A
rod
ct
m
B
C
III
100µm
A
ep
rod
n
m
ct
B
m
ct
C
IV
100µm
rod
A
n
m
ep
ct
A
B
C
D

PORE MORPHOLOGY AND DISTRIBUTION

Isopores

Pore pairs, where both pores are approximately the same size and shape, can be separated into a number of categories according to the pore shape, the size and position of the neural canal, and the morphology of the interporal partition.

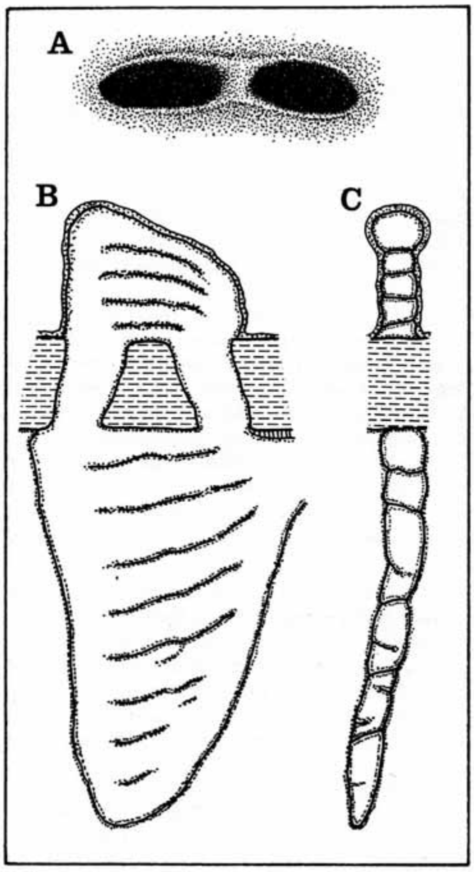
1. *Conjugate isopores* (Pl. 1, figs. 1–3; text-fig. 2). The two pores each have a rounded outline and are similar in size. The major axis of the isopore parallels the adoral plate suture and, in some cases, comes to overlie this suture. The neural canal is feebly developed and may be absent. Where present, it lies meso-adorally in the perradial pore. The interporal partition is broad and at least equal in breadth to the diameter of one pore. The interporal partition is crossed by a narrow furrow which links the pores.

Conjugate isopores were found aborally in a number of cassiduloids and in some clypeasteroids and spatangoids. They have also been found aborally in cidaroids and arbacioids (Smith 1978*b*). In all groups of irregular echinoids these isopores were never found to possess any specialized attachment area. In those species where the histology of the associated tube foot was examined (*Apatopygus recens*, *Cassidulus cariboearum*, *Echinocyamus pusillus*, and *Echinodiscus bisperforatus*), the tube foot was found to be specialized for gaseous exchange. A central, partitioned region is present in all tube feet and this is unbranched. In *Apatopygus* and *Cassidulus* the tube foot is relatively tall and narrow but in *Echinodiscus*, where the interporal area is very much broader, the tube foot is relatively short. These tube feet possess a small sensory tip which is skewed towards the adradial side. The walls of the central, partitioned region attach to the side walls of the interporal furrow.

2. *Elongate isopores* (Pl. 1, figs. 4, 5; text-figs. 4, 12). The isopore is long and narrow and lies parallel to the adoral ambulacral suture. Both pores are equally elongate along their common axis and each may taper slightly towards the interporal partition. The neural canal is small or absent. The interporal partition is usually rather narrow, though it may be quite broad in some cases, and is crossed by an area of raised stereom. This area links the two pores and may continue laterally, forming a narrow rim both adoral and adapical to each pore. The symmetrical taper of both pores and the narrow breadth of the raised band crossing the interporal partition give this isopore a waisted appearance.

Elongate isopores were found only in spatangoids and in fossil holasteroids. The histology of the associated tube foot was examined in only three species. In *H. expurgitus* and *Palaeostoma mirabile* the tube feet are small and each has a central, partitioned region which is unbranched (text-fig. 12). In *B. lyrifera* the central, partitioned region has side branches (text-fig. 4). The walls of the central, partitioned region attach to the margins of the raised interporal area and to the lateral rim of the pores. The morphology of tube feet associated with elongate isopores that possess a broad interporal area has not been investigated.

TEXT-FIG. 11. Longitudinal sections through dorsal funnel-building tube feet of spatangoids. I, *Brissopsis lyrifera*: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show the rosette; C, associated unipore; D, partitioned isopore associated with a similar tube foot in *Hemiaster expurgitus*. II, *Aeropsis rostrata*; distal part of tube foot: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show the rosette; C, associated isopore. III, *Echinocardium pennatifidum*: A, longitudinal half-section across the disc; B, transverse half-section of the disc to show arrangement of rods and small development of septa; C, associated unipore. IV, *E. cordatum*: A, longitudinal half-section across the disc; B, transverse segment of the disc; C, associated unipore from outer row; D, associated unipore from inner row.



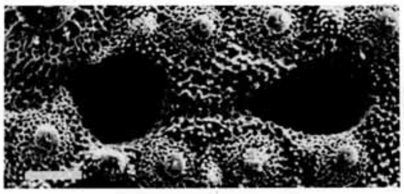
TEXT-FIG. 12. Aboral respiratory tube foot and ampulla of *Hemiaster expurgitus*. A, associated isopore; B, longitudinal section; C, sagittal section.

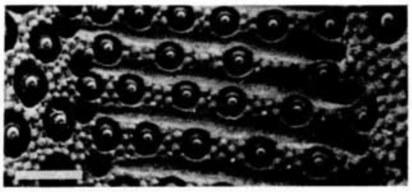
EXPLANATION OF PLATE 1

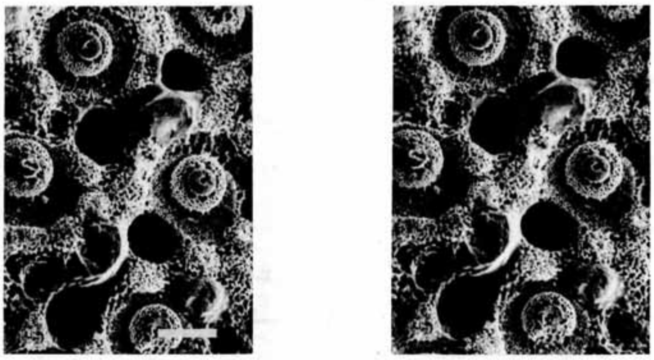
Figs. 1–8. *Petal isopores*. Top of photomicrograph adapical unless otherwise stated. 1, *Apatopygus recens* (Milne-Edwards). Conjugate isopore from aboral ambulacrum II. Top of photomicrograph adoral. 2, *Clypeaster rosaceus* (Linnaeus). Conjugate isopore from aboral ambulacrum II. 3, stereoview of conjugate isopores of *Echinocyamus pusillus* (Muller) from aboral ambulacrum IV. 4, stereoview of an elongate isopore of *Brissopsis lyrifera* (Forbes) from aboral ambulacrum II. 5, *Hemiaster expurgitus* Lovén. Elongate isopore from aboral ambulacrum IV. 6, *Clypeaster rarispina* de Meijere. Isopores with a flush interporal partition from aboral ambulacrum III. 7, *Paramaretia peloria* (Clark). Isopore with a flush interporal partition from aboral ambulacrum II. 8, *Echinocardium cordatum* (Pennant). Isopore with a flush interporal partition from aboral ambulacrum V.

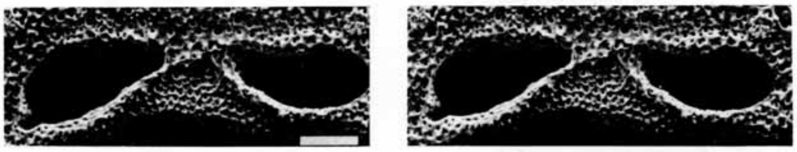
Scale bar in figs. 1, 3, 5 = 100 μm; 4, 6, 7 = 200 μm; 8 = 400 μm; 2 = 1 mm.

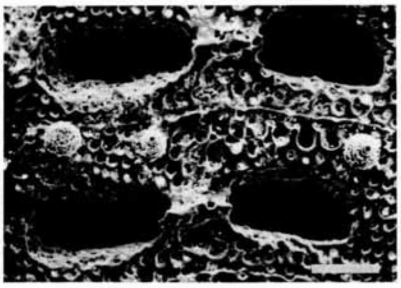
PLATE 1

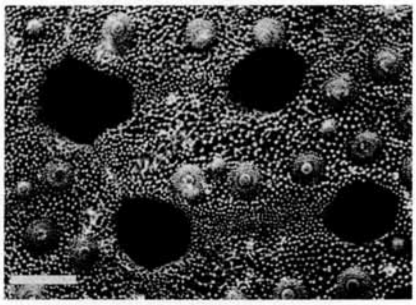

1

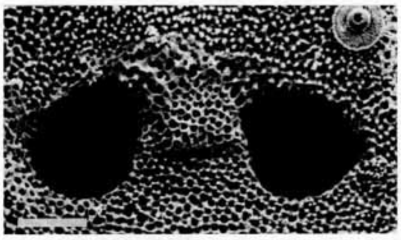

2


3


4

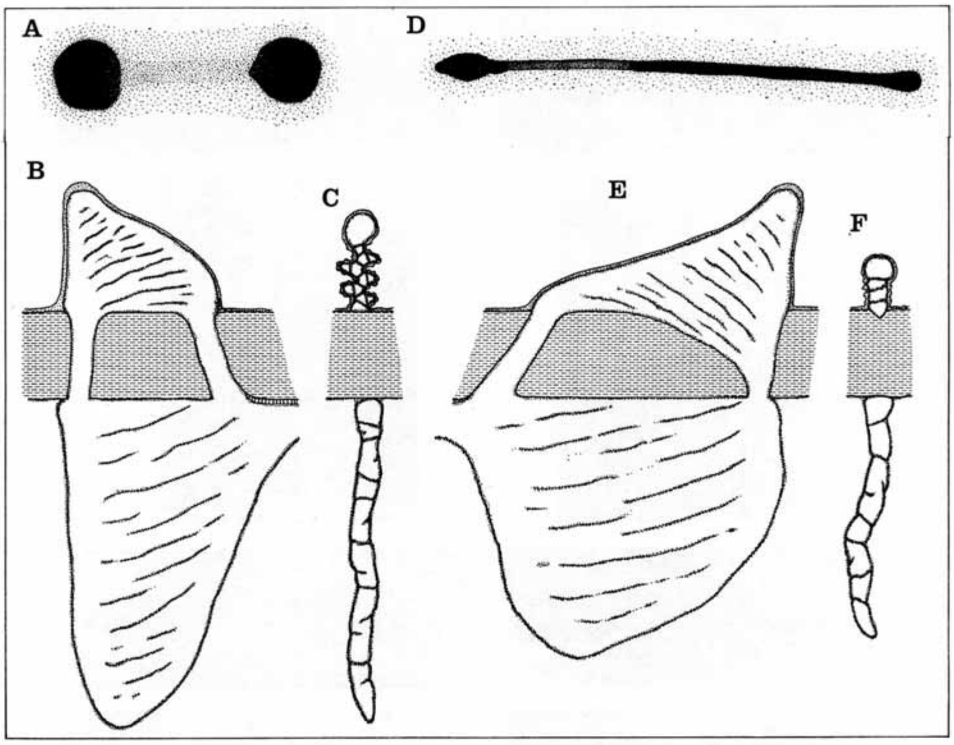

5


6


7


8

SMITH, Echinoid isopores



TEXT-FIG. 13. A–C, aboral respiratory tube foot and ampulla of *Clypeaster rarispina*: A, associated isopore with flush interporal partition; B, longitudinal section; C, sagittal section. D–F, aboral respiratory tube foot and ampulla of *Mellita quinquiesperforata*: D, associated conjugate anisopore; E, longitudinal section; F, sagittal section.

3. *Isopores with a flush interporal partition* (Pl. 1, figs. 6–8; text-figs. 4, 13). The pores are similar in size and may be circular or pear-shaped. If pear-shaped, each pore tapers towards the interporal partition and the major axes of each are not parallel but converge obliquely in an adapical direction. The relatively broad interporal partition lies more or less flush with the rest of the plate surface. The neural canal is typically feebly developed or is absent altogether. The interporal area is crossed by a band of stereom of different appearance from stereom of the surrounding plate surface (Pl. 1, fig. 7). In some cases this band is linear and is centrally positioned on the interporal partition. In others, the band lies adapical on the interporal partition and is gently curved. It also narrows considerably towards the centre of the interporal area.

Of the species examined only *Clypeaster rarispina* was found to have isopores with a flush interporal partition with a centrally positioned stereom band. These occur aborally and the associated tube feet have a central, partitioned area which has small side branches (text-fig. 13). Isopores that are adapically arched form the petals in a number of species of spatangoid. In *Echinocardium cordatum* and *Spatangus raschi*, the associated tube foot has a central, partitioned region with numerous side-branches, which may themselves be branched (text-fig. 4). The tube foot is skewed adradially. In both types, the central, partitioned region of the tube foot attaches on to the band of modified stereom which crosses the interporal partition.

4. *Partitioned isopores.* The term partitioned isopore encompasses all those isopores in which the two pores are not joined to one another by a furrow, a ridge, or a distinct stereom band, as described above. Partitioned isopores are separated by a well-defined interporal partition and possess a clear neural canal. An important subdivision can be made based on the positioning of the neural canal and this reflects a difference in the structure of the associated tube foot/ampulla system. The two groups of partitioned isopores are those with an axially positioned neural canal and those with a laterally positioned neural canal. The functional significance of this difference will be discussed in a later section.

Partitioned isopores with a laterally positioned neural canal (Pl. 2, figs. 1–3; text-fig. 6). These are the typical isopores present in all groups of regular echinoids and they have been grouped by Smith (1978*b*) according to the breadth of their attachment area. The major axis of these isopores lies parallel or only slightly oblique to the adoral suture of the plate. The neural canal lies in a meso-ventral position on the perradial pore and is always in contact with the adradial suture.

Partitioned isopores with a laterally positioned neural canal are not common in irregular echinoids but do occur in two groups of primitive irregulars, the pygasteroids (Smith 1978*a*) and the holectypoids. Both oral and aboral tube feet of the Recent holectypoid *Echinoneus cyclostomus* terminate in a sucking disc, described previously (text-fig. 6). The associated isopores have a narrow attachment area which is slightly better defined in oral isopores than in aboral isopores (Pl. 2, figs. 1, 3). Fossil holectypoids, such as *Holectypus depressus* (Leske) (Pl. 2, fig. 2) have a similar pore morphology.

This type of partitioned isopore was observed in only two other irregular echinoids that were examined. In both the Jurassic galeropygoid *Galeropygus agariciformis* (Forbes) and in the Recent spatangoid *Genicopatagus affinis* Agassiz, a single row of P1-type isopores occurs in each aboral ambulacral column (excluding the anterior ambulacrum of *Genicopatagus*). These presumably bear thin-walled, suckerless tube feet as in regular echinoids.

Partitioned isopores with an axially positioned neural canal (Pl. 2, figs. 5, 7; Pl. 3, fig. 1; text-figs. 10, 11, 14). In these, the neural canal is positioned so as to lie on the major axis of the isopore in alignment with the two pores. In the primitive condition, the isopore is orientated so that the adradial pore lies adapical to the perradial pore, whilst the neural canal typically abuts on to the adoral plate suture. Where 'plate-crushing' occurs, packing the isopores close together, the adradial pore returns to an adradial position so that the major axis of the pore parallels the adoral plate suture. The neural canal retains its axial position, sometimes maintaining contact with the adoral plate suture but, more often than not, becoming separated from the suture. Unlike the majority of partitioned isopores with a laterally positioned neural canal, the two pores show little divergence as they pass inwards through the plate. Indeed many isopores have slightly convergent pores which may coalesce to produce a single pore at the inner surface of the plate. On the external surface the interporal partition may be raised, planar, or even depressed. A distinct attachment area is commonly, though not always developed around the pores.

Partitioned isopores with an axially positioned neural canal are found in many groups of echinoids. The peristomial tube feet of many regular echinoids are associated with this type of isopore. The early galeropygoids and cassiduloids, such as *Galeropygus* and *Clypeus* possess oral and ambital isopores with this structure (Pl. 2, fig. 7) as do early disasteroids such as *Pygomalus*. Finally these isopores are often found in spatangoids and holasteroids, typically in the sub-anal region or dorsally in the anterior ambulacrum: they may also be found surrounding the peristome as in *Echinocorys*, *Micraster*, and *Infulaster*.

It is hoped to be able to present the results of a study on the morphology of peristomial tube feet and their pores elsewhere. The following discussion will therefore be limited largely to the spatangoids where the morphology of tube feet in a large number of species is known, some having been examined by the author, others described by Lovén (1883).

Sub-anal tube feet are remarkably uniform in their construction. Although many are associated with unipores, six of the species examined have sub-anal isopores with axially positioned neural canals. Of these, four (*Brissaster fragilis* (Düben and Koren), *Brissopsis luzonica* Gray, *Metalia sternalis* (Lamarck), and *M. dichrana* Clark) have sub-anal tube feet similar in external appearance to those of *B. lyrifera* (text-fig. 10). On the other hand, *Breynia australasia* (Leach) has, according to Lovén (1883), a disc covered in papillae, resembling the sub-anal tube feet of *Echinocardium cordatum*. Tube feet of the sixth species, *Paraster compactus* Koehler, were not examined.

Dorsal, funnel-building tube feet of ambulacrum III are more variable in their structure and are often associated with this type of isopore. In *B. australasia* and *P. floridiensis* Kier and Grant, the dorsal tube feet (illustrated by Lovén 1883, and Chesher 1966, respectively) have a disc bearing only a few large papillae and are similar in external appearance, to those of *E. pennatifidum* (text-fig. 11III). Others, such as *Hemiaster expurgitus* and *Palaeostoma mirabile*, have tube feet which terminate in a flat disc with a circular or scalloped outline and with a rosette composed of radiating rods, much like *Brissopsis lyrifera* (text-fig. 11I). Dorsal, funnel-building tube feet of *Moira atropos* (Lamarck) (illustrated by Chesher 1963), *Schizaster canaliferus* (Lamarck), and *Metalia sternalis* (Lamarck) have a similar rosette of radiating rods but deep indentations of the margin between each rod give the disc a fingered appearance. Tube feet of *Paraster compactus* and *P. doderleini* Chesher have discs with long and slender rods joined by a membrane. This is taken to an extreme in the dorsal tube feet of *Aeropsis rostrata* (text-fig. 11II). All these types of tube feet are found associated with partitioned isopores. Although there is some variation in the detailed morphology of these isopores, it is not possible to identify the nature of the tube foot disc from the structure of the isopore.

Phyllode pores in *P. compactus* and occasionally in the holasteroid *Urechinus wyvilli* Agassiz are this type of partitioned isopore and in these species the associated tube feet have a disc covered in papillae. Finally, because of their size, no survey of the minute ambital pores of spatangoids was carried out at the light microscope level. In those spatangoids examined with the SEM all ambital tube feet (which are sensory in function) were found to be associated with unipores. Lovén (1883), however, gives illustrations of some minute isopores which he found ambitally in certain species. The very small size of these isopores and the probability of their possessing little or no attachment area should make these readily distinguishable from larger isopores which support tube feet that possess a terminal disc.

From the preceding discussion it is obvious that partitioned isopores are associated with a number of tube feet of differing structure and function. Some correlation can, however, be drawn between the structure of the isopore and the morphology of the tube foot/ampulla system.

(i) All tube feet found in association with partitioned isopores have cylindrical stems and are not especially modified for gaseous exchange.

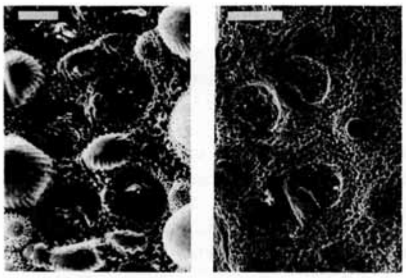
(ii) The ampullae found with partitioned isopores with a laterally positioned neural canal are broad and flat and are partitioned by septa. The ampullae which occur with partitioned isopores where the neural canal is axially placed are cylindrical, with a well-developed contractile fibre layer and with no septa crossing the lumen.

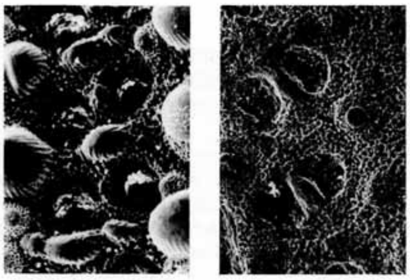
EXPLANATION OF PLATE 2

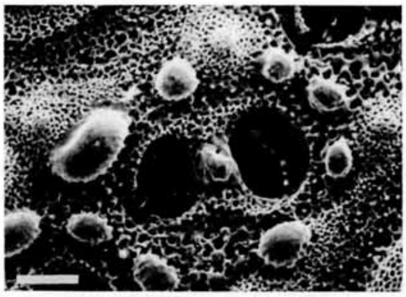
Figs. 1–7. Top of photomicrographs adapical unless otherwise stated. 1, stereoview of two partitioned isopores with laterally positioned neural canals from the aboral ambulacrum III of *Echinoneus cyclostomus* Clark. 2, stereoview of two partitioned isopores with laterally positioned neural canals from the aboral ambulacrum IV of *Holectypus depressus* (Leske). 3, *E. cyclostomus* Clark. Oral partitioned isopore with a laterally positioned neural canal. 4, *Echinocardium cordatum* (Pennant). Unipore with an extensive periporal area from the phyllode. 5, stereoview of three partitioned isopores with axially positioned neural canals from aboral ambulacrum III of *Moira atropos* (Lamarck). 6, stereoview of a broad-rimmed unipore present adapically in ambulacrum III of *Pourtalesia miranda* Agassiz. 7, isopore with an axially positioned neural canal from the phyllodes of *Clypeus* sp. Adapical to right.

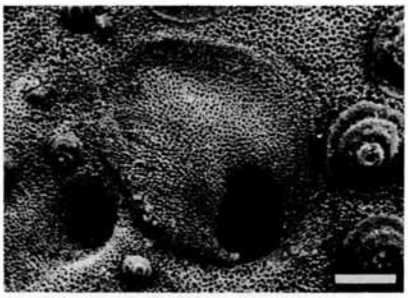
Scale bar in figs. 1–3, 6, 7 = 100 μm; 5 = 200 μm; 4 = 400 μm.

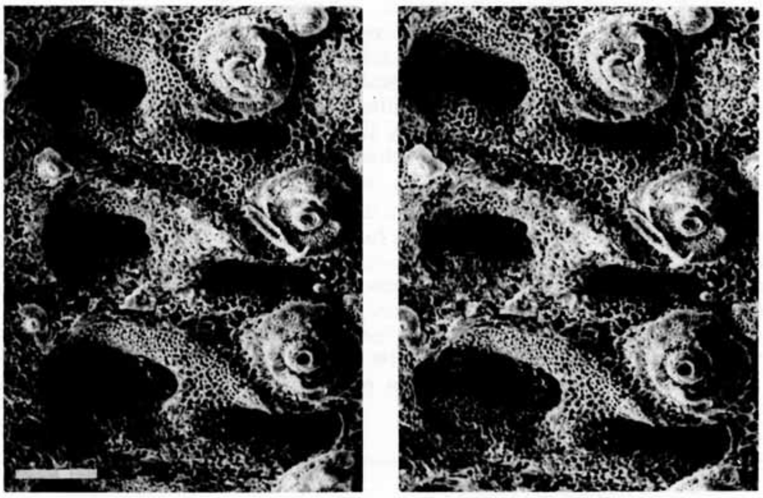
PLATE 2


1


2


3


4


5


6


7

SMITH, Echinoid isopores and unipores

(iii) Most tube feet found with partitioned isopores have some form of terminal disc. Those that do not can often be identified from the feeble development or complete absence of a specialized attachment area to the isopore. In spatangoids and holasteroids these isopores are relatively very small.

(iv) Partitioned isopores with a laterally positioned neural canal and an obvious attachment area are associated with tube feet that possess a terminal sucking disc. Partitioned isopores with an axially positioned neural canal, found in holasteroids and spatangoids, have tube feet whose flat or penicillate discs rely on mucus secretion for their adhesiveness. Similar isopores found in extinct members of the Cassiduloidea probably supported tube feet with sucking discs like those of their living relatives.

Anisopores

Ambulacral pore pairs, where the pores differ markedly in size and shape, are much more restricted in occurrence than either isopores or unipores. They are separated here into two groups, conjugate anisopores and non-conjugate anisopores.

1. *Conjugate anisopores* (Pl. 3, figs. 2–4; text-figs. 3, 13). These anisopores are extremely elongate and parallel, or even overlie, the adoral plate suture. The perradial pore is typically small and circular in outline with no more than a faint trace of a neural canal. The adradial pore is very elongate and is separated from the perradial pore by an often quite broad interporal partition. The two pores are linked by a furrow which crosses the interporal partition. The adradial pore tapers towards this furrow. In *Dendraster excentricus*, the adradial pore is partitioned by skeletal walls running perpendicular to the plate surface (Pl. 3, fig. 3). There is no specialized attachment area.

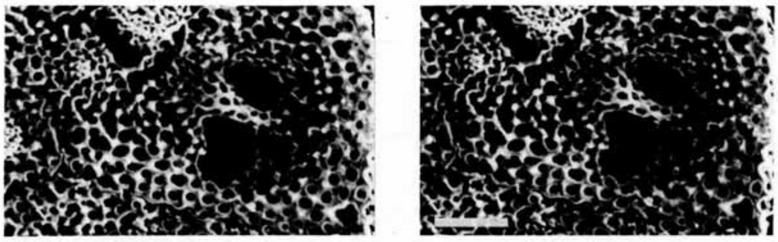
The associated tube feet are equally elongate and narrow. They extend only a short distance above the test, becoming taller adradially, where there may be a small sensory tip (text-fig. 3). Septa cross much of the central region leaving a main passageway running around the outer margin of the lumen of the tube foot. In *Dendraster* these septa attach to the skeletal walls that partition the adradial pore. The walls of the tube feet attach to the walls of the conjugate furrow and the margins of the pores. The ampulla is similarly thin-walled and partitioned by septa. Conjugate anisopores are found aborally in many cassiduloids and clypeasteroids.

2. *Non-conjugate anisopores* (Pl. 4, fig. 7; text-fig. 14). This category covers all those pore pairs in which one of the pores is markedly different in size or shape from the other and where these pores are not connected with one another by a furrow. In these anisopores there is always a clear periporal area. Such pores are not particularly common and only four examples are reported here. Non-conjugate anisopores are found within the sub-anal fasciole of *M. spatangus* (Lamarck) and *M. nobilis* Verrill. In these it is the perradial pore that is greatly reduced in size so that the neural canal is as large as, if not larger than, the pore itself. The neural canal is axially positioned and an obvious attachment area is developed (text-fig. 14F). The associated tube foot and ampulla were not examined in either species but they are, most probably, much like those of *M. sternalis* and *Brissopsis lyrifera*, described previously.

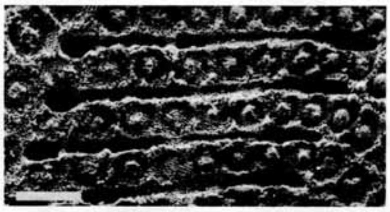
EXPLANATION OF PLATE 3

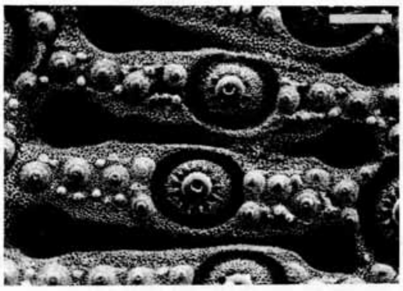
Figs. 1–6. *Isopores, anisopores, and unipores*. Top of photomicrograph adapical. 1, stereoview of a partitioned isopore with an axially positioned neural canal from aboral ambulacrum III of *Hemiaster expurgitus* Lovén. 2, *Mellita quinquiesperforata* (Leske). Conjugate anisopores from aboral ambulacrum IV. 3, *Dendraster excentricus* (Eschscholtz). Conjugate anisopore from aboral ambulacrum II. Adradial pores partitioned by calcite septa. 4, *Echinolampas crassa* (Bell). Conjugate anisopore from aboral ambulacrum III. 5, *Apatopygus recens* (Milne-Edwards). Funnelled unipore from the phyllode. 6, stereoview of a funnelled unipore from the phyllode of *E. crassa* Bell.

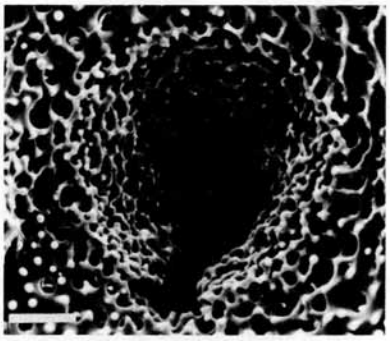
Scale bar in figs. 5 = 40 μm; 1, 6 = 100 μm; 2–4 = 400 μm.

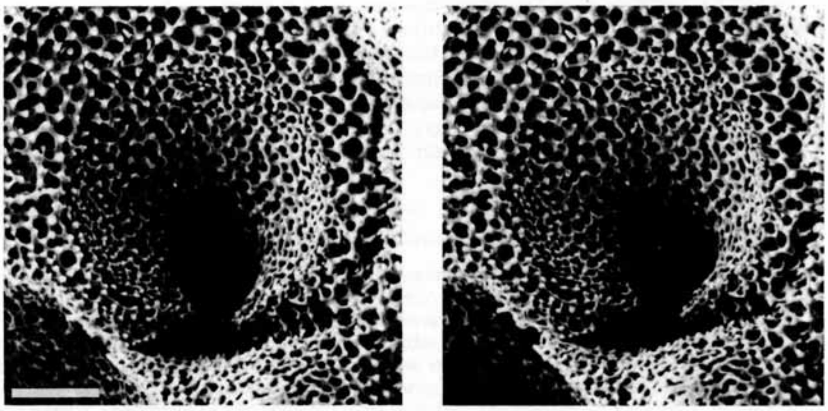

1


2

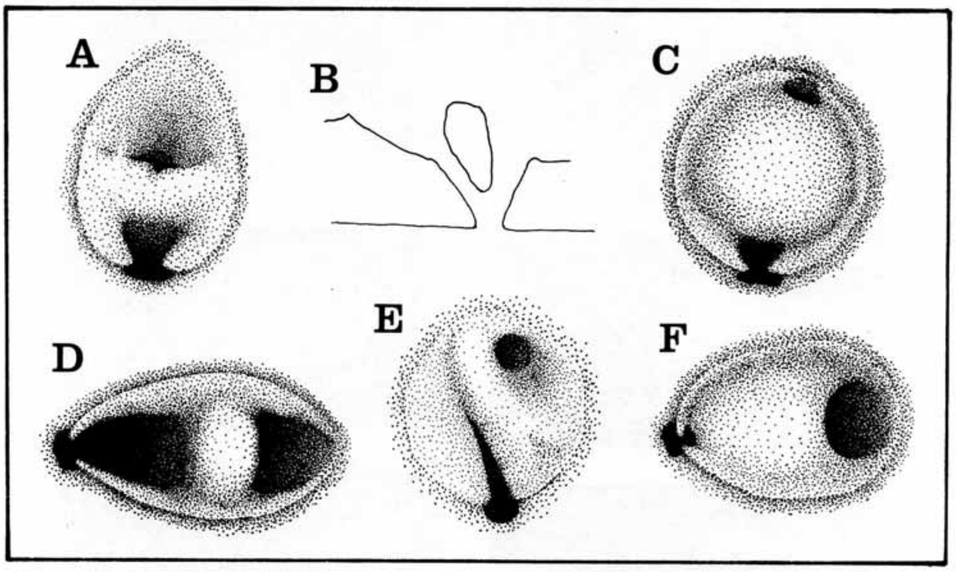

3


4


5


6

SMITH, Echinoid isopores, anisopores, and unipores



TEXT-FIG. 14. Ambulacral pores observed only at the light microscope level (not to scale). A, phyllode isopore of *Paraster compactus*; B, cross-section of A; C, aboral ambulacrum III isopore of *Faorina chinensis*; D, *Schizaster canaliferus*—aboral ambulacrum III isopore; E, sub-anal anisopore of *Linopneustes murrayi*; F, sub-anal anisopore of *Metalia nobilis*.

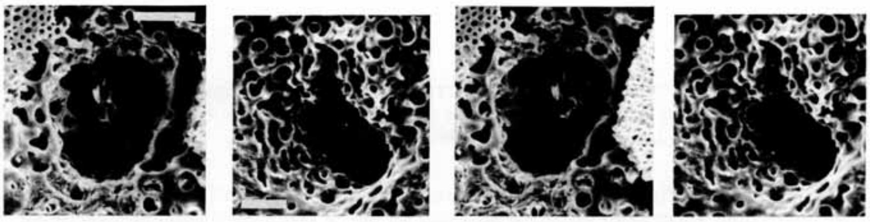
Another type of non-conjugate anisopore is found aborally in ambulacrum III plates of *Maretia planulata*. Here the perradial pore is reduced to a narrow slit, running perpendicular to the adoral plate suture. The adradial pore is circular and lies aboral of the perradial pore (Pl. 4, fig. 7). The neural canal is broad and lies on the major axis of the anisopore. Internally the pores sometimes merge to produce a single pore on the inner plate surface. The anisopore has a flat periporal area around the pores giving it a sub-circular outline. The associated tube foot is cylindrical and terminates in a sensory pad, as in text-fig. 1C. Connective tissue fibres of the tube foot stem insert around the margin of the periporal area. The ampulla is a tubular sack with contractile fibres and no septa. A similar pore structure is found associated with the penicillate sub-anal tube feet of *Linopneustes murrayi* Agassiz (text-fig. 14E). Here, however, the adradial pore appears to lie to one side of the anisopore. There is a broad, circular periporal area but no attachment area rim was seen using a light microscope.

EXPLANATION OF PLATE 4

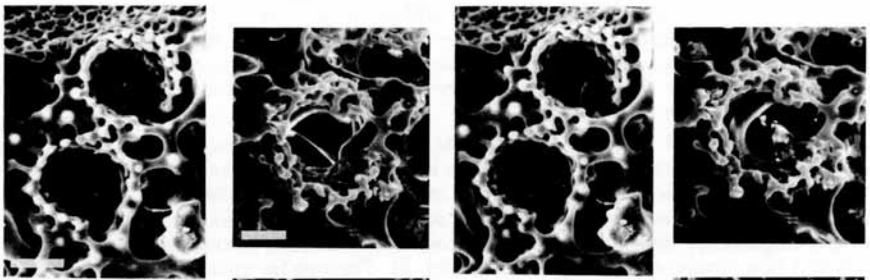
Figs. 1–7. *Anisopores and unipores*. Top of photomicrograph adapical unless otherwise stated. 1, stereoview of a simple unipore from ambital ambulacrum II of *Echinocardium cordatum* (Pennant). 2, stereoview of a simple unipore from ambital ambulacrum V of *Brissopsis lyrifera* (Forbes). Small periporal area to the adapical edge. 3, stereoview of two oral micro-unipores from *Encope michelini* Agassiz. Right side of photomicrograph adoral. 4, stereoview of an oral micro-unipore from *Mellita quinquiesperforata* (Leske). 5, stereoview of an oral micro-unipore from *Clypeaster rosaceus* (Linnaeus). 6, stereoview of two oral micro-unipores of *Dendraster excentricus* (Eschscholtz) from the floor of a food groove. 7, stereoview of a non-conjugate anisopore from aboral ambulacrum III of *Maretia planulata* (Lamarck).

Scale bar in figs. 4 = 10 μm; 3, 5 = 20 μm; 1, 2, 6 = 40 μm; 7 = 100 μm.

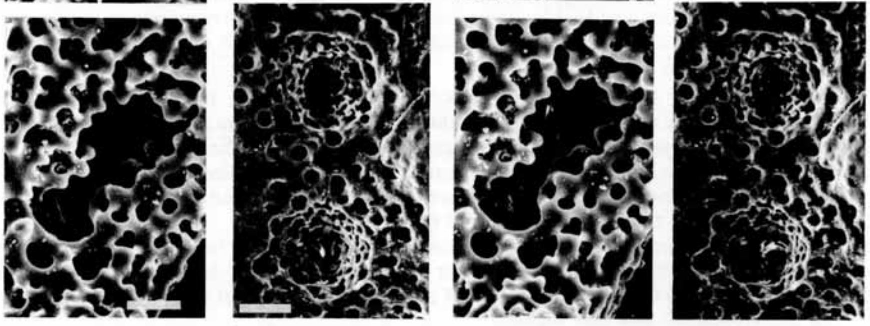
PLATE 4


1

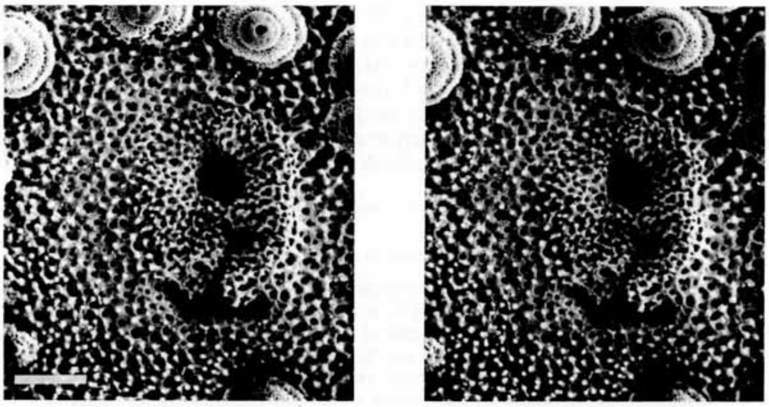
2


3

4


5

6


7

SMITH, Echinoid anisopores and unipores

Unipores

There is a great deal of variation in the structure of unipores in irregular echinoids and there is a corresponding variation in the morphology of the associated tube foot. Unipores can be grouped according to the pore size, the presence or absence of an attachment area, and the extent of the periporal area.

1. *Simple unipores* (Pl. 4, figs. 1, 2). These are small pores, 50 μm to 100 μm in diameter, roughly circular in outline. There is no periporal area and no rim of specialized stereom forming an attachment area. The neural canal is large yet poorly differentiated with only a small ridge on either side of the pore to distinguish it. Simple unipores are found ambitally in the lateral and posterior ambulacra of many spatangoids. In *E. cordatum* much of the pore space is taken up with nervous tissue and the tube foot is reduced to a sensory hummock capable of little extension (text-fig. 1II). No ampulla is found in association.

2. *Micro-unipores* (Pl. 4, figs. 3–6; text-fig. 8). These are small pores, usually 20 μm to 50 μm in diameter though very occasionally up to 80 μm in diameter. They are surrounded by an attachment area of fine stereom which typically forms a rim to the pore. In most, there is a clearly defined neural canal though this may be absent from some of the larger pores.

Micro-unipores are found only in clypeasteroids where they are associated with minute tube feet which end in a functional sucking disc (text-fig. 8). The smaller micro-unipores, with a distinct neural canal, bear slender and highly active tube feet. The larger micro-unipores, which are only found in or adjacent to food grooves, have much shorter tube feet with relatively broader discs. All ampullae are cylindrical and lack septa.

3. *Funnelled unipores* (Pl. 3, figs. 5, 6; Pl. 5, figs. 1, 2; text-fig. 7). In these unipores there is a narrow attachment area which forms a horse-shoe-shaped rim, 100 μm to 500 μm in diameter. The area inside this rim slopes inwards fairly steeply to a single pore. There is a neural canal on the adoral side of this pore. The unipore may be circular or oval in outline. In larger pores, near the peristome, the unipore rim may be partially surrounded by a depressed region of the plate surface which accommodates a tract of sub-epidermal nervous tissue.

Funnelled unipores are found in association with oral and ambital tube feet of cassiduloids and with buccal tube feet of clypeasteroids. In the cassiduloids all such tube feet have a functional sucking disc (text-fig. 7) but buccal tube feet of clypeasteroids may not be suckered. In either case, ampullae are cylindrical and lack septa.

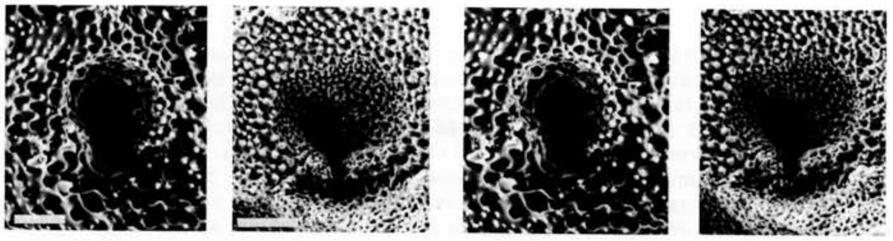
4. *Unipores with an extensive periporal area* (Pl. 2, fig. 4; Pl. 5, fig. 7; Pl. 6, figs. 1–3; text-fig. 9). These are very large and very distinctive unipores with a diameter of between 500 μm and 2 mm. There is a relatively small pore, with a clear neural canal, situated on the adoral or perradial margin of the unipore. The rest of the unipore is formed from a very extensive periporal area which commonly forms a platform but which may be developed into a bulbous dome centrally (Pl. 6, fig. 3). Surrounding the periporal area is a narrow attachment area, either forming a marginal rim or forming the outer slope to the periporal platform.

EXPLANATION OF PLATE 5

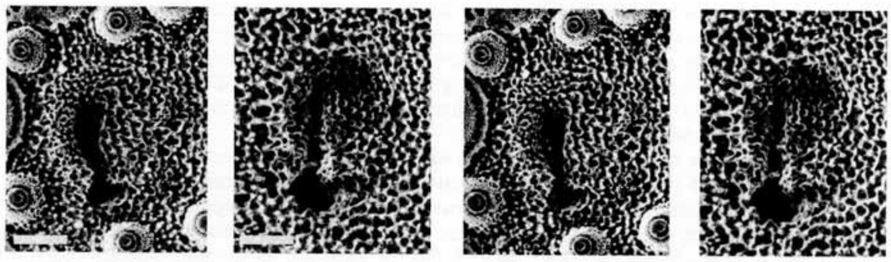
Figs. 1–7. *Unipores.* Top of photomicrograph adapical unless otherwise stated. 1, stereoview of a funnelled unipore of *Apatopygus recens* (Milne-Edwards) from ambital ambulacrum II. 2, stereoview of a funnelled unipore of *Echinolampas crassa* (Bell) from ambital ambulacrum III. 3, stereoview of a broad-rimmed unipore of *Brissus latecarinatus* (Leske) from aboral ambulacrum III. 4, stereoview of a broad-rimmed unipore of *Paramaretia peloria* (Clark) from aboral ambulacrum III. 5, stereoview of a broad-rimmed unipore of *Echinocardium pennatifidum* Norman from aboral ambulacrum III. 6, stereoview of a sub-anal unipore rimmed by an attachment area of *E. cordatum* (Pennant). Left side of photomicrograph adoral. 7, stereoview of a phyllode unipore with an extensive periporal area from *Brissopsis lyrifera* (Forbes).

Scale bar in figs. 1 = 40 μm; 2–5 = 100 μm; 6, 7 = 200 μm.

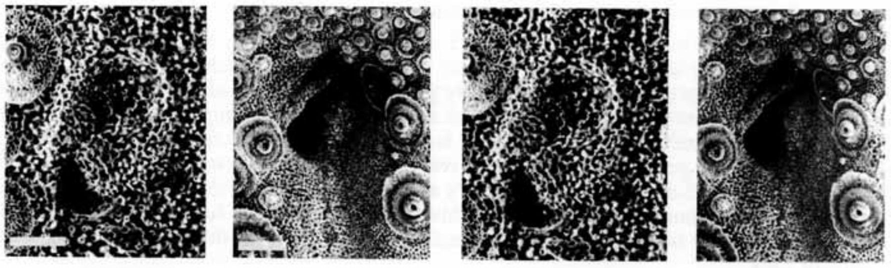
PLATE 5


1

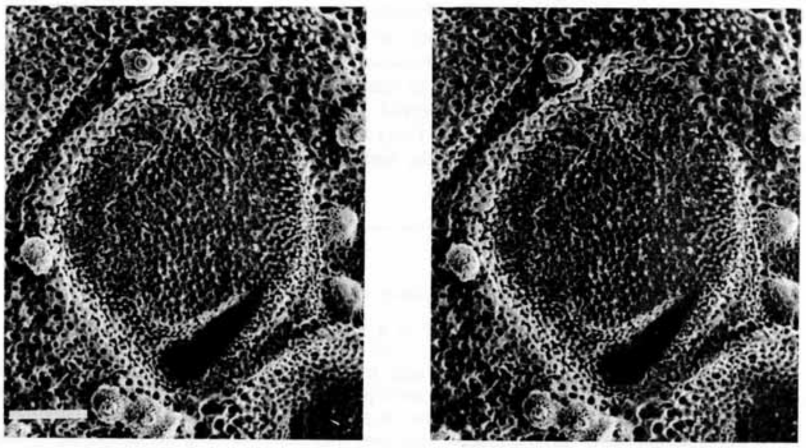
2


3

4


5

6


7

SMITH, Echinoid unipores

This type of unipore is found with penicillate tube feet of the phyllode in nearly all species of spatangoid examined as well as in the holasteroids *Plexechinus nordenskjoldi* Mortensen and *U. naresianus* Agassiz. In addition, the dorsal, funnel-building tube feet in four species of *Brissopsis* (*B. lyrifera* (Forbes), *B. luzonica* Gray, *B. alta* Mortensen, and *B. atlantica* Mortensen) are found with this type of unipore (Pl. 6, figs. 1, 3, and Chesher 1968, pl. 6, fig. f). Some funnel-building tube feet of the sub-anal fasciole are also associated with this type of unipore in *B. lyrifera*, *B. luzonica*, and *Agassizia scrobiculata* Agassiz and Desor. It therefore appears that unipores with an extensive periporal area bear penicillate tube feet and have tubular ampullae lacking septa.

5. *Constricted unipores* (text-fig. 10). Constricted unipores are obviously incomplete isopores where, either growth of the interporal partition has ceased before the two ridges, which go to form the partition, have met and fused, or where later resorption has removed the central part of the interporal partition. This central constriction gives the pore a very distinctive appearance. An axially positioned neural canal is present and there is a fairly obvious rim to the margin which, no doubt, marks the attachment area.

Constricted unipores tend to be found along with isopores. In *U. wyvillei* (Agassiz) many of the penicillate tube feet of the phyllode are associated with constricted unipores. Sub-anal pores of *Protenaster australis* (Gray), *Schizaster canaliferus* (Lamarck), and *Diploporaster savignyi* (Fourtau) may be isopores or may be constricted unipores. The associated sub-anal tube feet have not been examined but it seems likely that they have a disc of papillae, as in other species. Kier (1974) records similar pores in a number of other spatangoids.

6. *Unipores rimmed by a periporal area* (Pl. 2, fig. 6; Pl. 5, figs. 3-5; text-fig. 1III). In these, the pore is typically rather elongate and narrow and the neural canal, which lies at the adoral end of the pore, is often elongate in a direction roughly perpendicular to that of the pore. These unipores vary in size from about 100 μm up to 400 μm in length. In small unipores, generally less than 200 μm in length, the neural canal is relatively large and the periporal rim narrow and U-shaped. In larger unipores the periporal area becomes relatively broad and is circular or ovoid in outline. The pore in these broad-rimmed types forms only a small, central part of the unipore (Pl. 5, figs. 3, 4). The periporal rim is planar. Connective tissue fibres of the stem of the tube foot insert around the margin of the unipore but the stereom construction is not always modified to produce a distinct attachment area.

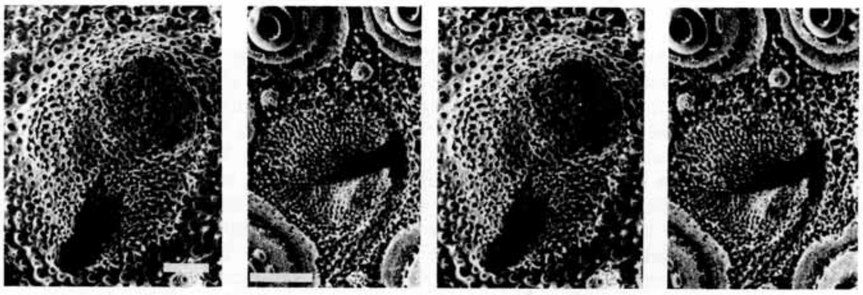
Small, rimmed unipores are developed ambitally in many spatangoids where they are associated with small, cylindrical tube feet which terminate in a sensory pad. Similar pores are found aborally in all ambulacra of the holasteroids *U. naresianus* Agassiz and *U. wyvillei* (Agassiz). The larger broad-rimmed unipores are found aborally in ambulacrum III of a number of spatangoids and adapically in ambulacrum III of the holasteroid *Pourtalesia miranda* Agassiz. These bear large sensory tube feet which are again suckerless. Only in *E. pennatifidum* were broad-rimmed unipores found bearing penicillate, funnel-building tube feet (text-fig. 11III; Pl. 5, fig. 5).

EXPLANATION OF PLATE 6

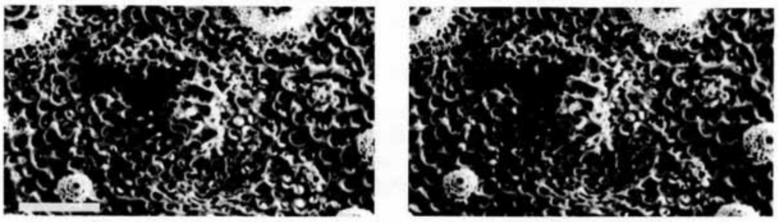
Figs. 1-5. *Unipores and isopores.* 1, stereoview of a unipore with an extensive periporal area in aboral ambulacrum III of *Brissopsis lyrifera* (Forbes). Left side of photomicrograph adoral. 2, stereoview of a sub-anal unipore with an extensive periporal area from *B. lyrifera* (Forbes). Top of photomicrograph adapical. 3, stereoview of a unipore with an extensive periporal area in aboral ambulacrum III of *B. atlantica* Mortensen. Left side of photomicrograph adoral. 4, stereoview of unipores rimmed by an attachment area in aboral ambulacrum III of *Echinocardium cordatum* (Pennant) showing the difference in shape of perradial and adradial unipores. Left side of photomicrograph adoral, perradius to bottom. 5, stereoview of two aboral petal isopores seen on the inner plate surface of ambulacrum V in *E. cordatum* (Pennant).

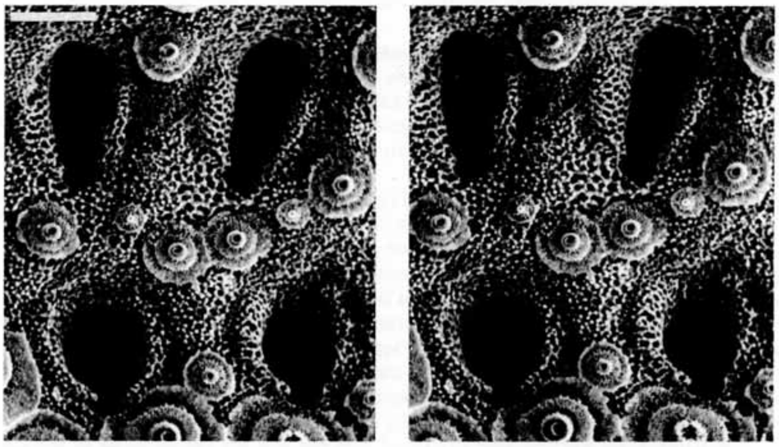
Scale bar in figs. 1, 3 = 100 μm; 2, 4 = 200 μm; 5 = 400 μm.

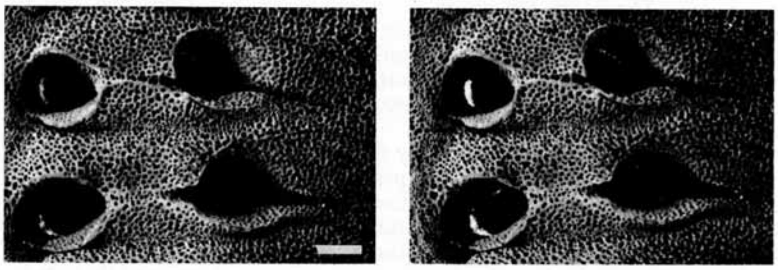
PLATE 6


1

2


3


4


5

SMITH, Echinoid unipores and isopores

7. *Unipores rimmed by an attachment area* (Pl. 5, fig. 6; Pl. 6, fig. 4; text-figs. 10, 11IV). These are large unipores, between 300 μm and 800 μm in diameter, which are circular to ovoid in outline. There is no periporal area but a narrow rim of attachment area borders the pore. A neural canal is present in a perradial position. Adradially the attachment area becomes less clearly defined. These unipores are, in some respects, similar to funnelled unipores but have more or less vertical pore walls. They can be distinguished from unipores rimmed by a periporal area by the size and shape of the pore, which, in this case, forms a very large part of the unipore.

Unipores rimmed by an attachment area are found in aboral ambulacrum III of *E. cordatum* where they bear penicillate, funnel-building tube feet (text-fig. 11IV). They are also found within the sub-anal fasciole in *E. cordatum* and *Spatangus raschi* where they again are associated with penicillate, funnel-building tube feet. The accompanying ampullae are bulbous tubes, lacking septa and with a well-developed layer of contractile fibres.

FUNCTIONAL SIGNIFICANCE OF THE STRUCTURE OF TUBE FEET

Respiratory tube feet. All specialized respiratory tube feet are connected to a large and flattened ampulla by two pores. This permits a one-way flow of coelomic fluid through the tube foot/ampulla system with one pore carrying fluid into the tube foot while the other carries fluid out of the tube foot (see Fenner 1973 for details). The aboral tube feet of most irregular echinoids are modified for gaseous exchange in a number of ways.

1. The tube feet and ampullae are very thin-walled possessing only a single layer of epithelial cells on either side of a very thin layer of connective tissue fibres, which generally is only 1 μm to 5 μm in breadth. Muscle fibres, although present, are sparsely distributed. Both connective tissue and muscle act as a barrier against the diffusion of gases, and therefore tube feet specialized for gaseous exchange are much thinner-walled than other tube feet.

2. Elongation of the tube foot not only increases the total surface across which gaseous exchange can occur but also increases the surface area to volume ratio making a more efficient system for gaseous exchange.

3. The development of a central, partitioned region in specialized respiratory tube feet serves two main functions. First, the septa, which connect the opposing walls, ensure that the tube foot maintains its narrow, elongate shape during expansion and contraction. Secondly, these septa separate the inflowing coelomic fluid into many streams ensuring that full use is made of the entire central region of the tube foot. This central region not only increases the surface area of the tube foot but also isolates the inflowing, oxygen-poor current from the outflowing, oxygen-rich current. In unspecialized tube feet these two currents are separated simply by a thin septum and depletion of oxygen from the outflowing oxygenated fluid can occur across the septum.

4. Lateral extension of the tube foot is accompanied by a reduction in its height. This is a direct result of the infaunal mode of life led by irregular echinoids. In regular echinoids, such as *Arbacia*, respiratory tube feet are able to extend well beyond the spines so as to obtain a suitably large surface area. These tube feet are relatively tall and narrow. With the development of an infaunal mode of life in the irregular echinoids, respiratory tube feet have to be protected from abrasion by sediment particles and can therefore extend no further than the tips of the adjacent, protective spines. These spines can be very short, especially in sand dollars. Therefore, in order to maintain a large surface area for efficient gaseous exchange, the tube feet have to become very elongate.

5. The more elongate tube feet are typically skewed so as to be tallest above the adradial pore. This is the pore through which coelomic fluid passes into the tube foot and there is a major vertical passageway in the lumen of the tube foot directly above this pore. Presumably, by having this vertical passageway as the tallest part of the tube foot, the inflowing current is better distributed through all the pathways in the central, partitioned region.

6. The development of side-branches to the central, partitioned region of the tube foot increases the surface area for gaseous exchange without adding to the height of the tube foot.

There appears to be some correlation between the development of specialized respiratory tube feet and the size and habitat of the urchin. Small echinoids, such as *Apatopygus*, *Cassidulus*, *Echinocyamus*, *Hemiaster*, and *Palaeostoma* have less specialized tube feet than larger urchins such as *Echinolampas*, *Mellita*, *Spatangus*, and *Echinocardium*. This is likely to be the result of differences in the surface area to volume ratio of the urchins. Some deep-sea urchins have not developed specialized respiratory tube feet. *Urechinus* and *Pourtalesia* have only small, sensory tube feet, borne on unipores, in their aboral ambulacra. Another deep-sea echinoid, *Goniospatangus*, also appears to lack specialized respiratory tube feet, judging from its partitioned isopores. Only the pygasteroids and holectypoids have never developed respiratory tube feet aborally.

Funnel-building tube feet. The terminal disc of dorsal and sub-anal tube feet is often highly modified in comparison with the suckered tube feet of regular echinoids. Funnel-building tube feet differ from suckered tube feet in the following points.

1. The disc relies on mucus rather than suction for its adhesiveness although, in many cases, levator muscles are still present to control the shape of the disc. This enables the tube foot to transport a disc-full of small particles, which would be impossible using a sucking disc. Although some spatangoids live in shell gravels and have to cope with individual grains, most excavate in sands or muds where the particle size is much smaller than the size of the disc.

2. The surface area of the disc is increased. In the simpler forms of funnel-building tube feet the disc is broad and is largely covered by an epithelial pad with mucous glands. The surface area of mucous-producing epithelium is greatly increased by the development of papillae in more specialized tube feet.

3. The disc becomes more flexible. In regular echinoids, the rosette is usually made up of four or five elements firmly sutured together to produce a fairly rigid disc. In funnel-building tube feet of spatangoids, the rosette, where present, is composed of between eight and fifty radially arranged rods. The rods are bound together by connective tissue over much of their length in the least specialized tube feet, though distally they become independent from one another. In others, the rods are elongate and are bound together only at their proximal end. The increase in the number of elements which form the rosette presumably gives more flexibility to the disc since muscle fibres can now act on relatively small segments of the disc. Flexibility is increased by the indentation of the margin between rods, which produces a rim of finger-like papillae. The most flexible disc occurs where the rods have separated from one another proximally so that each papilla is independent of its neighbours. Where the papillae are numerous and form more than one row, muscle control on individual rods is reduced, since muscle fibres are arranged to act radially on the disc margin.

4. In penicillate tube feet the lumen extends into the disc. This coincides with the development of independent rods. With the loss of a cohesive rosette it becomes impossible to support a broad terminal disc and papillae would have to be arranged on a simple rounded tip. However, by extending the lumen laterally it is possible to support a broad disc by hydrostatic pressure. In order to maintain the shape of the disc during expansion and contraction of the tube foot, radially arranged septa cross the lumen of the disc, binding the upper and lower surfaces together. The extension of the lumen is therefore vital to the formation of a broad, penicillate disc. The presence of the lumen in the disc has another effect, in that the shape of the disc, although stabilized by septa, is apparently more flexible than in discs with rosettes. This makes the disc much more prehensile.

The development of penicillate tube feet appears to have resulted from a need to pick up and transfer sediment particles. Whereas all sub-anal and phyllode tube feet of spatangoids that were examined are penicillate, very few dorsal, funnel-building tube feet are known to be penicillate. In *E. pennatifidum* and *Breynia australasia* there is a ring composed of a few large papillae around the margin of the disc of dorsal, funnel-building tube feet. In *E. cordatum* and *Agassizia scrobiculata* these tube feet have discs with numerous papillae. All other species known have a rosette of rods in dorsal funnel-building tube feet.

Phyllode tube feet have to pick up particles and transfer them into the mouth. Sub-anal tube feet have also been reported to transfer sediment particles. These tube feet build either one or two horizontal tubes posterior to the animal. In *Brissopsis alta* (Chesher 1968) and *E. cordatum* (Nichols 1959*a*, *b*), sub-anal tube feet collect particles from the end of the tube and carry them back to the vicinity of the sub-anal tuft of spines where they are dropped and incorporated into the walls of the funnel. The extension of the lumen into the disc and the flexibility of the papillae are extremely important since they allow the disc to change shape, as observed by Nichols (1959*a*, *b*) and Chesher (1968). During protraction the disc is convex and the papillae splayed, but upon contact with a suitable area of sediment the disc flattens. Upon contraction the disc invaginates and the papillae converge to envelop the adhering sediment particles. When phyllode tube feet reach their destination the disc is everted to drop its load. The situation is probably similar in sub-anal tube feet.

In building a vertical respiratory shaft to the surface, the problem of transporting particles is much less critical. Chesher (1968) observed that dorsal, funnel-building tube feet of *B. alta* were pressed into the substrate, oscillated, and then removed, leaving a circular indentation. He was unable to ascertain whether sediment was compressed or whether it was removed by the tube feet. It may be that the uppermost few centimetres of sediment are less compact and that a funnel can be built by simply compressing the sediment. However, it seems more probable that the tube feet do pick up some particles and that those which do not adhere or that are knocked off, fall down the funnel into the chamber of the burrow. Thus adhesion and transportation of sediment particles is not particularly important since those particles that are loosened by the action of the tube feet are automatically lost from the funnel. In this respect it is interesting to note that *E. cordatum*, one of the two known spatangoids with well-developed penicillate tube feet in ambulacrum III, can extend these tube feet out of the respiratory funnel where they gather detritus from the surface layer of sediment and carry this down into the burrow (Robertson 1871; Buchanan 1966). *A. scrobiculata* may also feed in this way.

In a number of spatangoids the aboral tube feet in ambulacrum III are suckerless. Aboral sensory tube feet are present in species of *Brissus*, *Lovenia*, *Maretia*, *Meoma*, *Paramaretia*, and *Spatangus*. Most of these are known to live infaunally (Takahashi 1938; Tornquist 1911; Ferber and Lawrence 1976; Chesher 1969; Nichols 1959*b*) but they rarely maintain any connection with the surface and then only by means of their dorsal spines. These echinoids are therefore restricted to living in sands or gravels where interstitial water circulation can be promoted. The dorsal tube feet of ambulacrum III are used simply as sense organs.

Oral tube feet. Irregular echinoids feed mostly by ingesting large quantities of sediment. The tube feet that are involved in collecting and transporting sediment particles are suckered in the holectypoids, cassiduloids, and clypeasteroids but are penicillate in the holasteroids and spatangoids. This seems to be related to the grain size of the substrate ingested. Recent cassiduloids and holectypoids live in coarse sands and shell gravels which they ingest with only limited selectivity (Higgins 1974; Thum and Allen 1976; Gladfelter 1978; Rose 1978). Suckered tube feet are quite satisfactory for picking up and transporting individual grains which are equal to or larger in size than the disc. Other groups have, however, invaded finer-grained substrates. The problem of feeding in these finer substrates has been solved in three ways:

1. In clypeasteroids, which live largely on or within sands, the tube feet have become extremely small but have retained a functional sucking disc. They have also become exceedingly numerous. These minute tube feet have a small enough sucking disc to be able to pick up the small sand and detritus particles which surround them. These can then be transferred to a near-by mucous rope, which lies in each food groove, or directly to the mouth.
2. In spatangoids and some holasteroids, large penicillate tube feet are developed around the peristome. Each tube foot can pick up a disc-full of fine sediment particles by mucous adhesion. These prehensile tube feet are even retained in spatangoids that live in coarse sands and shell gravels.
3. In *Pourtalesia* only sensory tube feet occur around the mouth. Unlike other irregular echinoids the anterior ambulacrum is deeply invaginated below the ambitus and the walls and roof of this cavity are covered in highly modified spatulate spines. This echinoid probably ploughs through the

surface layer of sediment using its specialized spines to shovel material into the peristome. This explains why *Pourtalesia* leaves behind a shallow furrow as it moves forward. This is illustrated in Southward *et al.* (1976) and has also been observed in bottom photographs by D. S. M. Billett (pers. comm.).

Ampullae. There are only two types of ampulla in irregular echinoids. Firstly there are those which are very large and elongate and which are crossed by numerous septa. These septa maintain the shape of the ampulla during contraction and expansion and also help to partition the flow of coelomic fluid so as to make full use of the large surface area available. Although there are contractile fibres in the walls, these ampullae are primarily designed for gaseous exchange. They are always connected to their tube foot by two pores. The corrugated ampullae in *E. cordatum* are associated with a conjugate furrow on the inner plate surface (Pl. 6, fig. 5; text-fig. 5).

Secondly there are cylindrical or bulbous ampullae which connect with the branch of the radial water vessel by a relatively narrow neck. These ampullae have no septa crossing the lumen and have a well-developed layer of circular, interconnecting contractile fibres. These accompany non-divergent isopores and unipores and serve as reservoirs for the tube foot. Thus they permit rapid expansion and contraction of the tube foot, independent of the contraction or expansion of neighbouring tube feet.

Intermediates do occur, as, for example, in *Echinoneus cyclostomus*, where the ampulla is squat and crossed by relatively few septa (text-fig. 6).

FUNCTIONAL SIGNIFICANCE OF THE STRUCTURE OF PORES

Number of pores. Two pores connecting the tube foot with its ampulla allow a one-way flow of coelomic fluid, as observed by Fenner (1973). This is highly adaptive, since the continuous circulation that results enhances the efficiency of gaseous exchange across the test. Where known, fluid passes into the tube foot via the adradial pore and out of the tube foot via the perradial pore.

In unipores, fluid moves in and out of the tube foot only during expansion and contraction (Fenner 1973). Kier (1974) has noted an evolutionary trend in irregular echinoids for oral pores to change from double to single pores. Unipores come to replace pore pairs where the associated tube foot plays only a minor part in supplying the respiratory demands of the animal. This usually follows the development of specialized, aboral, respiratory tube feet.

Pore divergence. Not all isopores and anisopores bear tube feet that play an important role in gaseous exchange. The emphasis placed on gaseous exchange is reflected in the separation of the two pores. If the pores are well separated when they appear on the inner surface of the test, then the associated ampulla is large and flattened and is crossed by many septa. If the pores coalesce, or appear close together on the inner plate surface, then the associated ampulla is cylindrical or bulbous and is not crossed by septa. Therefore tube feet associated with divergent pores, or pores that are widely separated on the outer surface of the plate, have a primary or secondary respiratory function. Tube feet associated with closely spaced pores, which show little or no divergence and which may even coalesce internally, play no significant part in gaseous exchange across the test. It is often the case that areas of non-divergent isopores may include some constricted unipores.

Overall shape. Isopores that are circular or oval in outline bear tube feet which have a cylindrical stem and terminate either in a sensory pad or in a disc. Isopores that are obviously elongate bear specialized respiratory tube feet with a central, partitioned region. The same is also true of anisopores. The shape of the ambulacral pore obviously matches the shape of the base of the tube foot.

Most unipores are roughly circular in outline. Where they are dense and become arranged into more than just a single row, differences in shape are found. This occurs aborally in ambulacrum III of *Echinocardium cordatum* (Pl. 6, fig. 4) and in the phyllodes of certain cassiduloids, such as

Apatopygus recens. The pores that lie nearest the perradial suture are typically circular in outline, whilst those in an adradial position are more elongate. This does not signify a difference in the structure or function of the associated tube feet but appears to result from the angle at which the pore passes through the plate. Elongate unipores occur with the more oblique pores.

Size. The size of ambulacral pores is of little importance in interpreting the form of the associated tube foot. For example, in this survey the tube feet which were found to terminate in a sucking or adhesive disc are associated with unipores that range from 20 μm to 2000 μm in diameter, whereas sensory tube feet are associated with unipores that range from 50 μm to 500 μm in diameter. Pore size does, however, indicate the size of the associated tube foot and this can be useful when comparing the same type of ambulacral pore in different species.

Pore shape. In isopores, elongate pores are always associated with respiratory tube feet. Pores, that are approximately circular in outline, are found with sensory, suckered, adhesive, or respiratory tube feet. In conjugate anisopores the adradial pore is always very elongate. As this pore passes through to the interior of the test it narrows considerably (text-fig. 13E). This is the pore through which coelomic fluid flows into the tube foot and the reason for its great elongation lies in the fact that the associated tube foot, although very elongate, rises only a short distance above the level of the test. This, as was explained previously, is an adaptation found in infaunal echinoids to provide efficient, but protected, respiratory tube feet. Were the septa to be arranged parallel to the plate surface, as in tall respiratory tube feet, little separation of the outflowing current could take place. In order to avoid this the septa are arranged obliquely and the adradial pore is elongate. In this way the outflowing coelomic fluid can be separated efficiently and much better use made of the central partitioned region. Because the tube foot is so short, partitioning often starts within the pore before it reaches the plate surface. This may be done by extension of the septa into the pore or by the growth of calcite partitions within the pore, as in *Dendraster*.

In unipores, large, round pores are associated with active tube feet that terminate in some form of disc. Small, narrow, and elongate pores are usually associated with sensory tube feet though occasionally unipores with an extensive periporal area, that are associated with feeding or funnel-building tube feet, may have a slit-like pore. In spatangoids, where the pore is large and forms a large percentage of the area of the unipore, as in the aboral unipores of ambulacrum III in *E. cordatum*, the associated tube feet are highly extensible. These tube feet, in *E. cordatum* can build a tube up to 18 cm in length (Nichols 1959*b*). Unipores, where the pore forms only a small proportion of the unipore, support tube feet which are less extensible. These are commonly sensory tube feet but in species of *Brissopsis* and in *E. pennatifidum* funnel-building tube feet are associated with these unipores. It is interesting that none of these appear to be capable of building a respiratory funnel more than 2 to 3 cm in length (Chesher 1968; Buchanan, in Goldring and Stephenson 1970; Gage 1966). Unipores associated with phyllode tube feet also have a relatively small pore and again appear to be only moderately extensible. The large area of pore is presumably required for the efficient movement of large volumes of coelomic fluid in and out of the tube foot.

Funnelled unipores are so shaped because of the construction and growth of the plate. In Recent cassiduloids there is a thick outer plate layer. The pore funnels outwards as it passes through this layer, presumably due to the expansion of the tube foot during growth of the outer plate layer. In fossil cassiduloids, such as *Clypeus* and *Galeropygus*, this outer plate layer is not developed and ambulacral pores, although partitioned, are not funnelled and are rimmed by an attachment area (Pl. 2, fig. 6).

Neural canal. The neural canal houses a branch of the radial nerve, part of which extends up the tube foot and part of which merges with the sub-epidermal nerve plexus of the plate surface. A neural canal is absent, or only feebly developed, in pores associated with respiratory tube feet, since very little nervous tissue passes up the perradial pore. A neural canal is present in pores supporting other tube feet. The neural canal is nearly always separated from the perradial pore by a constriction.

A thin membrane of connective tissue stretches across here, separating the nervous tissue from the lumen of the pore. The pore, in simple unipores, is analogous to a neural canal, since it is taken up largely by nervous tissue. In this case the narrow lumen of the water vascular system is not usually separated from the nervous tract by a constriction. It is similar, in this respect, to the terminal tube foot of the ocular plates.

In some instances the neural canal may become separated from the perradial pore by the closure of the constriction to form an unbroken attachment area, or becomes separated on its passage through to the interior of the test. Both are relatively rare occurrences and the formation of an independent neural pore is an abnormal situation of little functional significance.

Whether the neural canal lies on, or is displaced from, the major axis, is an important feature of partitioned isopores. This is linked with the presence or absence of pore divergence. General-purpose tube feet, involved in gaseous exchange across the test as well as in sensory reception and/or adhesion, have flattened and elongate ampullae. In order to attain a suitably elongate ampulla, the two pores must diverge as they pass through the test. In order to optimize this divergence, the major axis of the isopore is aligned parallel with the branch of the radial water vessel serving it. This is the direction in which the ampulla is flattened. The neural canal always maintains contact with the adoral plate suture and therefore lies to one side of the axis of the isopore.

With the development of specialized respiratory tube feet, other tube feet do not have to assist in gaseous exchange across the test. The ampullae therefore become cylindrical or bulbous tubes with narrow necks. No pore divergence is necessary and, rather than having a pore for inflowing coelomic fluid positioned perradially and one for outflowing coelomic fluid positioned adradially, both pores come to lie side by side, more or less equidistant from the radial water vessel. This is brought about by a shift of the adradial pore to an aboral position relative to the perradial pore. The neural canal remains in an adoral position, in contact with the adoral plate suture and thus comes to lie in an axial position.

This trend is evident in the partitioned isopores of regular echinoids. In the isopores that accompany the most muscular tube feet (P4-type), the adradial pore is shifted so that the major axis of the pore lies oblique to the adoral plate suture. The neural canal therefore comes to lie almost in an axial position. The pore divergence that occurs in these isopores is less than in most other types of partitioned isopore found in regular echinoids and the associated ampulla is also smaller and squatter.

The adapical/adoral isopore orientation is presumably the primitive condition and is still found in many spatangoids. However, with the development of more numerous tube feet aborally in ambulacrum III, the adradial pore shifts back to an adradial position to permit closer packing of the tube feet. The two pores still run parallel to one another and the axial position of the neural canal has been maintained. The attachment in such isopores is well developed adapically and adorally but is feebly developed adradially and is interrupted by the neural canal perradially. The axial-positioning of the neural canal is therefore not fortuitous but is brought about by the fact that funnel-building tube feet of ambulacrum III have to work largely in one plane.

Attachment area. Compared with most ambulacral pores of regular echinoids, the attachment area is poorly developed in the ambulacral pores of irregular echinoids. This is because the tube feet of irregular echinoids, with the possible exception of *Echinoneus cyclostomus*, are never involved in anchorage and require little tensile strength. Stem muscle fibres are therefore poorly developed and form only a thin layer, rarely more than a few fibres thick and often less. These muscle fibres simply control the posture of the tube foot. The development of the attachment area is not as useful in determining the structure of the overlying tube foot in irregular echinoids as it is in regular echinoids. It is important, however, that the attachment area, an area of fine labyrinthic stereom, be distinguished from the periporal area, an area of coarser and denser stereom overlain by squamous epithelium.

Even in partitioned isopores the development of the attachment area does not give much information. In most there is a clear but narrow attachment area. This may, however, be very indistinct in small pores (Pl. 3, fig. 1), and it may be difficult to correctly identify suckerless tube feet from the structure of the pore.

Periporal area. A large periporal area is developed in certain unipores. It lies within the base of the tube foot and is covered by a single layer of squamous epithelium. It may be developed for one of two reasons. First the pore may be reduced in size, often to a slit-like opening, where extensive expansion and contraction of the tube foot with the associated shifting of coelomic fluid is not important. This is common in sensory tube feet where the associated unipore has a small central pore surrounded by a horse-shoe-shaped periporal area. Secondly the associated tube foot may terminate in a very broad disc. The stem required to support it has to have a large diameter so that the pore, although not small, forms only a small part of the unipore. The pore has a marginal position and the periporal area may be depressed, flush, or raised and is sometimes developed into a broad, bulbous dome. There is no obvious functional significance underlying this variation though a central dome may help to maintain coelomic fluid movement in the lumen by increasing the surface area of rather sparsely ciliated epithelium.

Interporal partition. The interporal partition may be crossed by a furrow, a narrow platform, or by a band of distinctive stereom linking the two pores together. In all cases the associated tube foot is specialized for gaseous exchange. The narrow zone that crosses the interporal partition marks the position of the central, partitioned region of the tube foot. The more complex and branched tube feet have isopores in which the connecting band of distinctive stereom is displaced adapically in an arc. This may be in response to the lop-sided development of lobes in the central, partitioned region, noted by Fenner (1973) in spatangoid respiratory tube feet.

In partitioned isopores and anisopores the interporal partition is commonly raised above the level of the plate surface, but may also be flush or sunken. A septum joins on to the interporal partition in partitioned isopores with a laterally positioned neural canal, as in *Echinoneus*, but is absent from tube feet associated with partitioned isopores with an axially positioned neural canal. In some pore pairs the pores coalesce internally so as to produce an interporal partition that bridges the pore on the outer surface (text-fig. 14A, B; Kier 1974, fig. 24B). In constricted unipores the partition has obviously been breached or left incomplete. Kier (1974) has shown that, during evolution, the interporal partition is lost from oral pore pairs of irregular echinoids. Thus with the loss of its role in gaseous exchange, a tube foot loses its septum and the interporal partition becomes redundant and may be lost at a later stage.

The identification of funnel-building tube feet in fossil echinoids. From the preceding descriptions it must, by now, be apparent that funnel-building tube feet of spatangoids can be associated with several different kinds of pores. The ability to identify these tube feet in fossils would be extremely useful to the palaeoecologist and has prompted three workers to suggest features distinctive of the associated pores. Nichols (1959*b*) used the presence of a large interporal bulge and a surrounding non-tuberculated area to indicate that the associated tube feet were muscular and terminated in some form of disc. Kier (1974) also noted that a deep adapical pit was often found in the peripodia which bore funnel-building tube feet and suggested that this also might act for muscle attachment. We now know, however, that funnel-building tube feet need not be particularly muscular and that the interporal bulge and adapical depression have nothing to do with muscle attachment. Bromley and Asgaard (1975) suggest that spatangoids capable of forming an apical funnel of any great length require more than fifty aboral tube feet and an associated fasciole. No reason is given why so many tube feet are required dorsally when six to ten sub-anal tube feet suffice, in many cases, for building an extensive sub-anal funnel.

Although the results of this work show that it is not possible to reconstruct the form of the terminal disc from the pore morphology it is usually possible to distinguish between those pores that bear sensory tube feet and those that bear funnel-building tube feet. The following features are important when trying to reconstruct the tube feet in fossil spatangoids.

1. The presence or absence of an appropriate fasciole cannot be used to infer the presence or absence of funnel-building tube feet. Although Recent spatangoids, which lack an aboral fasciole, possess only sensory tube feet in the aboral part of ambulacrum III, this is unlikely to hold true for the more primitive fossil spatangoids, such as *Micraster*. In *Micraster* the whole of the aboral surface is covered in miliaries interspersed with tubercles (a situation not encountered in Recent spatangoids), and these are likely to have borne small, and presumably well-ciliated, spines. In addition the tube feet within a fasciole are not always specialized for funnel-building. For example, *Meoma ventricosus* (Lamarck) has a peripetalous fasciole and *Lovenia elongata* (Gray) has an inner fasciole yet in both species all the aboral tube feet of ambulacrum III are sensory and lack a terminal disc.

The pores that lie within a sub-anal fasciole are associated with funnel-building tube feet, though occasionally an undeveloped tube foot or two may be present along with the funnel-building tube feet. The absence of a sub-anal fasciole does not rule out the presence of sub-anal funnel-building tube feet. These are found in spatangoids, such as *Agassizia scrobiculata* Agassiz and Desor and *Brissaster fragilis* (Düben and Koren), were there is no sub-anal fasciole.

2. There is almost always a pronounced change in the size of the peripodia, marking the change from sensory to funnel-building tube feet. If pores of the sub-anal region are obviously larger than other ambital pores then it is fairly certain that they bear funnel-building tube feet. Similarly for ambulacrum III, if there is a sharp change from very small, apical pores to much larger pores, away from the apex, and a similar, but less pronounced, change from large pores to small pores ambitally, then dorsal, funnel-building tube feet are present.

3. Where the aboral pores in ambulacrum III are so closely spaced as to more or less touch one another, the associated tube feet are modified for funnel-building. Where aboral pores are more widely spaced the associated tube feet may be sensory in function, as in *Maretia* or *Brissus*, or may be used for funnel-building, as in *Brissopsis atlantica* or *Hemiaster expurgitus*.

4. If ambulacrum III is flush with the test surface, or even slightly raised, the associated tube feet are, in most cases, sensory in function. Only *Echinocardium pennatifidum*, of the species examined, have funnel-building tube feet and an ambulacrum that is not sunken. Anterior ambulacra, that are deeply sunken, all possess funnel-building tube feet in the spatangoids examined. This is not true for holasteroids, such as *Cardiaster* and *Infulaster*, where the deeply sunken ambulacrum is more or less vertical over much of its length. The pore morphology and arrangement tend to suggest that dorsal tube feet of the anterior ambulacrum in these species were sensory. A slightly depressed anterior ambulacrum may have either sensory or funnel-building tube feet.

5. Unipores rimmed by an attachment area, unipores with an extensive periporal area, and constricted unipores are all associated with funnel-building tube feet. In nearly all cases broad-rimmed unipores are associated with sensory tube feet. The only exception found was again in *E. pennatifidum*, where broad-rimmed unipores support both sensory and funnel-building tube feet. Partitioned isopores with an axially positioned neural canal, found in Recent spatangoids that were examined, all bear funnel-building tube feet. This, however, is unlikely to be true in more primitive echinoids. For example, in the holasteroid *Infulaster*, partitioned isopores are found in ambulacrum III. These do not vary in size or construction along most of the ambulacrum and are similar in size and shape to other ambital isopores. They are likely to have borne sensory tube feet.

Clearly then, it is not always possible to be certain as to whether a particular pore was associated with sensory or funnel-building tube feet. However, by considering the pore structure and arrangement and the size variation of pores over the test it is often possible to be reasonably certain of the type of tube foot supported.

THE EVOLUTION OF TUBE FEET AND ITS ADAPTIVE SIGNIFICANCE

Most workers are agreed that irregularity in echinoids evolved independently in two or more groups (see Durham 1966 for a comprehensive review). Tube feet in different groups of Recent irregular echinoids are often morphologically very different. They are, however, rarely, if ever, preserved in the fossil record and their evolution can be interpreted only through a study of the ambulacral pore morphology. Kier (1974) has realized this and has followed carefully certain evolutionary trends in pore morphology. He has interpreted these changes in terms of functional modifications of the associated tube feet. It is now possible to identify the probable evolutionary advances in tube foot morphology in rather more detail and to enlarge upon the adaptive significance of the changes that occur.

The pygasteroids are a short-lived group thought by Durham (1966) to have originated from a pedinoid ancestor. Members have both oral and aboral partitioned isopores with a laterally positioned neural canal in which the pores diverge. Both oral and aboral tube feet were probably suckered (Smith, 1978*a*). Pygasteroids appear to have retained the suckered tube foot and ampulla of regular echinoids with little or no modification.

The holectypoids, which originated either from a diadematoid ancestor (Mortensen 1948; Devries 1960) or from a pseudodiadematoid ancestor (Durham 1966), are represented by only two living genera. The tube feet of *Echinoneus cyclostomus* are only slightly modified with respect to those of non-cidaroid regulars. The tube foot still retains a septum, a rosette and frame, and a sucking disc. However, the disc muscles are well developed and the ampulla is squatter than would be expected. Both oral and aboral tube feet are suckered. The development of disc muscle fibres may be linked with the size of the disc which is very much smaller than the sucking disc in tube feet of regular echinoids. The pore morphology and arrangement in the earliest holectypoid genus *Holectypus*, is more or less identical to that found in the Recent *Echinoneus*. It seems safe to assume that the tube feet and ampullae of *Holectypus* were similar to those of *Echinoneus* and that little morphological change has occurred in the tube feet of the holectypoids.

The galeropygoids, which gave rise to both the cassiduloids and the disasteroids are believed to have originated from an acrosaleniid ancestor (Mintz 1968), though Devries (1960) suggested a diadematoid ancestry and Markel (1978) rules out a stirodont ancestor. Both *Galeropygus* and *Hyboclypus* have partitioned isopores aborally which presumably bore simple, suckerless, and somewhat flattened tube feet. Highly specialized respiratory tube feet were quickly evolved in the early cassiduloids. The primitive *Clypeus* species *C. michelini* Wright has compact anisopores with little separation of the two pores. The associated tube feet may have had a narrow partitioned region developed between the pores. In later species of *Clypeus* conjugate anisopores are highly developed and often extremely elongate. This trend towards more elongate anisopores represents a change from tall and slender tube feet to short and elongate tube feet. This helps maintain the efficiency of the tube feet as they shorten to become better protected following the adoption of an infaunal mode of life. It does not necessarily mark the development of more efficient respiratory tube feet.

Partitioned isopores with an axially positioned neural canal are found on the oral surface of galeropygoids and Jurassic cassiduloids. These are oval and have a narrow attachment area and a slender interporal partition. Although these isopores superficially resemble isopores of peristomial plates in some regular echinoids, the large area of pore space suggests that the associated tube feet were highly active and were most likely similar to those found in Recent cassiduloids. Kier (1974) has noted that the partition in oral isopores of cassiduloids is gradually lost during the late Cretaceous and early Tertiary.

Cassiduloids and holectypoids are known to use their tube feet in feeding (Thum and Allen 1976; Gladfelter 1978; Rose 1978). They pick up and transport suitable particles by means of their suckered tube feet and not, as suggested by Kier (1974), by means of mucous adhesion and prehensile grip, as is found in spatangoids. Because of the diameter of their disc, these tube feet are capable of handling only coarse sand and gravel-sized particles. Jesionek-Szymanska (1978) has shown that galeropygoids probably became irregular following a change in feeding habits and the loss of the dental apparatus. Galeropygoids may therefore have evolved from an ancestor which inhabited a suitably coarse substrate where organic-rich particles could be selectively ingested without grazing. A similar life style has been postulated for the unrelated pygasteroid *Plesiechinus ornatus* (Buckman) which is known to have inhabited oncoid-rich substrates (Smith 1978*a*). Cassiduloids and disasteroids rapidly evolved from galeropygoids and all quickly diversified to cope with life in substrates of lower organic content where large quantities of substrate had to be ingested. This necessitated the development of a posterior sulcus or the posterior migration of the periproct to deal with the increased discharge of sediment from the anus. Holectypoids appear to have evolved in parallel and likewise rapidly adapted to feeding by sediment swallowing.

The disasteroids evolved from a galeropygoid ancestor (Mintz 1968). Early forms, such as *Pygomalus ovalis* (Leske) and *Pygorhytis ringens* (Agassiz), have small partitioned isopores on both oral and aboral surfaces. They therefore lacked specialized aboral respiratory tube feet. The morphology and arrangement of partitioned isopores on the oral surface is very similar to that found in contemporary galeropygoids and cassiduloids, as pointed out by Kier (1974). Like cassiduloids, the associated tube feet were almost certainly suckered and the ampullae cylindrical. These disasteroids presumably fed on substrate particles collected and transported by their tube feet as did other Jurassic irregulars.

It therefore appears that all groups of primitive irregular echinoids relied on suckered tube feet for collecting the particles on which they fed. If this were indeed the case then the early irregulars would have been capable of handling only relatively coarse substrates leaving vast areas of the sea floor unexploited.

The holasteroids, which were descended from the disasteroids (Mintz 1968), had developed aboral linked isopores indicating that respiratory tube feet were present. These tube feet were presumably relatively tall and narrow. Kier (1974) has noted that, in the disasteroid–holasteroid lineage, there is a progressive reduction in the number of isopores surrounding the peristome and a corresponding increase in their size. In echinoids such as *Echinocorys*, *Infulaster*, and *Holaster* the partitioned isopores with an axially positioned neural canal, present around the peristome, are large. The associated tube feet must have terminated in a considerably larger disc than tube feet in any other position. The change towards increasingly large phyllode isopores, which started some time during the early Cretaceous, almost certainly marks the change from suckered tube feet to tube feet which relied on mucous adhesion. This innovation permitted holasteroids to feed on finer substrates than had hitherto been possible.

Spatangoids also evolved from a disasteroid ancestor (Devries 1960; Fischer 1966; Mintz 1968). The presence of more or less identically structured penicillate tube feet around the peristome in all spatangoid families examined by Lovén (1883) or by the author, as well as in the holasteroid *Urechinus*, suggests that penicillate tube feet may have already evolved in the disasteroids prior to the evolution and diversification of the holasteroids and spatangoids. Indeed it is quite possible that the development of mucous adhesive tube feet, permitting irregular echinoids to colonize fine-grained substrates, was a major factor giving rise to this rapid burst of evolution. In the spatangoids, funnel-building tube feet were evolved as an adaptation for an infaunal mode of life within a fine substrate. Fossil holasteroids, examined by the author, do not appear to have developed funnel-building tube feet. This adaptation permitted spatangoids to feed on sub-surface sediments inaccessible to the holasteroids.

Funnel-building tube feet can be arranged into a morphological series which may represent a true evolutionary progression. The simplest funnel-building tube feet differ from suckered tube feet in having a greater number of rosette elements. These elements may be broad and flat but more commonly they are elongate and narrow. In some the rods may be extremely long and slender and are connected by a web of connective tissue to form a flexible umbrella-like disc. In others the margin of the disc has become indented. The next morphological advance comes with the separation of rosette elements and the penetration of the lumen into the disc. In the most specialized tube feet the skeletal elements are reduced in size and increased in number while the disc lumen becomes more extensive. The functional significance of this morphological development has been discussed previously. Basically it results in a larger surface area of mucus-producing epithelium and a more flexible disc capable of picking up sediment in a prehensile manner.

Aboral tube feet in all but the anterior ambulacrum are mostly specialized for gaseous exchange in the spatangoids. Respiratory tube feet can also be arranged into a morphological series in which the trend is towards increasing their surface area without increasing their height. Sensory tube feet in holasteroids and spatangoids retain 'juvenile' characteristics seen in the developing suckered tube feet at the apex of some regular echinoids. The developing adapical pores are unipores which later change into isopores by the growth of an interporal partition. They are associated with simple suckerless tube feet. Sensory tube feet in irregulars are probably the result of paedomorphism.

The origin of the clypeasteroids is under some dispute. Durham (1966) argues for their derivation from a holectypoid ancestor whereas Phelan (1977) favours a cassiduloid ancestor. Recent work on the comparative morphology of the lantern and teeth of cassiduloids (Markel 1978) supports the view that clypeasteroids were derived from the cassiduloids. The minute, suckered tube feet of clypeasteroids bear a striking resemblance to the suckered tube feet of cassiduloids, especially to the small ambital tube feet where the rosette is much reduced. Ambital unipores of cassiduloids are also very similar to unipores of clypeasteroids (cf. Pl. 5, fig. 1 and Pl. 4, fig. 3). It would be a relatively simple step to multiply the number of tube feet and ampullae arising from each lateral branch of the radial water vessel to derive the simplest clypeasteroid arrangement. The reduction in size and increase in number of tube feet in clypeasteroids is an adaptation to cope with feeding in the finer sands. Although their tube feet still rely on suction for collecting particles, the small size of the terminal disc permits sand-sized particles to be handled. Clypeasteroids were therefore able to evolve and diversify in a niche previously inaccessible to cassiduloids.

A summary of the postulated evolutionary changes that have occurred in post-Palaeozoic echinoids is given in text-fig. 15.

Acknowledgements. I wish to thank Miss A. M. Clark (British Museum, Natural History), Dr. D. L. Pawson and Dr. P. M. Kier (Smithsonian Institution), Dr. F. W. E. Rowe (Australian National Museum), Dr. A. N. Baker (New Zealand National Museum), and Mr. C. Griffiths (University of Cape Town) for making specimens available to me. I am extremely grateful to Professor David Nichols for all his encouragement and help during this research. This work was financed by an S.R.C. research studentship.

REFERENCES

BELL, B. M. and FREY, R. W. 1969. Observations on the ecology and the feeding and burrowing mechanisms of *Mellita quinquiesperforata* (Leske). *J. Paleont.* **43,** 553-560.

BROMLEY, R. G. and ASGAARD, U. 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. *Bull. geol. Soc. Denmark*, **24,** 261-281.

BUCHANAN, J. B. 1966. The biology of *Echinocardium cordatum* (Echinodermata: Spatangoida) from different habitats. *J. mar. biol. Ass., U.K.* **46,** 97-114.

CHESHER, R. H. 1963. The morphology and function of the frontal ambulacrum of *Moira atropos* (Spatangoida). *Bull. mar. Sci. Gulf Caribb.* **13,** 549-573.

—— 1966. Redescription of the echinoid species *Paraster floridiensis* (Spatangoida; Schizasteridae). *Bull. mar. Sci.* **16,** 1-19.

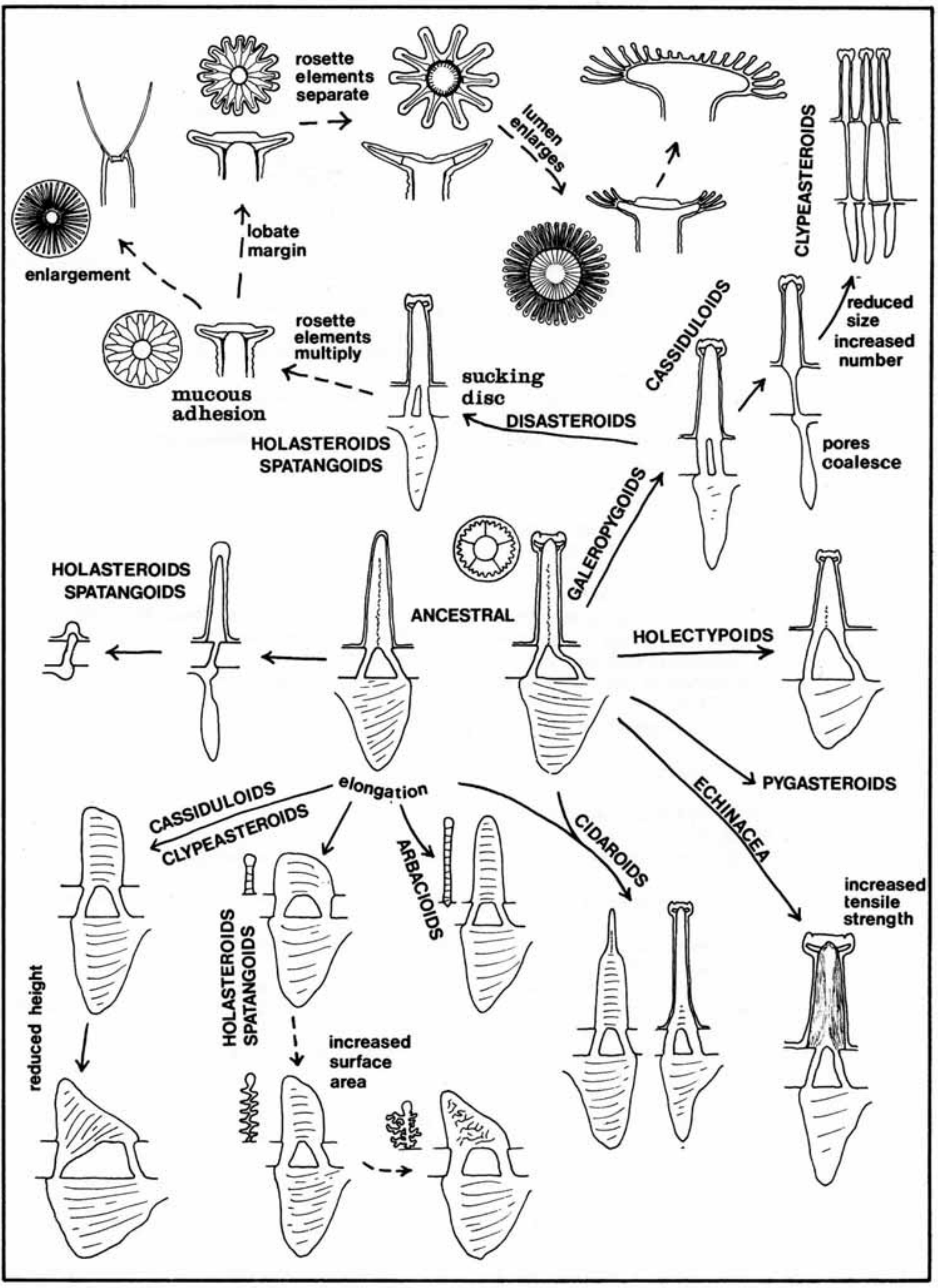
—— 1968. The systematics of sympatric species in West Indian spatangoids. *Stud. trop. Oceanogr. Miami*, **7,** viii + 168 pp.

—— 1969. Contributions to the biology of *Meoma ventricosa* (Echinoidea; Spatangoida). *Bull. mar. Sci.* **19,** 72-110.

CHIA, F. S. 1969. Some observations on the locomotion and feeding of the sand dollar *Dendraster excentricus* (Eschscholtz). *J. exp. mar. Biol. Ecol.* **3,** 162-170.

DEVRIES, A. 1960. Contribution à l'étude de quelques groupes d'échinides fossiles d'Algérie. *Publ. Serv. Carte géol. Algér., new ser. Paléont. Mem.* **3,** 1-278.

DURHAM, J. W. 1955. Classification of clypeasteroid echinoids. *California Univ. Publ. Geol. Sci.* **31,** 73-198.



TEXT-FIG. 15. Evolutionary diversification of tube foot structure in post-Palaeozoic echinoids. Dashed lines indicate morphological series. Tube feet/ampullae not to scale.

DURHAM, J. W. 1966. Classification. *In* MOORE, R. C. (ed.), *Treatise on Invertebrate Paleontology. U. Echinodermata 3*, University of Kansas Press, 270–296.

FENNER, D. H. 1973. The respiratory adaptations of the podia and ampullae of echinoids (Echinodermata). *Biol. Bull. mar. biol. Lab., Woods Hole*, **145**, 323–339.

FERBER, I. and LAWRENCE, J. M. 1976. Distribution, substratum preference and burrowing behaviour of *Lovenia elongata* (Gray) (Echinoidea; Spatangoida) in the Gulf of Elat ('Aqaba), Red Sea. *J. exp. mar. Biol. Ecol.* **22,** 207–225.

FISCHER, A. G. 1966. Spatangoids. *In* MOORE, R. C. (ed.). *Treatise on Invertebrate Paleontology. U. Echinodermata 3*, University of Kansas Press, 543–627.

GAGE, J. 1966. Observations on the bivalves *Montacuta substriata* and *M. ferruginosa*, 'commensals' with spatangoids. *J. mar. biol. Ass., U.K.* **46,** 49–70.

GLADFELTER, W. B. 1978. General ecology of the cassiduloid urchin *Cassidulus caribbearum*. *Mar. Biol.* **47,** 149–160.

GOLDRING, R. and STEPHENSON, D. G. 1970. Did *Micraster* burrow? *In* CRIMES, T. P. and HARPER, J. C. (eds.). *Trace Fossils*. Geol. Jour. spec. issue no. 3, 179–184.

GOODBODY, I. 1960. The feeding mechanisms in the sand dollar *Mellita sexiesperforata* (Leske). *Biol. Bull. mar. biol. Lab., Woods Hole*, **119,** 80–86.

HAMANN, O. 1887. *Beiträge zur Histologie der Echinodermen. Heft 3. Anatomie und Histologie der Echiniden und Spatangiden*. Verlag von Gustav Fischer, Jena. 168 pp.

HIGGINS, R. C. 1974. Observations on the biology of *Apatopygus recens* (Echinoidea: Cassiduloida) around New Zealand. *J. Zool., Lond.* **173,** 505–516.

JESIONEK-SZYMANSKA, W. 1978. On a new galeropygid genus (Echinoidea) from the Jurassic (Upper Lias) of Morocco. *Acta palaeont. pol.* **23,** 187–193.

KIER, P. M. 1974. Evolutionary trends and their functional significance in the post-Paleozoic echinoids. *J. Paleont.* **48,** Supplement no. 3, Mem. 5, 95 pp.

LOVÉN, S. 1883. On *Pourtalesia*, a genus of echinoidea. *K. Svenska Vetensk-Akad. Handl.* **19,** 95 pp.

MARKEL, K. 1978. On the teeth of the Recent cassiduloid *Echinolampas depressa* Gray, and on some Liassic fossil teeth nearly identical in structure. *Zoomorphologie*, **89,** 125–144.

MINTZ, L. W. 1968. Echinoids of the Mesozoic families collyritidae d'Orbigny, 1853 and disasteridae Gras, 1848. *J. Paleont.* **42,** 1272–1288.

MORTENSEN, T. 1948. *A monograph of the Echinoidea.* IVi. *Holectypoida, Cassiduloida.* C. A. Reitzel, Copenhagen.

NICHOLS, D. 1959*a*. The histology of the tube-feet and clavulae of *Echinocardium cordatum*. *Quart. Jl microscop. Sci.* **100,** 73–87.

—— 1959*b*. Changes in the Chalk heart-urchin *Micraster* interpreted in relation to living forms. *Phil. Trans. R. Soc., Lond.* **B 242,** 347–437.

—— 1959*c*. The histology and activities of the tube-feet of *Echinocyamus pusillus*. *Quart. Jl microscop. Sci.* **100,** 539–555.

—— 1961. A comparative histological study of the tube-feet of two regular echinoids. Ibid. **102,** 157–180.

PHELAN, T. F. 1977. Comments on the water vascular system, food grooves and ancestry of the clypeasteroid echinoids. *Bull. mar. Sci.* **27,** 400–422.

ROBERTSON, D. 1871. Notes on *Amphidotus cordatus* (Penn.). *Quart. Jl microscop. Sci.* **11,** 25–27.

ROSE, E. P. F. 1978. Some observations on the Recent holectypoid echinoid *Echinoneus cyclostomus* and their palaeoecological significance. *Thalassia Jugosl.* **12,** 299–306.

SMITH, A. B. 1978*a*. A comparative study on the life styles of two Jurassic irregular echinoids. *Lethaia*, **11,** 57–66.

—— 1978*b*. A functional classification of the coronal pores of regular echinoids. *Palaeontology*, **21,** 759–789.

SOUTHWARD, A. J., ROBINSON, S. G., NICHOLSON, D. and PERRY, T. J. 1976. An improved stereocamera and control system for close-up photography of the fauna of the continental slope and outer shelf. *J. mar. biol. Ass., U.K.* **56,** 247–257.

STEPHENSON, D. G. 1963. The spines and diffuse fasciole of the Cretaceous echinoid *Echinocorys scutata* Leske. *Palaeontology*, **6,** 458–470.

TAKAHASHI, K. 1938. On some castings of sand in Korror Island of the Palao group. *Palao trop. biol. Sta. Studies, Tokyo*, **3,** 459–468.

THUM, A. B. and ALLEN, J. C. 1976. Reproductive ecology of the lamp urchin *Echinolampas crassa* (Bell, 1880) from a subtidal biogenous ripple train. *Trans. roy. Soc. S. Afr.* **42,** 23–33.

TIMKO, P. L. 1976. Sand dollars as suspension feeders: a new description of feeding in *Dendraster excentricus*. *Biol. Bull. mar. biol., Woods Hole*, **151,** 247–259.

TORNQUIST, A. 1911. Die biologische Deutung der Umgestaltung der Echiniden im Paläozoikum und Mesozoikum. *Z. indukt. Abstamm. -u. VererbLehre*, **6,** 29–60.

A. B. SMITH

Department of Geology
Brownlow Street
Liverpool L69 38X

Typescript received 20 November 1978

Revised typescript received 24 March 1979