Fossil Echinoidea from the Barton Beds (Eocene, Bartonian) of the type locality at Barton-on-Sea in the Hampshire Basin, England.

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Abstract: The known species of fossil echinoids found in the Barton Beds of the type locality at Barton-on-Sea, Hampshire, England, are examined. Nine are described, of which three are new, and three are left in open classification. The new species comprise: *Echinopedina paucituberculata*, *Ambipleurus? quaylei*, and *Spatangus (Phymapatagus) grandituberculatus*; those left in open classification include: indeterminate cidaroid, *Porosoma? sp.*, and *Coelopleurus sp.*; the remaining three species are: *Schizaster (Hypselaster) branderianus* (Forbes), *Eupatagus (Eupatagus) hastingiae* Forbes, and *E. (E.) excentricus* (Gregory).

The original description of *Echinopsis edwardsi* Forbes was based on two specimens. One, subsequently destroyed by pyrite decomposition, came from Hordle, Hampshire, presumably from bed J, and was probably the same species as *Echinopedina paucituberculata*. The other came from Bracklesham, Sussex, and is assigned to *Leiopedina*.

Schizaster durbani Forbes from the Barton Beds, Alum Bay, Isle of Wight, is here regarded as a junior synonym of *Schizaster (Hypselaster) branderianus* (Forbes) which it strongly resembles. A 'transfer method' was used to extract well preserved specimens of *S. (H.) branderianus* from clay matrix and enable the true generic identity to be established. The technique revealed lateral and anal fascioles not seen before, and well preserved peripetalous fascioles and other fine details of the test.

Preservation of echinoids is briefly discussed in relation to their modes of life, and an attempt made to correlate modes of life with preservation of the Barton echinoids. The ecology of the fossil echinoids is discussed and their conditions of life interpreted on the basis of comparisons with living relatives. The fossil echinoids probably lived in water about 50 - 100 metres deep.

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INTRODUCTION

The purpose of this work is to describe the systematics, distribution and palaeoecology of fossil echinoids found in the Barton Beds of Christchurch Bay in the counties of Hampshire and Dorset, England. Some of the species have been recorded and described by earlier workers, and others are new. For the convenience of identification, all species are described in detail herein, whether or not they have been described before. The fauna of the Barton Beds is rich and varied, and has long been collected by amateur and professional palaeontologists. The most spectacular fossils are, perhaps, the larger molluscs, but other phyla are present which are equally interesting and sometimes locally more abundant than the molluscs. Ernest St.John Burton (1929) described the Barton Beds in detail and identified 14 horizons by letter, from A1, A2, A3-L, a scheme which has been used by serious collectors subsequently.

Burton (1933:151-161) listed some 600 species of fossils, of which most were molluscs. Other taxa represented in his list included plants, foraminifera, coelenterates, annelids, bryozoans, brachiopods, crustaceans, echinoderms, and vertebrates - fish, reptiles, mammals. Continued enthusiastic collecting by many people has added new taxa to many of these groups, notably the crabs (Quayle & Collins 1981), fish otoliths (Stinton 1975-84), asteroids and ophiuroids (Rasmussen 1972), and mammals (Hooker 1986). New species of echinoids have also been discovered during the last decade or so, and the quality of the specimens of known species has improved by careful collecting and better preparation techniques.

Conditions for collecting from the Barton Beds are deteriorating, but continued work may still bring new species to light, or better specimens of known species.

THE LOCALITY (Text-figs 1a, b)

The Barton Beds form part of the sea cliffs of Christchurch Bay in Hampshire and Dorset (but originally entirely in Hampshire until the county boundaries were changed in the early 1970's) and extend in the west from National Grid Reference SZ 194927 at Friars Cliff, west of Highcliffe Castle, to SZ 261923 near Long Mead End in the east. Barton-on-Sea, from which the strata take their name, is situated about midway along the bay. The cliffs reach a maximum height of about 30 metres and are cut by two streams in steep-sided valleys, known locally as 'bunnies'. Chewton Bunny is situated in the western part of the bay and now marks the boundary between Hampshire and Dorset, and Becton Bunny is situated in the eastern part of the bay. The cliff between the two bunnies is known as Barton Cliff. The shape of the cliff is constantly changing, partly because of erosion and partly because of attempts to prevent erosion.

Coastal defence schemes have stabilized parts of the cliff, notably to the west of Chewton Bunny, and below Barton-on-Sea, but the cliffs between Chewton Bunny and the western end of the Barton defences, below Naish Holiday Estate, and eastwards from the eastern end of the Barton defences to the end of the section are as yet unprotected. At their eastern ends, the defences have accelerated erosion of these unprotected parts of the cliff by initiating a swirling, scouring action by waves deflected by either the projecting strongpoints or by the groynes. This effect can be clearly observed when there is a strong onshore wind and rough seas.
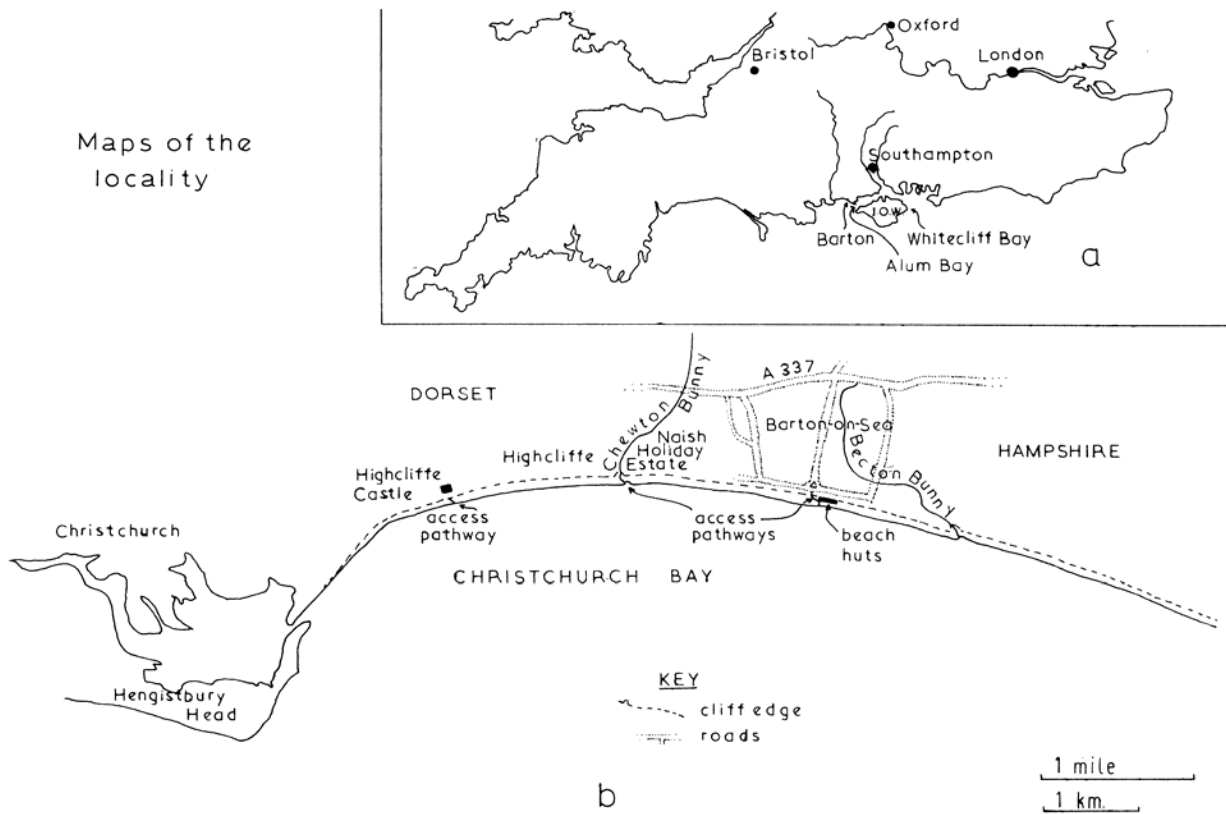
Text-fig. 1. Maps showing: (a) the location of Barton-on-Sea, Hampshire, England; (b) the location of Christchurch Bay; the exposures of the Barton Beds are found in the vicinity of Barton-on-Sea.

During collecting work in 1982, there was a distinct horizon above the A2/A3 beds at beach level which contained numerous Wellington boots protruding out of the clay, like the large fossils their previous owners had been attempting to collect.

STRATIGRAPHY.

A detailed account of the stratigraphy of Christchurch Bay is not within the scope of this work. The geology of the area has been adequately described by many authors, and their works have been summarized by Hooker (1986), and Edwards & Freshney (1987).

In his discussion of the stratigraphy, Hooker has proposed that the term Barton Clay Formation be adopted for the beds between the Pebble Bed and the base of bed A1, beds A1 to the lower half of bed H, and bed J. According to him, the age of the Formation is Bartonian, comprising the Auversian and Marinesian substages, plus part of the Ludian stage. He places the boundary between the Auversian and Marinesian substages somewhere within beds A1-C and the top of the Marinesian substage of the Formation in the middle of bed H. He also includes bed J in the Formation where it is Ludian in age.

Hooker has proposed that the term Becton Sand Formation be adopted for the upper half of bed H, beds I and K (except the uppermost green clay). The Lignite Bed, equivalent to bed L, is not included because Gardner et al. (1888) regarded it as belonging to the Headon Beds, and because it is lithologically different. He places the Formation in the Marinesian to early Ludian, with the upper part of bed H to the top of bed I included in the Marinesian, and bed K (along with bed J of the Barton Clay) in the Ludian. In order to demonstrate that bed J belongs in the Barton Clay Formation, Hooker has compared the Barton section with that in Whitecliff Bay, Isle of Wight. In Whitecliff Bay, a bed containing small siderite nodules like those in parts of bed J at Barton is found in a bed which overlies, with a sharp junction, blue-grey sandy clays. The dinocyst evidence (see Bujak et al., 1980) correlates these lower beds with upper H bed/lower I bed at Barton, suggesting that bed I wedges out towards

the east or northeast (see Hooker, 1986, text-fig. 68). Furthermore, at Barton, in the cliff section just behind the beach huts (see Text-fig. 1) east of the easternmost access pathway, bed K lies directly on top of bed I, and then very rapidly bed J achieves considerable thickness, separating beds I and K.

Hooker dates both the Barton Clay Formation and the Becton Sand Formation as late middle/late Eocene. He uses the Ludian stage in his correlation rather than the Priabonian stage because of the ease of referring the European fossil mammal faunas to the Ludian.

Curry (1981) defined the Bartonian as being the time of deposition of the Barton Beds (*sensu* Gardner *et al.* 1888), extending from the *Nummulites prestwichianus* bed below to the base of the Lower Headon Beds above. This definition excluded the Pebble Bed and those beds above it up to the *Nummulites prestwichianus* bed.

The term 'Barton Beds' used herein is informal and refers to all the beds as described by Burton (1929), from the basal pebble bed upwards, through A1 to L. Both terms are used simply for convenience and do not imply disagreement with Hooker. The echinoid fauna described in this work is confined to the Barton Clay Formation.

PRESERVATION.

Introduction.

The echinoids of the Barton Beds were first described by Forbes (1852) and by Gregory (1891) and were based mostly on rather poorly preserved and inadequate material. They have been mentioned in the works of other authors, (e.g. Desor 1857-58; Cotteau 1887) and have been included in faunal lists, such as those of Gardner *et al.* (1888:633); Prestwich (1888:370) and Burton (1933:152).

Forbes (1852:21-28) described the following echinoids from the Barton Beds of Barton:-

> *Cidaris Websteriana* (p. 22, pl.III, fig. 4), based on radioles.
> *Echinus Dixonianus* (p. 22, pl. III, fig. 3), based on radioles.
> *Echinopsis Edwardsi* (p. 23, pl. III, figs. 2a-f), based on tests from Barton and Bracklesham.
> *Hemiaster Branderianus* (pp. 25-26, pl. III, figs. 8a-c), based on tests.
> *Eupatagus Hastingiae* (pp. 26-27, pl. III, figs. 7a-d), based on tests.
> *Spatangus Omalii* Galeotti (p. 28, pl.III, figs. 9a-c), based on tests.

Forbes also described *Schizaster D'Urbani*, from the Barton Beds of Alum Bay (text-fig. on p. 36).

Gregory (1891:18-28, text fig. 1 on p. 27) described the following echinoids from the Barton Beds of Barton:-

> *Cidaris websteri* Forbes (p. 28), recording a radiole, and *Echinus* (!) *dixoni* Forbes (p. 28), recording a radiole; of the two species he said that radioles "...for comparison with other faunas are valueless..."
> *Hemiaster? branderi* (Forbes) (p. 22), based on tests;
> *Maretia grignonensis* (Desmarest) (p. 26), based on fragments of test;
> *Euspatangus hastingiae* Forbes (p. 26), based on tests;
> *Euspatangus excentricus* n. sp. (pp. 26-28), based on a single test.

Burton (1933:152) listed the following echinoids, together with their horizons (see Burton 1929:223-229), on the basis of specimens observed in situ and sometimes collected:-

> *Cidaris websteriana* Forbes from beds G, H;
> "*Echinus*" *dixoni* Forbes from bed E;
> *Echinopedina edwardsi* Forbes from beds A3, E, G, H;
> *Hemiaster branderi* Forbes from beds A3, F, H, ?J;
> *Maretia grignonensis* (Desmarest 1837) (= *Spatangus omalii* Forbes) from bed A3.

These lists show the uncertainty about the taxonomic position of most of the echinoids from the Barton Beds, due usually to the lack of well preserved specimens, to insufficient preparation of material, or to the fragmentary nature of some of the tests.

Both Forbes and Gregory were aware of the limitations of their material. For example, Gregory (1891:22) said of *Hemiaster? branderi* that "...The species is very imperfectly known and the genus uncertain. ...It has been referred by Desor and others to *Brissopsis*. As I am unacquainted with any evidence in support of this conclusion the species is here left in *Hemiaster*. If the species were better known it would not improbably have to be transferred to *Schizaster*. ..." Forbes (1852:26) thought that if the echinoid should have a "...caudal fasciole...the species must be referred to *Brissus*...".

Careful preparation of *Eupatagus excentricus* revealed features not seen by Gregory. Thus, he saw neither the sub-anal fasciole nor the peristome because both were embedded in matrix, and he missed seeing traces of the peripetalous fasciole, and assumed that its presence was "...indicated by the structure of the test and distribution of the tubercles..."

The species of echinoids from the Barton Beds described herein include the following, together with known and recorded horizons:-

	Name:	Bed recorded by Burton	Bed recorded by Lewis, Quayle
1.	*"Cidaris" websteriana* Forbes herein as indeterminate cidarid	G, H	A3
2.	*Echinopedina paucituberculata* sp. nov. previously as *Echinopsis edwardsi* Forbes	A3, E, G, H	J
3.	*Porosoma?* sp. previously as *Echinus dixonianus* Forbes	E, G	A3
4.	*Coelopleurus* sp.	---------	A2
5.	*Ambipleurus? quaylei* sp. nov.	---------	E
6.	*Schizaster (Hypselaster) branderianus* (Forbes)	A3, F, H, ?J	A2, A3
7.	*Eupatagus (Eupatagus) hastingiae* Forbes	---------	A2, A3, F
8.	*E. (E.) excentricus* (Gregory)	---------	A3?
9.	*Spatangus (Phymapatagus) grandituberculatus* sp. nov. (previously as *Maretia grignonensis* (Desmarest))	A3	A2, A3

Of these, three species herein remain unchanged (6,7,8), with additional information given for their generic assignment, one of the new species represents a new discovery (5), and two other new species have been renamed from original assignments after examination of type material and of new specimens (2,9). One species cannot be assigned to a genus because it is only known by its radioles (1), and the remaining species can be referred only to genera in open classification because of lack of evidence (3,4).

Taphonomy of Echinoids.

The tests of echinoids are not usually preserved complete after the death of the animal because they are constructed of many components held together partly by soft tissues. Fossil echinoid remains may be almost complete or may consist only of isolated radioles, individual plates, or fragments of test, or they may be complete or nearly so. The completeness of the remains may depend on predators which crush tests and scatter fragments, on scavengers which enhance the disintegration of the test, on submarine water currents, on wave action, or on the particular structure of the test.

Schäfer (1972:104) recorded that when a regular echinoid dies on the sea-bed, the radioles and pedicellariae are the first parts of the test to fall off, taking about a week to do so. The peristomial and periproctal plates fall away next as the membranes which support them decompose, this occurring after about two weeks. At the same time, the lantern breaks up into component parts which are lost through the peristome, and the collagen holding together the coronal plates is decayed

enough for the individual plates to separate from one another. If the plates of the apical system also fall into the test, this further weakens the structure and speeds the collapse. The disintegration can be accelerated by the action of scavengers.

Kier (1977), in his comparisons between fossilisation of regular and irregular echinoids, said that the tests of irregular echinoids are very fragile, but if they live buried, and remain so after death, are much less prone to disintegration than are the tests of regular echinoids which live on the surface. However, the radioles of irregular echinoids are attached by much less organic matter than those of regular echinoids, and consequently may be lost within hours of death if the echinoid is not buried. When the organic tissues which hold the coronal plates together have decayed, the test does not necessarily collapse because the stereom of one plate interlocks with that of adjacent plates, preventing separation. According to Smith (1984), the degree of interlocking varies with the type of echinoid - cidaroids and diadematoids have very weakly interlocking stereoms, whereas clypeasteroids are well interlocked by means of large, spiny protrusions of the stereom which so produce one of the strongest forms of test. Other groups fall between these extremes (see Schäfer, 1972:102-104; Kier 1977; Smith 1984:15-17, for discussions on the disintegration of echinoid tests, and Mortensen 1943, for some examples of methods of plate interlocking in temnopleuroids).

Tests may be broken up by a predator, in which case the break tends to occur across plates rather than along the sutures, for these are well endowed with collagenous tissue. Fossil tests which have suffered this fate can sometimes be recognized (Schäfer 1972:102).

A further factor influencing whether or not a test will be preserved is the mode of life. Kier (1977) has pointed out that only 20% of named/known Tertiary echinoids were regular species, whereas the number of Recent species of regular echinoids is slightly greater than that of irregular species (see Kier, 1977:169, table 1) He indicated that the number of species of known fossil irregular echinoids has increased from the Lower Jurassic, Hettangian, to the Pleistocene, when compared with the number of species of known fossil regular echinoids which have gradually decreased, but he was unsure whether the differences in the fossil record reflected the lack of preservation or actually fewer species. He pointed out that "...Regular echinoids predominate in areas of active erosion, such as rocky intertidal shores; whereas irregular echinoids are common in areas of active deposition, such as mud and sand fields...". Irregular echinoids which burrow will be preserved if they are not displaced following post mortem burial, but surface-dwelling regular echinoids after death are immediately exposed to scavengers, currents or wave action. Irregular echinoids living partly or wholly within the sediment, also extract food material from it. Because their guts are filled with sediment, on death the extra weight in the test helps prevent it from being worked to the surface and subsequent disintegration by scavengers or current activity (Kier 1977:171).

A very rapid influx of sediment may cause the death of an echinoid, whether regular or irregular. As a consequence of burial, the whole test complete with radioles, pedicellariae, apical disc and lantern may be preserved (see Lewis & Ensom 1982). Under a constant rate of sedimentation, burrowing echinoids can maintain their optimum depth within the sediment, but if the rate is increased, the echinoids may be unable to cope and may perish. Schäfer (1972:102) reported that the Recent burrowing spatangoid *Echinocardium* would be unable to dig its way out of "...an additional 30 cms of fine sand." He also recorded (p.104) that the regular echinoid *Psammechinus miliaris* was capable of coping with a sediment cover of between 5-20 cms thick by using its tube feet and radioles to turn itself on one side to burrow to the surface. If the covering is less than 5 cms, it does not turn on one side to reach the surface, but anything more than 30 cms of sediment will probably kill the animal. Schäfer pointed out that in areas of sudden rapid sedimentation, the rate of erosion is likely to be just as rapid and abrupt so that any echinoid so buried will later be eroded out and destroyed.

Burial Diagenesis.

The burrowing echinoids - *Schizaster, Eupatagus*, and *Spatangus* have a much better fossil record from the Barton Beds than do the regular echinoids. The more complete fragments of regular tests are of those whose stereom structure allows a more robust interlocking between individual plates, e.g. *Ambipleurus*?, a temnopleuroid with a peg and socket type of interlock (see Smith 1984:text fig. 2.5d). On the other hand, those with weak or non-existent interlocking mechanisms are represented by radioles or isolated plates only, e.g. cidarids and *Porosoma*. The presence of pyrite may also contribute to the destruction of the test - for example, specimens of *Echinopedina paucituberculata* from bed J are very poorly preserved because of depyritization. The specimens of *Eupatagus* from bed

F are less well preserved than those from beds A2 and A3. Those from bed F are frequently encrusted with small crystals of gypsum, which also pentrate parts of the test and cause it to crack and break up. Details of the test have to be revealed by careful removal of the gypsum crystals. The specimens from beds A2 and A3 are relatively well preserved but require careful removal of the matrix to reveal details of the test. *S. (H.) branderianus*, the most commonly found echinoid from the Barton Beds, is preserved either:

      i)   As internal casts from which the test has been lost;

or ii)   With the whole test preserved.

When preserved as internal casts, the shape of the test, the position of the peristome, periproct, ambulacral pores, genital pores, and plate sutures can be seen, but as no part of the actual test is preserved, the specimens are of no use except for measuring them and for recording their presence. On the other hand, specimens which have all or parts of the test preserved, if carefully prepared can reveal very fine detail (see Lewis 1986).

Specimens of *S.(P.) grandituberculatus* from bed A3 are frequently very well preserved. They are sometimes covered with small sand grains which have become embedded in the test and which are difficult to remove, but often the tests are clean and reveal excellent surface detail. Numerous fragments of test of this species have been found in sandy shell-drifts within bed A3, together with whole tests. A specimen of *E. (E.) excentricus*, - BMNH 49820 - recorded by Gregory simply as coming from the "Barton Beds" is similarly preserved and so most probably came from a shelly drift in bed A3. The surface detail is mostly lacking on this specimen, but remarkably, the periproctal and peristomial plates are preserved *in situ*. Its radioles were presumably lost quickly, but the test was buried before the membranes disintegrated.

The colour of the echinoids varies according to the bed in which they were preserved. Regular echinoids are generally pale cream or pale grey, rather like the molluscan fauna of the same beds, the important exceptions being the specimens of *Echinopedina* from bed J which are very dark in colour, and with much pyrite present obscuring detail. Some of the irregular echinoids are also pale in colour - specimens of *Schizaster* and *Eupatagus (E.) excentricus* are usually cream to reddish-cream in colour. Specimens of *E.(E.) hastingiae* from bed F are usually darker, either cream or brownish cream. Those same species from beds A2 and A3 are dark grey. Most specimens of *Schizaster* from bed A2 are dark grey, frequently with tiny crystals of pyrite developed which destroy the fine detail of the test.

The species of echinoids found in the Barton Beds have been preserved in many different ways:-

      "*Cidaris*" *websteriana*' (indet. cidarid) - radioles.

      Porosoma? sp. - radioles, fragments of test, including interambulacral plates and portions of ambulacra.

      Echinopedina paucituberculata - heavily pyritized tests, internal casts and fragments of test.

      Coelopleurus sp. - fragments of test, including interambulacral plates and portions of ambulacra, plus an incomplete, damaged test.

      Ambipleurus? quaylei - broken but almost complete tests, plus fragments.

      Schizaster (Hypselaster) branderianus - internal casts, external moulds, almost complete tests - some with radioles.

      Eupatagus (Eupatagus) hastingiae - almost complete tests, some with radioles, some tests with overgrowths of gypsum crystals.

      E. (E.) excentricus - a single worn test, but complete with peristomial and periproctal plates.

      Spatangus (Phymapatagus) grandituberculatus - well preserved tests, some with embedded sand grains.

METHODS.

Collecting.

Methods of collecting the various faunas from the Barton Beds vary according to which group of animals the collector requires. Commonly, larger specimens are extracted with trowel or knife blade, and put in a bag along with any other specimens. A second method is to take bulk samples of clay or shell-drifts and to sieve them, either in the sea nearby, or in the laboratory. The first method can be used for most groups of fossils which are large enough and robust enough to survive being stored alongside others. The second method may be used if the fossils are robust enough to survive the sieving, or if fragmentary remains are acceptable. Bulk sampling is, of course, a much more random method of collecting, and fossils of a particular group being sought may not be found, even when detailed and thorough sampling is carried out. It yields echinoids usually as a by-product of processing for other faunas, and mostly only fragments of tests and radioles are recovered, whereas close examination of the clay can provide more complete specimens, although collecting individuals in this way can be very time consuming. The horizon at which the fossils were found, using either method for collecting, ought always to be recorded.

Preparation.

A suitable method for the removal of fragile tests from clay was described by Lewis (1986) and involved the use of a transfer method. Alternatively, a mounted needle and very careful preparation can be applied successfully to more robust specimens, especially those which have not broken into several parts. Also, crystals of gypsum can be removed in this way from the tests of *Eupatagus* from bed F.

All specimens, however thay are prepared, may benefit from the application of a hardening plastic, so long as it is not applied too thickly. The exact dilution is variable and is applied on a trial-and-error basis, and depends on an individual specimen. A starting dilution of plastic to hardener may be 1:10, with greater quantities of either being added as required. If the plastic is applied too thickly it can obscure details.

During examination under a microscope, (and also during photography) the details of the test can be enhanced by the application of ammonium chloride sublimate (see Dean & Nuttall, 1960). Lighting is adjusted as required to cast shadows for contrast, or to remove them, as necessary. If a plastic hardener has been applied too thickly, the detail will be obscured when ammonium chloride is used. The one exception to thick application of plastic is to a specimen which has a very irregular, pyritized test, where details are lost when viewed normally under a microscope. A thick layer of plastic removes the masking effect of the rough surface and allows details of the plate boundaries and ornament to be seen.

TAXONOMIC DESCRIPTIONS.

Key: **GSM** =   Prefix to registration numbers of specimens in the British Geological Survey, Keyworth, Nottinghamshire.

          BMNH =   British Museum (Natural History), London.

             E =   prefix to the registration numbers of specimens of fossil echinoderms in the Department of Palaeontology, BM(NH). Older collections do not have the `E' prefix.

The classification follows that of the `Treatise' (Moore 1966) and Jensen (1981). Specific comparisons refer only taxa of closest similarity. Synonymies are selective rather than exhaustive and include references which add descriptive data or taxonomic emendation.

Class   Echinoidea Leske 1778.
Order   Cidaroida Claus 1880.

Cidaridae indet.

(Pl.1, figs. 1,2.)

1852 *Cidaris Websteriana* Forbes : 22, pl.3, fig.4

Type material of *C. websteriana*: lectotype, selected herein - GSM 11821 (the figured syntype of Forbes, pl.3, fig. 4), the horizon is not known but other specimens have been recorded from beds A3-H; paralectotypes - GSM 11822-4.

Other material: 49812; E 1093; E 12261; E 17716; E 41456-69; E 76525 (from bed H); E 76529; E 76771 (bed G); E 76772 (bed H); E 79065; E 79719; E 79782.

Description

This `species' is known from slightly worn primary radioles only. In specimens E 41456-69, the radioles range in size from about 10mm to at least 24mm long. The shaft is straight, slender, slightly inflated in the middle or just proximal to the middle, has a circular cross-section and tapers to a point (e.g. E 17716). The thick, sharply defined cortex layer is a characteristic of cidaroids. In cross section the thickness of each layer in a specimen from a group numbered E 79719 is: medulla - 0.16mm; radiating layer - 0.8mm; cortex - between 0.096mm (valley between spinules) and 0.1mm (thickness of spinules). The ratio of the thickness of each layer is 1:5:1. The proximal end of the radiole has a neck with fine longitudinal striations which are also present over a thin collar (e.g. E 41456-69). The base has a smooth rim and the acetabulum is perforated, more noticeable in some specimens than in others. The shaft has ornament which consists of about 20 rows of fairly coarse, globular, elongate, or tear-drop shaped spinules (e.g. 49812), each one joined along its longitudinal axis to its neighbour by a narrow, raised portion and formed from the cortex layer. The rows of spinules have a certain amount of axial twist and occasionally bifurcate. Some radioles with fine striations between the rows of spinules are much smaller in diameter (e.g. E 41456-69).

All the specimens preserved are primary radioles. Smaller specimens may either be from smaller tests, or from those parts of larger tests which bear smaller radioles.

Discussion

Although a number of these radioles have now been found in the Barton Beds, no associated plates of the test have been recorded and their generic and specific affinities remain unknown. The cidaroid type of internal structure and the coarse ornament of globular or tear-drop shaped spinules formed from the thick cortex layer, suggests that the radioles belong with the cidarids. The preservation of most specimens indicates that they may have been transported, possibly far from their origins, or that they were not buried immediately after death.

Subclass   Euechinoidea Bronn 1860.
Superorder   Pedinacea Jensen 1981.
Order   Pedinoida Mortensen 1939.
Family   Pedinidae Pomel 1883.
Genus   Echinopedina Cotteau 1866.

Echinopedina paucituberculata sp. nov.

(Text-figs. 2a-b, 3; Pl.1, figs. 3-7.)
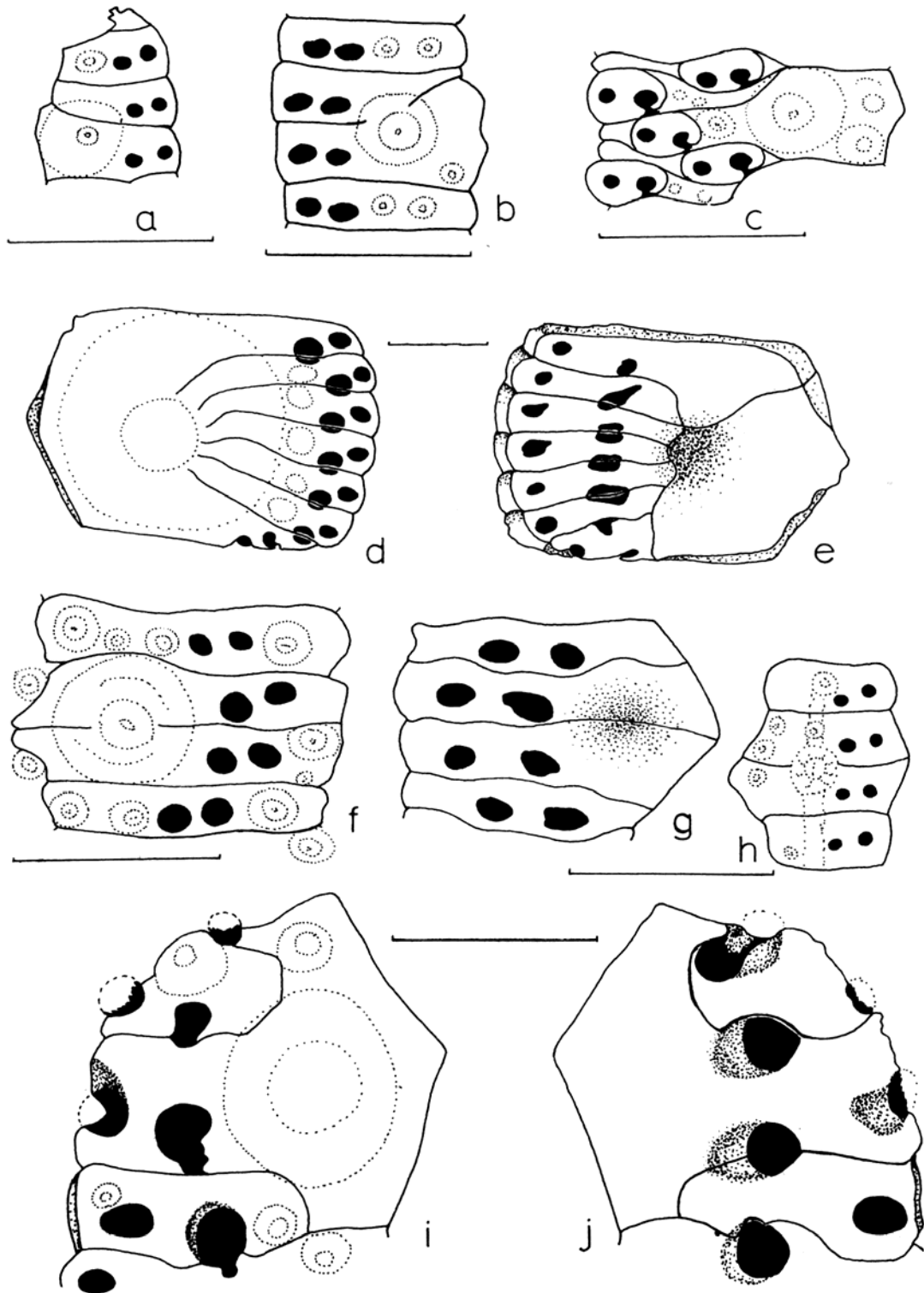
Text-fig. 2. Camera-lucida drawings of plate compounding of: (a) *Echinopedina paucituberculata* sp. nov. E 76425, plates near the apical disc; (b) E 76581, the holotype, plates at the ambitus. (c) *Leiopedina edwardsi* (Forbes), GSM 54920, the lectotype; plates at the ambitus. (d) *Porosoma* sp. E 76920, anterior surface of an ambulacral plate; (e) the inner surface. (f) *Ambipleurus quaylei* sp. nov. E 76923, outer surface of an ambulacral plate; (g) inner surface; (h) E 76822a, the holotype, ambulacral plates at the ambitus. (i) *Coelopleurus* sp. E 76520, outer surface of an ambulacral plate; (j) inner surface. Scale bars: 1mm.

1852 *Echinopsis Edwardsi* Forbes : 23 (*pars*).
1856 *Echinopsis Edwardsii* Forbes; Salter : Dec.V, pl.3 p.6 (*pars*).
1856 *Echinopsis Edwardsii* Forbes; Woodward in Salter : Dec.V, pl.3 p.6 (*pars*).
1856 *Echinopsis Edwardsi* Forbes; Desor : 100 (*pars*).
1866 *Echinopedina edwardsi* Forbes; Cotteau : 262 (*pars*).
1889 *Echinopedina edwardsi* Forbes; Duncan : 83 (*pars*).
1891 *Echinopedina edwardsi* Forbes; Gregory : 19 (*pars*)

Material: Holotype - E 76581; paratypes - E 76425; E 76573-80; E 79701; E 79821 (all from bed J).

Derivation of name: paucituberculata = having few tubercles; a reference to the relatively small number and size of the primary tubercles present on the test.

Preservation: All specimens except for E 76425 are heavily pyritized and much of the detail of the test is lost. Some specimens are internal casts.

Diagnosis: An echinopedinid with 9-15 ambulacral and 8-10 interambulacral primary tubercles, small and regularly spaced; about seven secondary tubercles forming contiguous, incomplete scrobicular circles around interambulacral primary tubercles.
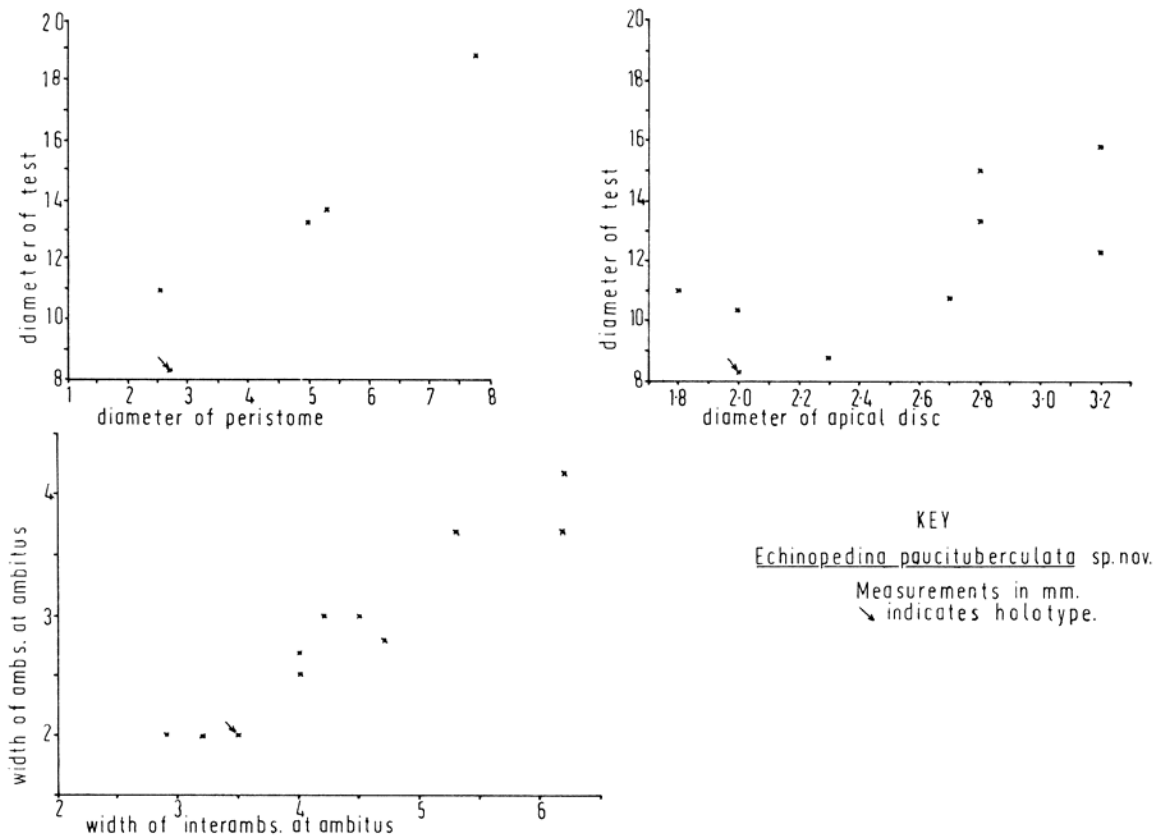
Text-fig. 3. Scatter diagrams of measurements taken from specimens of *Echinopedina paucituberculata* sp.nov.

Description

Shape: Sub-spherical, rounded adorally, slightly conical adapically; diameter from 8mm to 16mm, height from 5.5mm to 10mm. (Text-fig.3.)

Apical system (Pl.1, fig.6): This is small, dicyclic, but probably with ocular plates I and V insert and has five approximately pentagonal genital plates. The madreporic genital plate 2 is more prominent than the others. The ocular plates are not always preserved or visible. The periproct appears to be slightly elongated, but this may be a preservational artifact caused by crushing; the apical disc is best seen in E 79701 (the anterior half) and E 76577 (the posterior half).

Ambulacra (Text-figs. 2a,b, Pl.1 figs. 3,7): These are fairly wide at the ambitus, being half, or a little over half the width of the interambulacra. Each ambulacrum broadens gradually from the apical disc to the ambitus and adorally narrows only slightly towards the peristome. On the oral surface the ambulacra are about the same width as the interambulacra (e.g. E 76574, E 76578).

The plating shows diadematoid compounding (e.g. E 76581, E 79701). There are three components to each ambulacral plate; the two adapical plates bear a perforate, non-crenulate primary tubercle, the adapical-most component plate may barely reach the perradius, or may be a demi-plate (e.g. E79701). The pore-pairs are circular, similar, are horizontal and are arranged in very shallow inverse arcs of three, forming a single column in each half of an ambulacrum. The diameter of each primary tubercle is about a third of the height of the compound plate and is situated in the centre of the two adoral component plates and close to the perradial margins of the pore-pairs. The tubercle has a shallow basal terrace, low convex boss and a hemispherical, perforate mamelon on a narrow platform. Two small tubercles are present in the centre of the adapical component plate. Several small, widely spaced secondary tubercles form an incomplete scrobicular circle which is open on the adoral margin of the plate. The primary tubercles form two straight columns on each ambulacrum, with between 9-15 tubercles per ambulacral column, depending on the size of the test.

Interambulacra: Individual plates are about twice the size of adjacent ambulacral plates and the length is 80% greater than the height at the ambitus. Each primary tubercle is small and occupies a position just adoral to the centre of the plate. The diameter of the boss is about half the height of the plate. Each tubercle has a low, convex boss which rises gently from the basal terrace to a narrow platform. The mamelon is small, hemispherical and perforate. Surrounding the boss there are at least seven small, widely spaced secondary tubercles forming an incomplete, contiguous scrobicular circle. There are also three secondary tubercles on the adradial side of the plate and one on the adapical interradial part of the plate. Each interambulacral plate has several facets along its adradial margin for the adjacent ambulacral component plates. There are between eight and ten tubercles per column. They taper sharply towards the apical disc and more gently towards the peristome.

Peristome (Pl.1, fig.5): The peristome is half the diameter of the test and is circular. The margin has shallow buccal notches (e.g. E 76574). A latex rubber mould of the peristome of E 76578 shows some of the inner structure of the peristome. There are incomplete remains of five auricles, which are small peg-like protuberances about 2mm long. They have grooves along their adapical or inner surfaces, marking the attachment points of the radial compass muscles and the retractor muscles. The arch is not replicated in the mould, but it may remain within the matrix in the specimen.

Lantern: Within the cast of the test of E 76578 there is preserved a single demipyramid. This is reserved without its epiphysis and is 2.25mm high and 1mm wide at the lowest part of a narrow, shallow foramen magnum. The retractor muscle scar on the demipyramid is long, narrow and shallow and has a thin rim towards the interpyramidal edge and a thicker rim towards the pyramidal suture.

Radioles (Pl.1, fig.5): Several radioles are present in and around the peristome of E 76578. The length of the remaining portion of the longest is 4mm. Each radiole tapers to a distal point. The base tapers gently and is rounded and smooth at the proximal end. The shaft has ornament consisting of longitudinal striae which are continuous with milling on the collar. The radioles are hollow in cross-section with large calcite wedges around a central lumen which tapers from the base to the tip.

Comparisons

Echinopedina paucituberculata differs from the type species *Echinopedina gacheti* (Desmoulins 1837) (Middle Eocene of Blaye, Gironde, France), by having fewer primary ambulacral and interambulacral tubercles - *E. paucituberculata* has 9-15 ambulacral and 8-10 interambulacral tubercles, whereas *E. gacheti* has 29-30 ambulacral and 24-25 interambulacral tubercles and is much larger. The interambulacral plates of the Barton species are much smaller than those of the type species, with a length to height ratio of about 1.5:1. The length to height ratio of those of the type species is about 3:1. The length to height ratio of the interambulacral plates of *E. biarritzensis* Cotteau 1893, (Upper

Eocene, La Gourèpe, near Biarritz, France) is about 3:1 and it has more interambulacral plates than the Barton species. *E. granulosa* Lambert 1902, (Eocene, Vilelista, near Barcelona, Spain) has interambulacral plates with a length to height ratio of 4:1 and many more primary tubercles. *E. edwardsi* (Forbes 1852:23) (Eocene, Bracklesham Beds, Bracklesham, Sussex) differs from *E. paucituberculata* by its very oblique plate compounding and is assigned to *Leiopedina* (Lewis 1989).

Until proper populations are available to determine ranges of variation in ontogeny, distinguishing between species must remain uncertain.

Discussion

This species has previously been included in *E. edwardsi* Forbes. *Echinopsis edwardsi* Forbes, 1852:23 (Pl.1, figs. 8a, b herein) was based on two specimens - one was a poorly preserved specimen from "...the uppermost marine beds at Barton...", (probably bed J of Burton 1929); the other specimen was a much better preserved individual from "Brackelsham". Both specimens were deposited in the Museum of Practical Geology, where in the late 1930's the specimen from Barton was destroyed by pyrite decomposition. The specimen from Bracklesham was the one used by Forbes for his description of the species. It is highly likely that the decomposed specimen from Barton was the same species as the one decribed herein - its locality was recorded on its label as "Hordwell" (= Hordle) which is approximately where bed J outcrops at beach level. If this was so then was based on two different species.

The taxonomic position of *Echinopsis edwardsi* has been discussed by many authors, but notably by Forbes (1852:23), Woodward (*in* Salter 1856:6, pl.3), Desor (1856:100), who referred it to *Echinopsis* and by Cotteau (1866:262), Duncan (1889:83), Gregory (1891:19), Mortensen (1940:119), who referred it to *Echinopedina*, but all of them were referring to the Bracklesham specimen. Burton (1933:152) listed the species as *Echinopedina*.

Mortensen (1940, 1943) gave detailed generic descriptions of *Echinopsis* and *Echinopedina*. In his discussion of *Echinopsis* (1943:36), he included the following characters: "...trigeminate compound plates of the echinoid type; the pores arranged in a straight line even at the peristome...", tubercles "...perforate and finely crenulate...". The characters of *Echinopedina* (Mortensen 1940:118-121) included: trigeminate ambulacral plates with pores arranged in arcs, perforate, non-crenulate tubercles. By grinding down the surface of the test of a specimen of *Echinopedina gacheti* he was able to reveal that the compound plate included a demiplate (Mortensen 1940:65, text fig.30c). Mortensen also examined - GSM 54920 - *Echinopsis edwardsi* (from Bracklesham, the specimen figured and described by Forbes 1852) and concluded that the arrangement of the pore-pairs was that of *Echinopedina*. Further examination of the surviving type specimen of *E. edwardsi* (Text-fig.2c, Pl.1, figs.8a,b), shows that the compounding does not resemble that of *Echinopedina gacheti*, but does resemble closely that of *Leiopedina tallavignesi* Cotteau 1856b (*in* Leymerie & Cotteau), as illustrated by Mortensen (1940:125, text figs.71a,b), having compound plates consisting of one large central component plate and two demiplates. Therefore, the syntype of *Echinopsis edwardsi* from Bracklesham and in the collections of the British Geological Survey, number GSM 54920 and figured by Forbes (1852:pl.3, figs.2a-d) becomes *Leiopedina* edwardsi (Forbes).

The plate compounding of *Echinopedina paucituberculata* is similar to that of *Echinopedina gacheti* as illustrated by Mortensen (1940:65, text. fig.30c) and by Cotteau (1866:264, pl.14, fig.6), but not to that of *Leiopedina* edwardsi as illustrated by Forbes (1852:pl.3, fig.2c). The presence of hollow primary interambulacral radioles (seen in specimen E76578) with a structure typical of some of the diadematoids suggests that the species does not belong with the pedinids, but the primary tubercles have pedinid structure, i.e. they are perforate and non-crenulate. Mortensen (1940:118) said that the radioles of *Echinopedina* were unknown.

Further research needs to be carried out on the Pedinidae to establish the true nature of the fossil forms. It is quite likely that some genera will have to be removed from this family because they possess some of the characters of both the Pedinidae and the diadematoids.

Superorder   **Echinacea Claus 1876.**
Order   **Phymosomatoida Mortensen 1904.**
Family   **Phymosomatidae Pomel 1883.**
Genus   *Porosoma* **Cotteau 1856a.**

Porosoma? sp.

(Text-figs. 2d,e, Pl.2, figs. 1-5.)

1852 *Echinus Dixonianus* Forbes: 22, pl.3, fig.3.

1891 "*Echinus*"(!) *dixoni* Forbes; Gregory: 28.

Material: Holotype of *E. dixonianus* - GSM 118225, no horizon known; other material - 49826, E 41518-21, E 76767a-d, E 76924, E 79781, all radioles; isolated ambulacral plates: E 76920 (bed A3), E 41522, E 76922, (Middle Barton Beds); isolated interambulacral plates: E 76766 (bed A3), E 41505 (bed E), E 41523-5 (Middle Barton Beds). All the plates are worn, some are broken.

Description

Isolated ambulacral plates (Text-figs. 2d, e; Pl.2 figs. 3a, b, 4): these show phymosomatoid compounding. E 41522 comes from the adapical part of the test, close to the apical disc and is taller than long. The primary tubercle is small - the diameter is less than half of the length of the plate - and has a convex boss which rises abruptly from the surface of the plate. The mamelon is hemispherical, imperforate and has an undercut neck. The narrow platform has a crenulated parapet with seven crenulations preserved; other crenulations have been broken off. There are very worn remains of about six secondary tubercles along the adradial side of the plate, perradial to the pore-pairs. There are five complete pore-pairs and one incomplete pair at the adoral side of the plate. The pores are similar, very slightly elongated and arranged in an adradially convex arc. They are each surrounded by a low wall which is open at the adoral margin of the perradial pore. A groove extends from the perradial pore adradially, passing between adjacent adradial pores. The sutures between the component plates can only be seen alongside the pores.

The isolated ambulacral plate E 76922 is longer than tall and has a large tubercle covering most of the plate. The boss rises steeply from a shallow sloping basal terrace and has straight sides. The terrace has 12 strong crenulations. The mamelon is hemispherical, imperforate and has a thick,undercut neck. There are ten secondary tubercles, each with a large hemispherical mamelon with an undercut neck. One of the secondary tubercles has a boss whose diameter is three-quarters that of the primary mamelon and is situated on the adapical perradial corner of the plate. There are six pore-pairs, with a seventh adoral pair divided horizontally along the adoral plate-margin. The two most adapical pore-pairs are incomplete, the adradial pores having been lost.

Isolated interambulacral plates (Pl.2, fig.5): The plates are longer than they are tall and each has a large, oval primary tubercle covering most of the plate. The sides of the boss are straight and rise steeply from a narrow, shallow sloping scrobicule to a crenulate platform with 12 crenulations. The mamelon is imperforate, hemispherical and has a thick, undercut neck. There are at least nine secondary tubercles on the largest plate and were probably more, but the plate is incomplete. The largest secondary tubercle is situated on the interradial adapical edge of the plate and has a tubercle whose diameter is slightly greater than that of the mamelon of the primary tubercle. The mamelon of the secondary tubercle is large and hemispherical; the boss is low, steep sided and has a broad platform.

Radioles (Pl.2, figs.1,2): The largest radiole, specimen E 79781 (Pl.2 fig.1), is 27.5mm long and is straight and tapers gradually from the collar to the pointed distal end. The shaft is 25mm long and 2.5mm thick near the collar, the cross-section from the collar to about halfway along the shaft is oval. From here to the tip of the radiole the cross-section is circular. Some other examples have a circular cross-section along the whole length. The ornament of the radioles consists of up to 24 fine, straight,

longitudinal striae. These continue over the prominent collar, which is steep sided on the distal edge and shallow on the proximal edge. The base is nearly smooth and the acetabulum has 12-15 crenulations. There is a thin cortex preserved on the shafts of some of the specimens.Most of the radioles, including the holotype of *Echinus dixonianus* have a perforation in the centre of the acetabulum. The perforation varies greatly in size and outline. A few radioles (e.g. E 76767c) have no perforation but resemble the perforated ones in other respects.

Discussion

The species *Echinus dixonianus* was described by Forbes from a single radiole (Forbes 1852:22). At the time of his writing there was "...no body, or even plate of any true *Echinus*..." found in the British Eocene. The number of crenulations and the size of a primary tubercle on a plate matches the number of crenulations and size of the acetabulum of a radiole. Therefore it is extremely likely that radioles and plates described herein belong to the same species. The structure of the ambulacral plates is characteristic of the phymosomatids, i.e. the compounding and the crenulate tubercles. Most genera of the phymosomatids can be rejected for various reasons.

The plate compounding of *Porosoma*? sp. as described herein closely resembles that of the *Porosoma* species illustrated by Mortensen (1935:473, text fig. 274), but without further evidence, such as the apical disc, it is not possible to be more definite in assigning the Barton species to this genus. Furthermore, without better and more complete material, a specific determination cannot be made and so the species is best left in open classification.

The presence of a perforate acetabulum in many of the radioles is at first puzzling. However, examination of the tubercles and radioles of the Cretaceous species *Phymosoma koenigi* (Mantell 1822) shows that this echinoid also had imperforate tubercles and perforated radioles. In both *Porosoma*? sp. and *Phymosoma koenigi* the perforation is simply a hole in the acetabulum, with no attachment surface for a ligament. The hole therefore is an extension of the canal in the core of the radiole. The perforations in the radioles of *Porosoma*? sp. vary considerably in size and shape, with some radioles (e.g. E 79781) having very small perforations and others (e.g. E 76924a) much larger ones. The irregular, rough outline of some perforations (e.g. E 41518) suggests that the enlargement was caused by erosion at this thin part of the acetabulum.

Order   **Arbacioida Gregory, 1900.**
Family   **Arbaciidae Gray, 1855.**
Genus   *Coelopleurus* **Agassiz, 1840.**

Coelopleurus sp.
(Text-figs. 2i, j; Pl.2, fig. 8; Pl.3, figs.1a, b, 2)

Material: E 76768, a poorly preserved but fairly complete specimen from bed E; E 76520, E 76522, fragments of ambulacra and interambulacra from bed E; E 76921, labelled as coming from the Middle Barton Beds.

Preservation: Although the test of E 76768 is almost complete, it is badly weathered and has been damaged by pyrite decomposition which has cracked the test. It has also been crushed slightly so that some plates are displaced. Mineral impregnation has coloured the specimen a reddish brown and the fine detail is no longer present. The other specimens are fragments of test: E 76520 and E 76921 are ambulacral plates and E 76522 is a fragment of an interambulacrum. These fragments have well preserved details.

Diagnosis: A trigeminate *Coelopleurus* with large, circular primary ambulacral and interambulacral tubercles, which are similar in size from the peristome to just above the ambitus; all interambulacral tubercles in this region very similar in size; very few small secondary tubercles on ambulacral plates.

Description

Shape: The test is low and has the outline of a rounded pentagon. It is flattened on the oral surface, with the rim of the periproct raised very slightly. The diameter of the test of the holotype is 6.3mm, the maximum height is about 3.3mm and the diameter of the peristome is 3.8mm.

Apical system: This is probably dicyclic, but it is incomplete in E 76768. There are three ocular plates and three genital plates preserved. (i) Ocular plates. The best preserved has a rounded diamond-shaped outline, but has no pore. Ornament consists of a few small, rounded granules. (ii) Genital plates. These make up the raised rounded rim of the periproct. There is a large, rounded granule present near the periproctal rim and several much smaller granules over the rest of the plate.

Ambulacra (Text-figs.2i, j; Pl.2,fig.8): These are raised slightly above the level of the interambulacra. E 76768, probably a juvenile specimen, has about five large primary tubercles per ambulacral column. Each column widens rapidly from the apical disc to the ambitus where it is 80% of the width of an adjacent interambulacral column. On the oral surface the ambulacra taper gently towards the peristome. Each primary tubercle (e.g. E 76520-1) is imperforate, non-crenulate, circular in outline and covers most of the plate. A tubercle consists of a large and prominent steep-sided boss, with a flat, well defined narrow platform. The mamelon is a little less than a hemisphere and has a thick, very slightly undercut neck. The basal terrace is raised above the level of the plate in all but the most adapical plates and is approximately circular. Next to the pore-pairs the terrace is a little lower than the general level of the plate. The basal terrace of adjacent ambulacral plates almost touch at the perradial suture. There are usually one or two secondary tubercles per plate, situated at the adapical perradial edge of the plate. Each has a low, convex boss and a tiny mamelon. They are about seven times smaller than the primary tubercles.

The plates of E 76768 have arbacioid compounding, with three slightly oblique pairs of pore-pairs in an adradially convex arc. The adradial pore of a pair is almost circular and the perradial pore is very slightly elongated at its adoral perradial margin, forming a tear-drop shaped outline. Between each component plate there is a shallow depression which extends from the adoral adradial edge of the perradial pore to the adradial suture. The adapical margin of each component plate is raised to form a low wall around the pore-pairs adapically and extends between the pores, with a slight dip in the middle. The adoral edge of each pair has no wall. Two spike-shaped granules are present on the adapical wall. The finer details are well preserved in E 76520 and E 76921.

Interambulacra (Pl.3, fig.2): Each interambulacrum of E 76768 widens rapidly from the apical disc to the ambitus and adorally tapers gently to the peristome. From the ambitus adapically, there is a broad naked zone with no tuberculation. On each plate from the apical disc to the ambitus there is one small primary tubercle situated close to the adradial margin of the plate. The tubercles are joined to each other down a column by a low rib from the apical disc to the ambitus, but on the oral surface the rib is not present. From the ambitus to the peristome there are two primary tubercles, (seen on individual plates from larger individuals). The interradial tubercle at the ambitus is about 3.5 times the size of an adradial tubercle next to the naked zone, but nearer the peristome the adradial tubercle is only a little smaller than the interradial one (e.g. E 76522).

E 76768 has about three large primary tubercles per interambulacral column, from the ambitus to the oral surface and about four small primary tubercles adapical to the ambitus. The structure of the primary tubercles at the ambitus and adorally is similar to that of the ambulacral tubercles (e.g. E 76522). Secondary tubercles have small bosses and tiny mamelons and are situated along the adapical margins of the interambulacra, up to five per plate, each one joined to its neighbour by a rounded ridge to form a horizontal rib-like structure.

E 76522 (Pl.3 fig.2) is a single plate 4mm. long, 2.5mm high and is from a specimen larger than E 76768. It has two large primary tubercles. The interradial margin is incomplete. The tubercles are imperforate, non-crenulate and 1.5mm and 2.0mm in diameter. Each has a circular basal terrace which is not flat but has a slight twist in its horizontal axis, so that the interradial adapical corner of the plate and the adoral corner of the plate are lower than the opposing corners. The basal terrace is slightly undercut and flared in the adoral adradial position. The remainder of the basal terrace is raised slightly above the level of the plate, except at the adoral interradial corner of the larger tubercle, which is flush with the plate. The boss is slightly concave, rising gently at first, then becomes vertical below a narrow platform. The mamelon is small, hemispherical and has a straight neck. The adapical edge of the plate has a facet along part of its length which is angled to the outside of the

plate. The adradial suture has four arcuate facets for the primary and demiplate components of the adjacent ambulacral plates. Along the adradial margin of the plate there are eight granules, two by each facet. Outside the basal terraces of the two primary tubercles, near their adapical rims, there are four small secondary tubercles, two per primary tubercle. There are two secondary tubercles present near the adoral margin of the interradial edge of the plate, one between the primary tubercles and one in the interradial corner. There are also the remains of other secondary tubercles present on other parts of the plate.

Peristome: This is circular and has shallow buccal notches. The diameter of the peristome of E 76768 is 3.8mm.

Comparisons

The Barton *Coelopleurus* sp. has circular tubercles whereas *C. delbosi* Desor 1857,(Middle Eocene, France), has primary interambulacral interradial tubercles whose basal terraces extend to the horizontal margins of their plates, so that the outline of the tubercles is oval. *C. agassizi* d'Archiac, 1846, *C. coronalis* (Leske, 1778), *C. munieri* Cotteau 1892 (all from the Upper Eocene of the Pyrenees) and *C. tounoueri* Cotteau, 1869 (Middle Eocene, France), have a greater number of secondary interambulacral tubercles and *C. agassizi* has much smaller adradial primary tubercles than does the Barton species.

The Barton *Coelopleurus* sp. is too poorly preserved and incompletely known for a specific determination to be made.

Order   **Temnopleuroida Mortensen 1942.**
Family   **Glyphocyphidae Duncan 1889.**
Genus   **Ambipleurus Lambert 1932.**

Ambipleurus? quaylei **sp. nov.**

(Text-figs. 2f-h, Pl.2, figs. 6a,b, 7.)

Type material: holotype - E 76822; paratypes - E 76823-4, E 76923. All specimens from a shell drift in bed A3.

Preservation: E 76822 and E 76823 are two fairly well preserved but incomplete tests. There are also two fragments: E 76824, comprising part of an ambulacrum and interambulacrum; and E 76923, a fragment from the oral surface, showing part of an ambulacrum, interambulacrum and buccal notches. The two tests do not have their apical discs preserved complete. E 76822 consists of about half of an uncrushed test without the apical disc and the flattened remains of the other half with a single ocular plate attached. E 76823 retains the shape of the test as an internal cast in clay with some of the test attached to the clay. All the specimens are from a shell drift in bed A3.

Derivation of name: the species is named after John Quayle, amateur collector from Southampton, for his generosity in donating so many specimens of echinoids and other fossils to the BMNH, including E 76822 and E 76823.

Diagnosis: a glyphocyphid with small, finely sculptured test with elongate excavations along horizontal ambulacral margins and irregular excavations perpendicular to them; interambulacral plates with small pits in surface; margins of plates distinct, including component plates of acrosaleniid compounding in ambulacra.

Description

Shape: Small, hemispherical, with a rounded oral surface and a large peristome. Dimensions of the holotype:- diameter of test: 8.7mm; height of test : 4.0mm at least; diameter of peristome: 4.2mm.

Apical system: One ocular plate is preserved on specimen E 76822. It is a 'U'-shaped plate with a circular ocular pore just to one side of the perradius. Ornament consists of a single tubercle just

adapical to the pore and a few others, randomly placed. There are also a few small pits in the surface. E 76823 has an indistinct internal clay cast of the periproct.

Ambulacra (Text-figs. 2f-h, Pl.2, figs.6b, 7): These are narrow, widest at the ambitus where they are about half the width of the interambulacra. The ambulacral plates have acrosaleniid compounding. One small, perforate, crenulate primary tubercle unites two of the component plates and a single tubercle about a third of the size, is present on the simple plate. Each tubercle is situated just perradial to the centre of the plate and has a small, convex boss, a narrow, finely crenulated parapet, with about 15 crenulations on the larger and about 11 crenulations on the smaller tubercles. The mamelon is hemispherical, perforate, with an undercut neck. The larger ambulacral primary tubercles are about 80% of the size of the adjacent interambulacral primary tubercles.

The pore-pairs are in single straight columns and are large, slightly oblique, and of standard structure. The sutures of the component plates between pore-pairs are fairly deeply excavated except at the tubercle.

There are three or four secondary tubercles arranged in an adapical perradial arc on the diad plates. One of these tubercles is situated near the adapical perradial corner of the diad and is about the same size as the primary tubercle on the simple plate. It is perforate and has about 12 crenulations. The other secondary tubercles of the arc are slightly smaller. Two more secondary tubercles are present at the adoral edge of the simple plate.

Sculpturing consists of many small circular and oval pits or excavations around the secondary tubercles and along the adradial margin of each plate. The holotype - E 76822 - has both kinds of sculpturing and paratype E 76823 has only the small pits. The boss of the primary tubercle is also excavated and undercut around its periphery, which defines its extent very clearly. Close to two adapical secondary tubercles on the diads and the two adoral secondary tubercles of the simple plate, the sculpturing produces an appearance of a thick, low rib which extends down each column of ambulacral plates. The perradial and adradial margins of the plates are excavated fairly deeply, whilst the horizontal margins of the simple plates and those of the component plates of the diads are less deeply excavated. The excavations along the central suture of the diad extend only as far as the primary boss. The outlines of the plates are very distinct because of these excavations.

Interambulacra (Pl.2, fig.6a): At the ambitus these are almost twice as wide as the ambulacra and taper gently adorally and adapically. Each plate is almost twice as wide as it is high and has a small, central, primary tubercle which has a small convex boss with a parapet with about 14 crenulations. The mamelon is hemispherical, perforated and has a short undercut neck. About seven perforate, crenulate secondary tubercles form a contiguous scrobicular semi-circle around the primary boss in the adapical half of the plate. Two more are present near the adapical adradial and adapical interradial edges of the plates and are aligned with the other seven secondary tubercles to form a flattened, rounded, `W'-shape. Tiny granular tubercles are present elsewhere on the surface of the plate.

The other ornament of the plates consists of many small pits and excavations. In the holotype, these are present:- at the interradial edges of the plates where they are elongated, parallel with the sutures; over the surface of the plate where they are sub-circular or elongated and irregular and form a coarse meshwork; along the horizontal margins where excavations form two thin wedge-shapes thickening towards the centre of the margin. These wedges are cut by perpendicular, parallel, elongated excavations which increase in length from the adradial and interradial ends of the margin towards the centre of the margin. At the centre of the margin the plate is not excavated and forms a small ridge, which together with the adjacent elongated excavations gives the appearance of a rib along each column of plates, forming ribs similar to those of the ambulacra. The adradial and interradial margins have shallow excavations along their lengths, to give a well defined outline to each plate.

Peristome (Pl.2, fig.7): This has shallow buccal notches and its diameter is about half that of the test. The holotype has the remains of a single auricle preserved as broken stumps.

Comparisons

Ambipleurus? quaylei differs markedly from all the species assigned by Mortensen (1943:30) to *Ambipleurus*, comprising *A. douvillei* (Lambert 1932) (Eocene, Priabonian, North Africa, Egypt), *A. duncani* (Lambert 1932) (Upper Eocene, India), *A. darchiaci* (Duncan & Sladen, 1882), *A. haimei*

(Duncan & Sladen, 1882), (Eocene, Sind, Pakistan), *A. neuvillei* (Lambert 1912), A. fabrei (Jeannet 1935), A. castexi (Jeannet 1936), A. daguini (Jeannet 1936) (Eocene, Lutetian, France).

A.? quaylei does not have such extensive excavations along the horizontal margins as, for example, do *A. douvillei* (Lambert), *A. duncani* (Lambert), or *A. darchiaci* (Duncan and Sladen). The ornament of the interambulacral plates is very much finer and much more complicated in *A.? quaylei* than in any of the other species.

Discussion

Unfortunately, none of the specimens of *Ambipleurus? quaylei* is complete and no complete apical disc has been preserved, so that no definite generic assignment can be made.

Genera of the Glyphocyphidae whose plate compounding is polyporous can be ignored. *Glyptodiadema* differs in having ambulacral pores in arcs of three near the peristome, unlike *A.? quaylei*, whose pores are in single columns. *Hemidiadema* has primary ambulacral tubercles on alternate plates so that a single series is produced down each ambulacrum. *Progonechinus* has interambulacral plates with up to four large tubercles. *Dictyopleurus* has a complicated network of raised ribs on its plates, similar to that of *Arachniopleurus*. *Echinopsis* has no sculpturing of the plate margins. *Glyphocyphus* (*Glyphocyphus*) and *G.* (*Rhabdopleurus*) both have extensively excavated horizontal plate margins. *Ambipleurus* has well excavated horizontal margins, but these are not as tall as the excavations of the plate margins of *Glyphocyphus*.

The horizontal marginal interambulacral excavations of *A.? quaylei* are thin wedge shapes, with excavations perpendicular to them, not like the horizontal excavations of any other glyphocyphids. The other ornament of the test is also very fine. *A.? quaylei* is tentatively assigned to *Ambipleurus* because it has fairly thin, wedge-shaped horizontal marginal excavations. The generic assignation is uncertain, however, because the horizontal excavations are more strongly developed in all previously known species of *Ambypleurus* and these lack vertical excavations seen in *A.? quaylei*. If these vertical perpendicular excavations of *A.? quaylei* are no more than a specific character, the species is best referred to *Ambipleurus*.

Superorder	**Atelostomata Zittel 1879.**
Order	**Spatangoida Claus 1876.**
Suborder	**Hemiasterina Fischer 1966.**
Family	**Schizasteridae Lambert 1905.**
Genus	***Schizaster* L. Agassiz 1836.**
Subgenus	***Hypselaster* Clark 1917.**

Schizaster (Hypselaster) branderianus (Forbes 1852) Lewis 1986

(Text-figs. 4, 5, 6, Pl.3, figs.3, 4a, b, 5, Pl.4, figs.1a, b, 2-4, Pl.5, fig.1)

1852 *Hemiaster Branderianus* Forbes: 25-26, pl.3, figs.8a-e.
1852 *Schizaster D'Urbani* Forbes: 27, woodcut fig.1 on p.36.
1858 *Brissopsis Branderiana* Forbes; Desor: 381.
1858 *Schizaster D'Urbani* Forbes; Desor: 390.
1862 *Brissopsis Branderiana* Forbes; Dujardin & Hupé: 598.
1862 *Schizaster d'Urbani* Forbes; Dujardin & Hupé:603.
1887 *Schizaster d'Urbani* Forbes; Cotteau:364.
1887 *Trachyaster branderianus* Forbes; Cotteau:406-407.
1887 *Ditremaster branderianus* Forbes; Cotteau:427.
1891 *Hemiaster? branderi* Forbes; Gregory:22.
1891 *Schizaster d'urbani* Forbes; Gregory:24.
1925 *Schizaster (Aplospatangus) Durbani* Forbes; Lambert & Thiéry: 27.

1986 *Schizaster (Hypselaster) branderianus* (Forbes); Lewis: 25-127, pl.1,figs.1-3.

Type material: lectotype, herein selected - GSM 118226 (the figured syntype of Forbes 1852:pl.3, figs.8a-c), horizon unknown, but possibly from bed A3; syntypes of *Schizaster durbani* Forbes - 33395 (two specimens), no horizon known. Paralectotypes are not selected because the unfigured syntypes of Forbes (1852) have not been identified. The other figured syntype (Forbes 1852: pl.3, figs. 8d,e) is a different species.

Other material: 33396, 40373, 49815, 49817-9, 57700, E 1701-2; E 76198, E 76455-8, 76468-71 (from bed A2); E 76517, E81671-6, E 81679-85, E 81716-9 (from bed A3); E 76591-9, E 76600-1, E 76862-5 (from bed A2 or A3).

Preservation: specimens are preserved in three ways: (i) as internal casts in clay, with or without test material attached; (ii) as external moulds in clay, with or without test material attached; (iii) with most or part of the test preserved, but embedded in matrix. Pyrite may also be present on moulds and casts and within the stereom of the calcite. Specimens are almost always crushed and broken to a greater or lesser extent. The lectotype - GSM 118226 - has been flattened and also slightly crushed antero-posteriorly. It is a pyrite-covered internal cast with only a small amount of test remaining.

Diagnosis: A *Hypselaster* with moderately inflated, broad test, about as wide as it is long; anterior unpaired ambulacrum in broad, flat, anteal sulcus which is 47% as wide as long; posterior paired petals about half as long as anterior paired petals; petals more deeply sunken in larger individuals than in smaller; peripetalous fasciole terminates petals; lateral fasciole sometimes present, anal fasciole present; posteriorly eccentric apical disc; periproct high on posterior end of test (Text-fig. 4).

Description

Apical system: This is ethmolytic (e.g. E 76862) and has two large gonopores in plates 1 and 4. The ocular plates have very small perforate tubercles surrounding the pores. Similar tubercles are also distributed irregularly over the other components of the apical system.

The apical system lies slightly posteriorly, about two-thirds of the way along the antero-posterior axis, but is not preserved complete in any specimen except as internal casts or moulds.

Apical surface (Pl.3, figs.3, 4a,b, Pl.4, figs.1a, 2, 4). Ambulacra: these are petaloid, with the anterior paired petals longer and sunk deeper into the test than the posterior paired petals. The posterior pair are almost twice as long as they are wide and are about half as long as the anterior pair. The unpaired ambulacrum is about 30% longer than the anterior paired petals and is also fairly deeply sunken into the test and has an interporiferous zone which is very wide and flat from the apical disc almost to the ambitus, where the two columns of pore-pairs begin to converge.
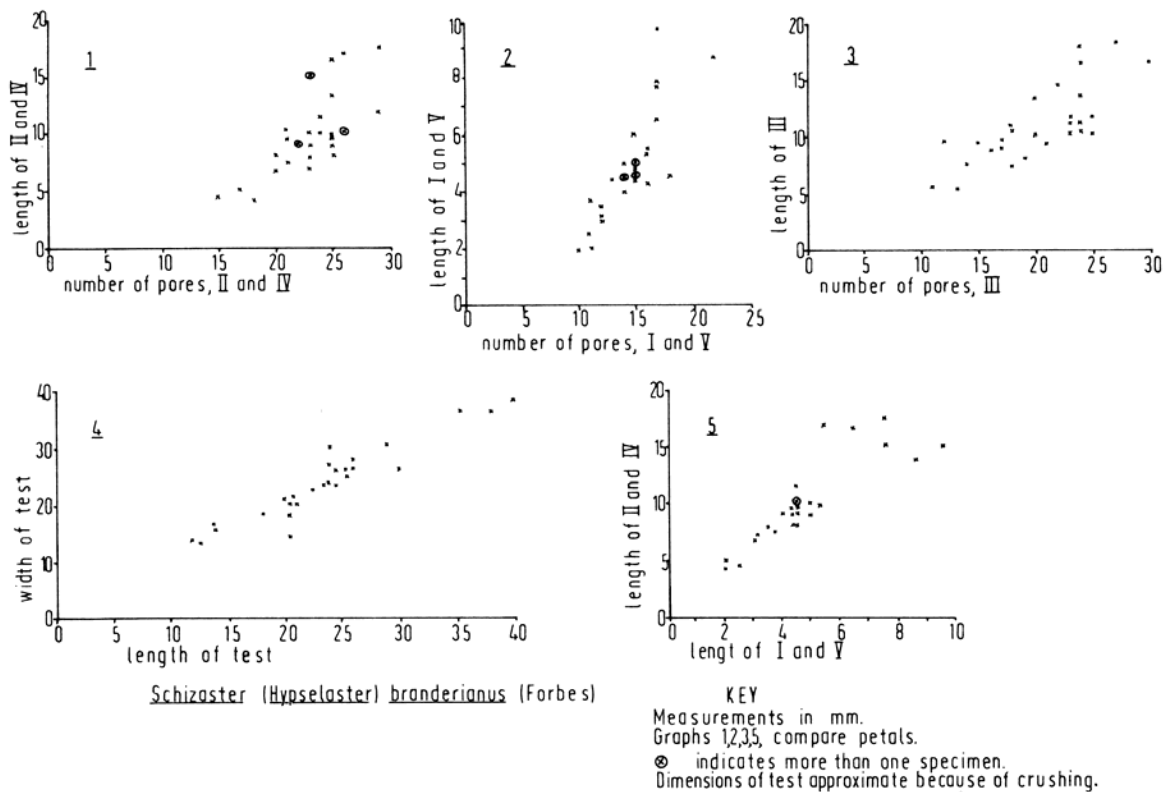
The posterior petals have straight posterior columns of pores and slightly curved anterior columns. The anterior paired petals are flexed, with the portions nearest to the apical disc at right-angles to the antero-posterior axis. They are about three times longer than wide at their widest part. The pores of the paired petals are straight and are situated in long thin plates. Each pore of a pair is an elongated tear-drop shape with the pointed ends directed towards each other and with a raised rim. The adradial pore is slightly longer than the perradial pore and together they occupy about 77% of the length of the plate. The two pores are connected by a short, low ridge, adoral to which is a broad, shallow, triangular depression. Each plate has up to three tubercles adapical to the adradial pore. The adradial sutures are rounded and arc-shaped, whilst the perradial suture of each plate has a hook-shaped outline which interlocks with its opposing neighbour. The interporiferous zone is narrow, about 23% of the width of the petals and about the same width at its widest part as a pore. The ornament consists of tiny tubercles - few at the adapical ends of the petals, slightly more at the adoral ends. The petals are abruptly truncated at the peripetalous fasciole (Pl.3, fig. 4b).

Adoral to the fasciole and as far as the ambitus, all five ambulacra consist of far fewer but much larger irregularly hexagonal plates, ornamented with a few primary and secondary tubercles. Each primary tubercle has a large, elongated scrobicule. The secondary tubercles are much smaller - about the same size as a primary mamelon and have a random distribution over the plate (e.g. E 81671). The pores are single, minute, with a diameter less than a quarter of the length of an adoral pore of the petal and are situated close to the adoral horizontal margins of the plates.

Ambulacrum III is about 20% broader than the paired petals and has a flat interporiferous zone which is about 2.75 times as wide as a pore-pair. The pores are slightly oblique, are much smaller than those of the paired petals, are much less elongate and have a triangular outline. Each perradial pore has a tall rounded rim around its adapical margin, while each adradial pore is situated in a steep-walled shallow pit. Between each pore of a pair there is a tall, flat-sided protuberance, aligned perradial-adapically. In the interpore zone the ornament consists of widely separated secondary tubercles arranged in approximately horizontal rows and large primary tubercles situated close to the adapical side of the perradial pore. Smaller primary tubercles also occur elsewhere on the plate. Close to the fasciole the scrobicule becomes slightly elongated at its perradial adoral side. Also close to the fasciole, the pores are reduced in size to about half that of those elsewhere on the ambulacrum, and the secondary tubercles are more numerous (e.g. E 76601, E 81671, E 81679-80).

Secondary tubercles are also present in horizontal rows between the adradial pore and the adradial suture.

Interambulacra: Adapical to the peripetalous fasciole these form 'spurs' between the inset ambulacral petals. The ornament consists of many primary tubercles which vary in size and fewer, small, secondary tubercles, which are of constant size. Adapical to the fasciole, the largest tubercles are close to the adradius, the smallest at the interradius and close to the fasciole and are half the size of the largest tubercles. Adoral to the fasciole only the smallest tubercles are situated adjacent to it, elsewhere the tubercles are larger and of equal size. The secondary tubercles are much smaller, about the size of a primary mamelon and are also perforate. They are distributed randomly between the primary tubercles.

Schizaster (Hypselaster) branderianus (Forbes)

KEY
Measurements in mm.
Graphs 1,2,3,5, compare petals.
⊗ indicates more than one specimen.
Dimensions of test approximate because of crushing.

Text-fig. 4. Scatter diagrams of measurements taken from specimens of *Schizaster (Hypselaster) branderianus* (Forbes).

KEY:

Matrix and
missing test:
Peristome : P

Text-fig. 5. Camera-lucida drawing of part of the oral surface of *Schizaster (Hypselaster) branderianus* (Forbes), E 81716, showing the labral plate (l), sternal plates (s), and adjacent periplastronal plates of ambulacra I and V. Scale bar: 1mm.

Oral surface (Text-fig.5, Pl.3, fig.5). Ambulacra: These have large polygonal plates with ornament consisting of very few, fairly small primary tubercles and more numerous tiny secondary tubercles, both irregularly distributed. The ambulacral plates on the oral surface are elongated antero-posteriorly and are slightly rounded polygons. Further away from the peristome, towards the peripetalous fasciole, the plates become less elongated and near the ambitus the height and length of the plates are about equal. Adorally the ambulacra are gently concave.

The primary tubercles each have a large saucer-like scrobicule which may be raised at one end. The boss is low, convex, has between seven and ten crenulations and may be tilted according to the position on the test. The mamelon is hemispherical and perforate, the perforation perhaps elongated. The long axis of the foramen of the mamelon is parallel with the axis of the tilt. The scrobicules are not attached to the test very firmly and are easily removed, leaving a faint scar on the plate.

The plates adjacent to the peristome have two oblique, approximately circular pores, each present in a shallow depression. The adoral pore has a thick, horse-shoe shaped rim around it, with the pore situated between two pointed protuberances near the open side of the horse-shoe. The aboral pore has no rim around it but has a curved, hook-like structure over it, dividing it in two. The pores with rims are situated nearer to the perradius and the pores with `hooks' are either central or adradial,

according to the size of the plate. Plates immediately aboral to those adjacent to the peristome have one pore situated at the adoral end of the plate between two protuberances, surrounded instead by a faint, shallow depression. Pores in the remainder of the periplastronal plates occur as small, single, elongated tear-drop shapes or slit-like grooves, with slightly raised margins on more adoral plates and without raised margins aborally. The pores are situated close to the adoral margins of the plates (e.g. E 81679, E 81683a, E 81716, E 81717b). The posterior end of the test is not preserved well enough in any of the specimens to show the ambulacra and pores.

Interambulacra: Interambulacra 1 and 4 form relatively flat, triangular areas of the oral surface; 2 and 3 are rounded and 5 forms a convexly rounded, wedge-shaped area of the oral surface. Plating in interambulacrum 5 is mesamphisternous (see Text-fig.5).

Peristome (Pl.3, fig.5): This is kidney shaped, with the labral plate protruding slightly into the peristomial space and raised above the other component plates. The peristome is about the same width as the anteal sulcus at the ambitus.

Periproct: No specimen has the complete periproct preserved. An adoral portion of the periproctal part of interambulacrum 5a is preserved in specimen E 81684a, where it shows that the adoral margin of the periproct is eliptical. Adapically, the periproctal outline appears to become semi-circular. Together, these outlines show that the periproct was vertically elongated.
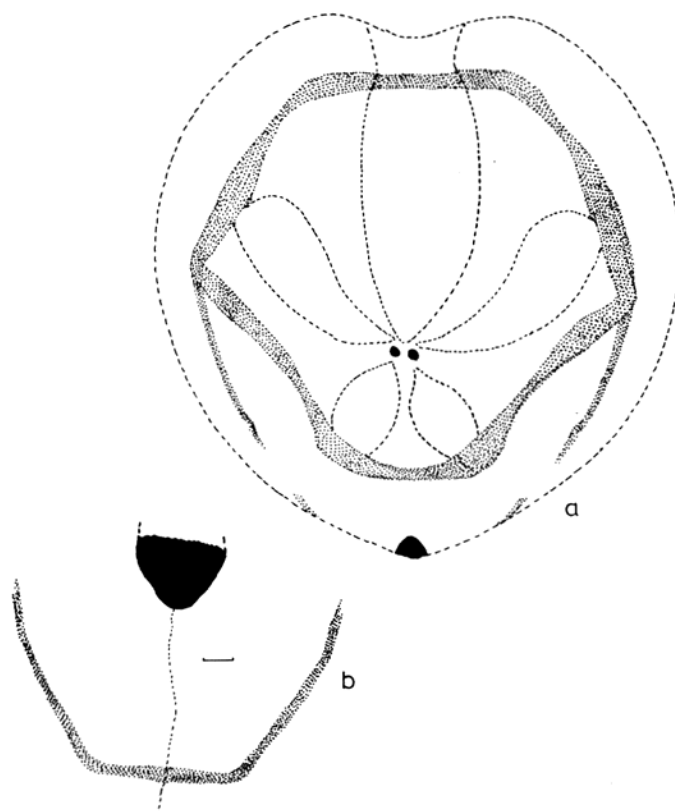
Text-fig. 6. *Schizaster (Hypselaster) branderianus* (Forbes); diagram to show (a) peripetalous and lateral fascioles, based on E 76598b, E 81673a, E 81679, E 81680. The dashed outlines show the position of test and petals relative to fascioles, and are stylized from several specimens of different sizes; (b) anal fasciole, based mostly on E 81684a. Scale bar: 1mm; cf. pl.4, fig.3.

Fascioles (Text-fig.6, Pl.3, figs.4a,b, Pl.4, figs.1a, b, 2, 3): There are three kinds of fascioles: peripetalous, lateral and anal. The peripetalous and anal fascioles are always developed; the lateral fasciole is only occasionally developed (e.g. E 76601, E 76862, E 81673,5,9, E 81680).

(i) Peripetalous fasciole (Pl.3, figs.4a,b, Pl.4, figs.1a,b): This forms a distinct band and marks the limits of the ends of the petals. The thickness of the fasciole varies according to the position on the test. The thickest parts of the fasciole, which taper away from the perradii, are present near the ends of the petals where there are up to 20 rows of minute tubercles at petal III, up to 18 rows at petals II and IV and up to 16 rows at petals I and V. The thinnest parts of the fasciole are present on interambulacra 1-4, close to the adradii and have up to nine rows on the anterior interambulacra, up to ten on the posterior paired interambulacra and about five at interradius 5. The fasciole is approximately semi-circular around the anterior half of the adapical test, but becomes more angular at about the middle of interambulacra 1b and 4a, where it turns sharply adapically and runs parallel with the anterior paired petals. Over interambulacrum 5 it forms a short, shallow arc.

(ii) Lateral fasciole (Pl.4, figs.1a,b,2): (e.g. E 76598b, E 81673a, E 81682.) This is most often not developed. Three specimens on which the lateral fasciole is certainly present are E 81673a whose test is almost complete and is 12mm long and 11.5mm wide; E 81682 which is a fragment of the postero-lateral part of a much larger test, the fragment being 18mm long and 12.5mm high; and E 76598b, an adapical portion of test which is 14mm long and 16mm wide and lacks the posterior-most part of the test. Between two and six rows of tubercles form the fasciole, which extends from the posterior and adoral end of the semi-circular part of the peripetalous fasciole, towards the posterior end of the test, where it may join the anal fasciole (e.g. E 81682).

(iii) Anal fasciole (Pl.4, fig.3): (e.g. E 81671, E 81681, E 81684a.) This is always present on specimens in which the posterior end of the test is preserved. It has a deep, angular `U'- shape and has between three and five rows of tubercles - fewer at the adapical end and more sub-anally. The adapical ends of the fasciole are usually not joined to the lateral fasciole, but E 82682 shows the joining of lateral with anal fasciole. The lateral fasciole here has only two rows of tubercles, but the anal fasciole has four.

Radioles (Pl.4, fig.1a): These are occasionally present in bunches, some almost in situ on or around the test, or are present as single individuals. The shafts are short, either straight or gently curved, sometimes spatulate. Each radiole has a reticulate pattern along its length and has a broadly flaring crenulate annulus. The base is very short and tapers to a narrow acetabulum.

Comparisons

Several species of *Schizaster* with two genital pores resemble *Schizaster (Hypselaster) branderianus* in outline and in proportions of the paired petals. *S. globulus* Dames (1877), (Middle Eocene, Landes) has a much more angular peripetalous fasciole and has a longer test. *S. leymeriei* Cotteau (1856a), (Upper Eocene, La Gourèpe; Landes; Pyrenees, France) has a much more rounded test and much shallower anteal sulcus. *S. foveatus* Agassiz (1840), (Upper Eocene, Landes, France) has much shorter petals in proportion to the test, a central apical disc and a shallower anteal sulcus. *S. africanus* de Loriol (1863), (Eocene, Egypt) has longer posterior petals and its peripetalous fasciole follows the outlines of the petals. *S. gaudryi* de Loriol (1880), (Eocene, Thebes, Egypt) is similar to *S. africanus* except that its peripetalous fasciole follows the outlines of the petals more closely. *S. mokattamensis* de Loriol (1883), (Eocene, Mokattam, Egypt) has a narrower anteal sulcus and its apical disc is not so posterior. *S. rohlfsi* de Loriol (1883), (Eocene, Mokattam, Egypt) has a central apical disc and a narrow anteal sulcus, but has an indistinct lateral fasciole, like the Barton species. All of these species except *S. rohlfsi* have distinct, continuous lateral fascioles and so are not referred to the subgenus *Hypselaster*, even though they may resemble in some respects *S. (H.) branderianus*. It is likely that *S. rohlfsi* should be assigned to *Hypselaster* because of its indistinct lateral fasciole.

Discussion

The type specimen of *S. (H.) branderianus* (Forbes, 1852) - GSM 118226 - consists of a flattened and crushed test, with some of the original test remaining on the adapical and adoral surfaces, but mostly the specimen is an internal cast. There is insufficient detail for a thorough description to be made of the species from this specimen, but it resembles closely other material of similar preservation from the Barton Beds.

Forbes (1852:25-26,27) described *Hemiaster branderianus* and *Schizaster durbani* (pl.5, fig.1) from the Barton Beds: *H. branderianus* he described as coming from Barton, plus another from Haverstock Hill, N.W. London and *S. durbani* he described as coming from the Barton Beds of Alum Bay, Isle of Wight.(Gregory 1891, however, referred to the specimen as coming from the Bracklesham Beds.). The

syntypes of the Alum Bay specimens - BMNH 33395 - have a similar state of preservation to the lectotype of *S.* (*H.*) *branderianus* from Barton and also to other material from Barton and so a detailed description of *S. durbani* cannot be made. In fact, Forbes stated (p.27) that "...it is impossible to pronounce upon its true identity with certainty." The specimens resemble material from Barton so closely that they may be considered to be the same species.

The specimens from Barton are found sometimes in large groups, sometimes as single individuals in the lower Barton Beds A2 and A3. The large groups contain specimens of various sizes, ranging from small individuals about 13mm long and 12mm wide, to very large ones about 39mm long and 37mm wide. Most of them, however, are about 23mm long and 22mm wide. Those specimens which are well enough preserved demonstrate that size is not correlated with the presence or absence of the lateral fasciole.

The generic and specific identity of the Barton species has been the subject of some debate. The generic assignment herein is to *Schizaster* (*Hypselaster*) because the species has two large gonopores, like many schizasterids and has an incomplete latero-anal fasciole, which is the definition of *Hypselaster* given in the `Treatise' (Moore 1966) and by Mortensen (1951:313).

There have been other suggestions made about the taxonomic position of the Barton species. These include:-

Hemiaster by Forbes (1852:26), describing *H. branderianus*, in which he saw the peripetalous fasciole, but not the latero-anal fasciole.

Schizaster, again by Forbes (1852:27), describing *S. durbani*, in which no fascioles were described, or figured.

Brissopsis branderiana by Desor (1858:381), in which he mentioned the peripetalous fasciole;

Schizaster by Cotteau (1887:364), describing *S. durbani* without reference to any fasciole;

Trachyaster, again by Cotteau (1887:406-407), describing *T. branderianus*, in which reference was made to the peripetalous fasciole (and to four genital pores). Strangely, Cotteau referred the same species to *Ditremaster* in the same work (p. 427), referring only to the peripetalous fasciole (and two genital pores).

Gregory (1891:22), mentioned *Hemiaster?* *branderi* and discussed other generic assignments given by various workers, but gave no further description. He did not support the opinion of Duncan (1889:248-249) who believed the species to be a *Brissopsis*, but preferred to call it *Hemiaster*, although he cautiously suggested that the genus could be *Schizaster*. Discussing *S. durbani* (p. 24) Gregory mentioned the confusion between the species *branderianus* and *durbani*, but preferred to keep the two as separate species, distinguishing *S. durbani* by its "...deep, broad and flat-bottomed anteal furrow."

Other authors have listed the Barton species under various genera and as either *branderianus* or *durbani*.

The arguments over the generic assignment has also led to confusion over the name of the species. Gregory (1891:22) summarized the causes of this confusion to palaeontologists as being poor material and descriptions; *Hemiaster branderi* was "...retained for some specimens from the London Clay..." although the description by Forbes "...was based on the Barton specimen...".

If the name *durbani* is to be retained at all, it should be reserved for the specimens from the Barton Beds of Alum Bay - but only if subsequent material proves that it is not conspecific with the specimens from the Barton Beds of the type locality.

The specific name *branderianus* is herein retained for specimens from the Barton Beds of the type locality because one of the original syntypes described by Forbes came from this locality. At present, the specimens from Alum Bay are also referred to this species unless better material proves otherwise.

Suborder   Micrasterina Fischer 1966.
Family   Brissidae Gray 1855.
Genus   *Eupatagus* Agassiz 1847 (In: Agassiz & Desor 1846/7).
Subgenus   *Eupatagus* Agassiz 1847 (In: Agassiz & Desor 1846/7).

Eupatagus (Eupatagus) hastingiae Forbes 1852.

(Text-figs.7, 8, 9, Pl.5, figs. 2-7)

1852 *Eupatagus Hastingiae* Forbes: 26-27, pl.3, figs.7a-e.

Holotype: GSM 118232, partly decayed by decomposition of pyrite. No horizon is known, but the specimen probably came from bed F.

Other material: GSM 118230-1, no horizon known, but probably from bed F; E 76457, E 76460-7, E 76515, E 76583-5, E 76588-9, E 76590, E 76917. (BMNH specimens from bed F.)

Diagnosis: Test low, of medium size; anteal sulcus very weak or virtually absent; paired petals long, almost flush with surface of test; anterior paired petals almost at right angles to antero-posterior axis of test, posterior pair close to interradius 5; test within peripetalous fasciole has few primary tubercles situated on shallow, depressed scrobicules; peripetalous fasciole has flattened slightly rounded `V'-shaped posterior end; apical disc situated about 60% along antero-posterior axis from posterior of test.

Description

Shape: Test almost oval in outline, slightly longer than wide, fairly low; anteal sulcus very weak; lateral margins rounded; oral surface generally flattened, with a slight inflation posteriorly and with a slight depression anteriorly, near the peristome.

Apical system (Pl.5, fig.6): This is ethmolytic and has four genital pores. It is anterior of the centre of the test, about 60% along the antero-posterior axis from the posterior of the test, approximately circular, small and is flush with the surface of the test.

Genital pores are large, circular. Each posterior pore has a low raised rim around it; the anterior pores have no rims (e.g. E 76463a). The madreporic part of plate 2 has a few small perforations and is slightly swollen. The ornament of the genital plates consists of small perforate tubercles randomly distributed.

The ocular plates are very small, approximately triangular in shape (e.g. E 76515) and are slightly lower than the general level of the test.

Apical surface (Pl.5, figs.2,3,5). Ambulacra: These are long and petaloid. The anterior and posterior paired petals are almost the same length and are flush with the surface of the test. The anteal sulcus is virtually absent. The anterior paired petals are nearly perpendicular to the antero-posterior axis, directed just slightly antero-laterally, but the posterior paired petals are much closer to the antero-posterior axis. The ends of the petals of both pairs are closed. Ambulacrum III has almost parallel sides and is straight.

There are between 22-28 pore-pairs in petals I and V; 17-24 in petals II and IV; and 6-12 in ambulacrum III, for tests with lengths between 30-38mm and widths between 23-28mm.

Both pairs of petals are fairly narrow and are widest halfway along their length. They have long, thin plates, wide interporiferous zones with ornament consisting of a few large, primary tubercles and many smaller secondary tubercles. There is one primary tubercle present on each plate, either near the perradial suture or near the perradial pore.
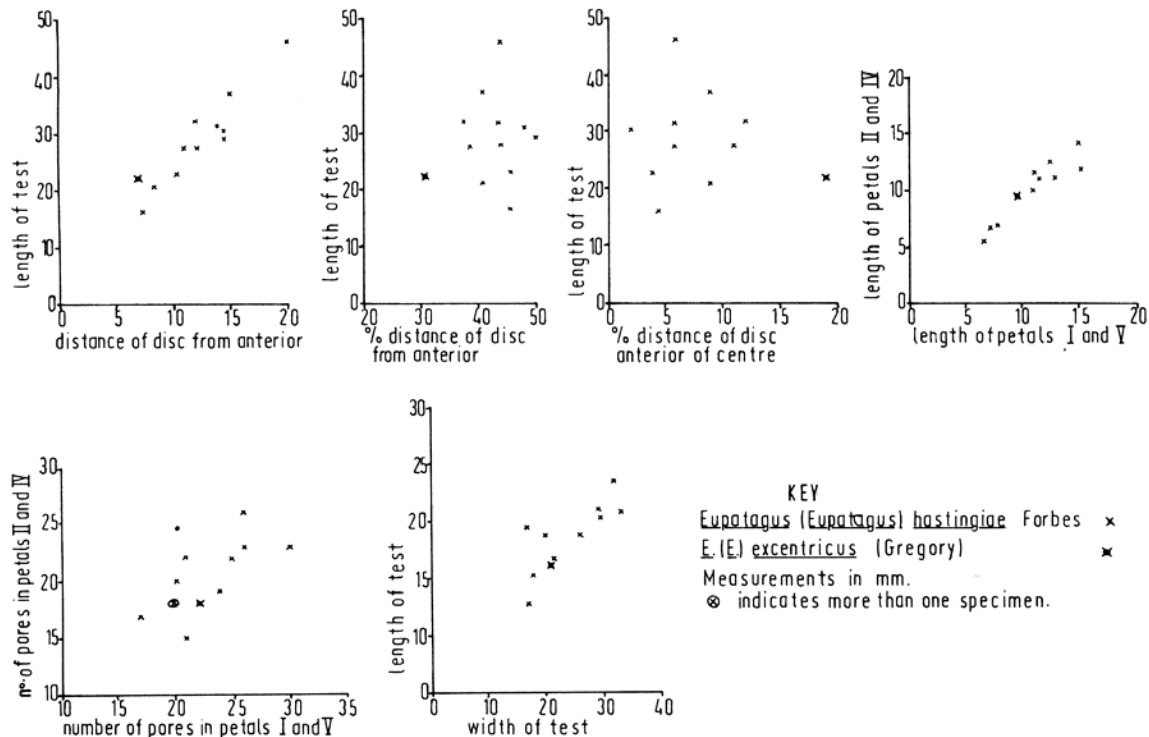
Text-fig. 7. Scatter diagrams of measurements taken from specimens of *Eupatagus (Eupatagus) hastingiae* Forbes and *E. (E.) excentricus* Gregory.

Adapical to each pair of pores there are about five or six secondary tubercles present on narrow ridges between adjacent pore-pairs and several others scattered over the interpore zone. The ridges are perpendicular to the perradius of the petal.

Each pore of a pore-pair has a tear-drop shaped outline, the perradial pore smaller than the adradial one. Each pore is surrounded by a thin raised rim, and there is a shallow, triangular pit between the two pores on their adoral sides.

From the ends of the petals to the ambitus, the ambulacral plates are non-petaloid and become much higher and longer, have a hexagonal outline and have minute, single, slit-like pores near the adoral margin of each plate. Their ornament consists of a few small primary tubercles and many tiny secondary tubercles. At the ends of the anterior paired petals there are one or two non-petaloid plates between the ends of the petals and the peripetalous fasciole, whilst the posterior paired petals end at the fasciole (e.g. E 76515).

The plates of ambulacrum III (e.g. E 76585) from the apical disc to between a third and halfway to the peripetalous fasciole, are similar in shape and structure to those of the paired petals. In the perradial adoral corner of the plate there is a single primary tubercle present which is structurally similar to those of the paired petals. Towards the ambitus, the plates increase in height and remain the same width. To the fasciole, the pores are single, reduced in size and each is situated slightly adradial to the centre of the plate and is present in a horse-shoe shaped depression. Ornament consists of a few small primary tubercles and many tiny secondary tubercles.

Interambulacra: Interambulacra 1-4 are wide and have ornament which is similar on each. Interambulacrum 5 is narrower and its ornament is different. (e.g. E 76466, E 76515, E 76583-5).

The plates of 1-4 are large and have irregular chevron-shaped outlines; those of the posterior columns are slightly larger than those of the anterior columns and so bear a greater number of large primary tubercles. There are between five and six plates per column to the ambitus.

Large primary tubercles confined to the adapical portion of the test within the peripetalous fasciole, are present on all plates except the smallest three or four nearest to the apical disc in each column of

interambulacra 1-4. There can be as many as seven tubercles on a plate, but usually there are between one and three. Each has a steep-sided boss with slightly convex sides and a basal terrace with irregularly developed coarse crenulations. The boss has a parapet with 9-11 coarse crenulations and a hemispherical mamelon with undercut neck and a circular foramen just posterior of the centre. Each tubercle is situated in the centre of a large, gently concave scrobicule, which is sunken into the test, slightly more so at the postero-medial side. The tubercles are about half the diameter of the scrobicule. On specimen E 76515, a typical scrobicule is 1.5mm in diameter. The position of the tubercles on each plate is variable and irregular.

The small primary tubercles are about the same size as the mamelon of a large tubercle. Each has a low, convex boss, a parapet with 10 or 11 crenulations, and a hemispherical perforate mamelon. Some on interambulacrum 5, adapical to the peripetalous fasciole, have narrow scrobicules with slightly raised edges on the adapical side. The distribution of small primary tubercles on the interambulacra adapical to the peripetalous fasciole appears to be random, except along the adapical margin of the peripetalous fasciole, where they are spaced at regular intervals.

Between the peripetalous fasciole and the ambitus, the smaller primary tubercles are tilted posteriorly and have scrobicules with raised rims, giving the appearance of a tilted saucer. The tubercles are evenly distributed and widely spaced.

The secondary tubercles form scrobicular circles around the large primary tubercles and are also distributed irregularly elsewhere on each plate. The secondary tubercles adoral to the fasciole are about two thirds the size of those adapical to it, are widely spaced, evenly distributed between the primary tubercles and along the adoral margins of the peripetalous fasciole.

Oral surface (Text-fig. 8, Pl.5, fig.7).

Ambulacra: Ambulacra II, III and IV are two thirds the width and about 80% of the length of I and V. The ornament consists of primary and secondary tubercles. The primary tubercles are present on the plates nearer to the ambitus in ambulacra II-IV, but are not present on ambulacra I and V, nor on the two or three plates nearest to the peristome. The primary tubercles of ambulacrum III are three quarters of the size of those of II and IV. There are very few primary tubercles; on ambulacra II and IV there are between one and four and on ambulacrum III there are up to five.

Secondary tubercles are more numerous and are distributed evenly over the surface of the plates and around the pores. Pores on plates next to the peristome occur in shallow depressions. Each pore is tear-drop shaped, with the pointed end adoral and if paired each is separated from its neighbour by a ridge. If the pores are single, there is a pit in place of the second pore. Paired pores are oblique and are present in plates Ia, IIa, IIIb, IVa and Vb. Single pores occur in plates Ib, IIb, IIIa, IVb and Va. All paired and single pores lie centrally in their plates. Plates adjacent to the marginal plates of the peristome each have a single, slit-shaped pore surrounded by a horse-shoe shaped depression, with the long axis of the slit parallel to the perradius. The pores are situated very close to the adoral margin of the plates and in successively aboral plates are single and much reduced in size, their shape gradually altering from being slit-like to circular in outline (e.g. E 76460, E 76465b).

Interambulacra: (e.g. E 76460, 3,6). The plastronal plating is ultramphisternous. The single plates of interambulacra 1-4 adjacent to the peristome have approximately the same shape, which is flask-like, with the thin neck of the flask separating adjacent ambulacral plates bordering the peristome. In contrast, the labrum spreads wide at the peristome and is long and narrow aborally. Two large, triangular sternal plates are present aboral to the labral plate and up to three ambulacral plates are in contact with it on either side.

The large primary tubercles are numerous and are distributed evenly and regularly except on interambulacra 1-4, where plates adjacent to the peristome have very few small primary tubercles, irregularly and widely spaced. On the labral plate the small primary tubercles are clustered in rows near the peristomial end of the plate.

Fascioles (Text-fig.9, Pl.5, figs. 4, 5): There are two fascioles - peripetalous and sub-anal:

(i) Peripetalous fasciole (Text-fig. 9, Pl.5, fig. 5). This is narrow, well defined and parallel to the ambitus on the anterior half of the test as far as perradii II and IV. It then curves slightly postero-adapically before continuing to interradius 5, where it forms a flattened, slightly rounded `V'-shape (e.g. E 76463a, E 81983b) at the interradius. The fasciole is composed of between five and seven

KEY:
Matrix and missing test:
Peristome: P
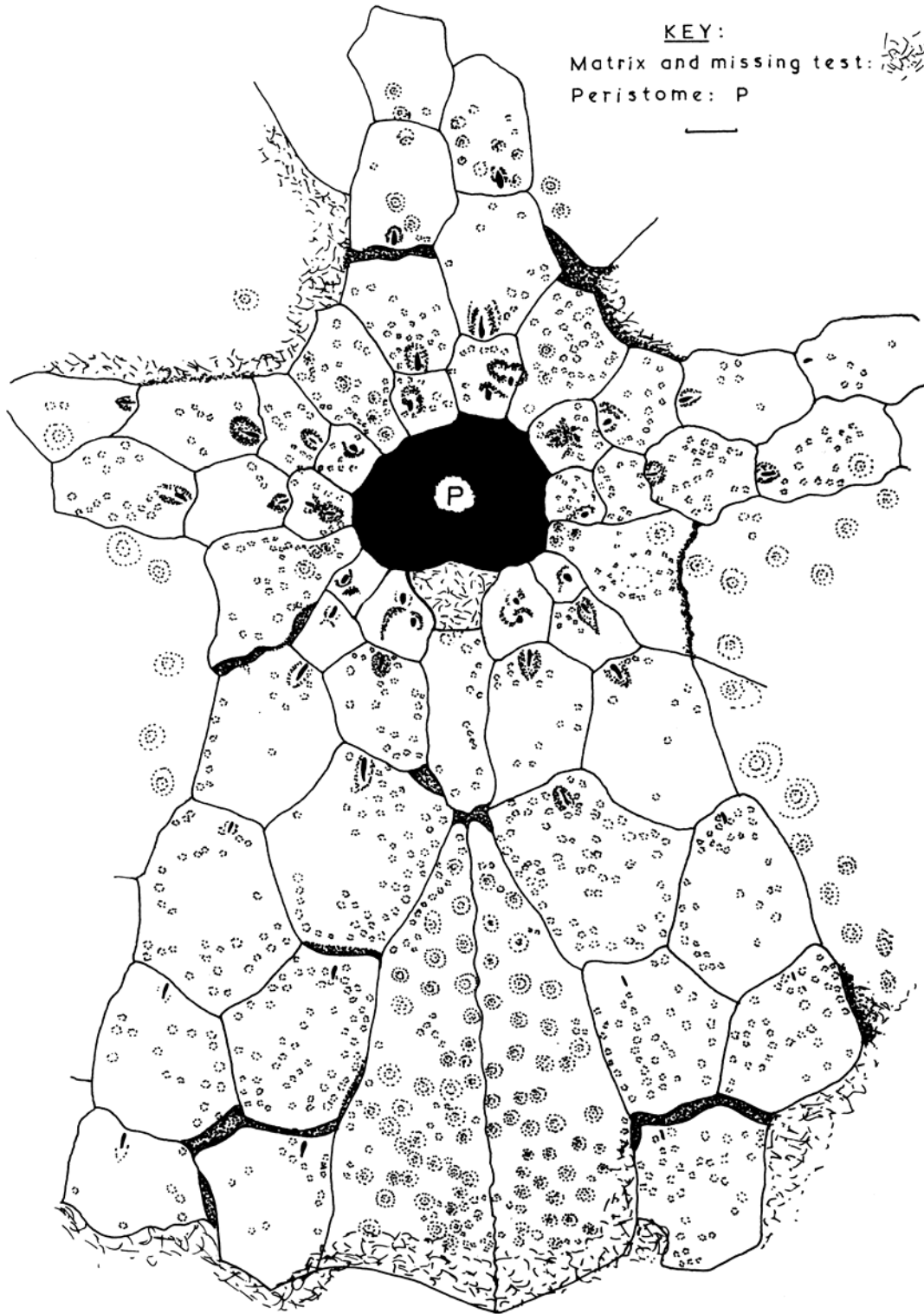
Text-fig. 8. Camera-lucida drawing of part of the oral surface of *Eupatagus (Eupatagus) hastingiae* Forbes, E 76460. Scale bar: 1mm.
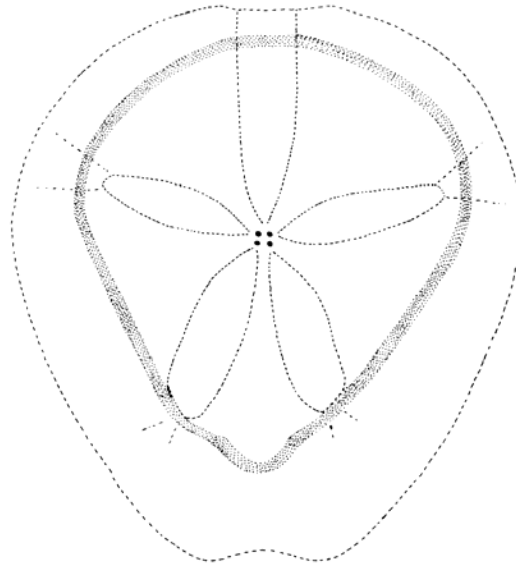
Text-fig.. 9. *Eupatagus (Eupatagus) hastingiae* (Forbes); diagrammatic representation of the peripetalous fasciole, based on E 76457a, E 76466, E 76515, E 76583a, E 76588, E 76589a. The dashed lines of the test and petals are stylized from several specimens. Because of the crushed tests the exact shape cannot be determined.

alternating rows of very small, regularly spaced, perforate tubercles. Similar, but slightly larger tubercles are present at irregular intervals along the border of the fasciole, adorally and adapically.

(ii) Sub-anal fasciole (Pl.5, fig. 4). This has between six and ten rows of very small, close-packed tubercles. Along the margin of the fasciole, in the enclosed area of the test, there is a row of regularly spaced, slightly larger tubercles (e.g. E 76463, E 76466), which increase in size away from the margin of the fasciole. The shape of the fasciole is not very well known because of poor preservation; the part furthest from the periproct is semi-circular, but that near the periproct is not preserved.

Peristome (Pl.5, fig. 7): This is small and kidney-shaped and is situated at about one third of the total length of the test from the anterior end. The labrum does not overhang the peristome (e.g. E 76460-1, E 76465-6).

Periproct (Pl.5, fig. 2): This is not known in detail, all specimens being incomplete or flattened. A single specimen - E 76466 - has the adapical half of the periproct preserved which is narrow and fairly tall and cuts interradius 5 adapically in a half elipse. The adoral half of the test is not preserved. The periproct is situated high on the posterior end of the test and notches the apical outline.

Radioles: Those preserved are incomplete, having lost their distal ends. They are short, fine and slightly curved and have a reticulate ornament together with longitudinal striations. E 76585 has radioles preserved on the oral surface of the test and these are directed posteriorly.

Comments

The holotype, GSM 118232, described and figured by Forbes in 1852, has been almost completely destroyed by pyrite decomposition, so that only small fragments of the test remain. The figure by Forbes is a fair representation of the species described herein.

Comparisons

Several species of *Eupatagus* resemble *E. (E.) hastingiae* reasonably closely, but differ in certain details. *E. duvali* Agassiz & Desor, 1846, (Middle Eocene, Calcaire Grossier, France) has an oval outline with no anteal sulcus and a much more even distribution of large primary tubercles enclosed by the peripetalous fasciole. *E. biarritzensis* Cotteau 1885, (Upper Eocene, Biarritz, France) has more evenly

distributed primary tubercles enclosed by the peripetalous fasciole. *E. vasseuri* Cotteau 1885, (Middle Eocene, Vendée, France) has its apical disc situated anterior of the centre of the test, about 63% along the antero-posterior axis from the posterior of the test. The peripetalous fasciole truncates the ends of the posterior paired petals, which are 25% longer than the anterior ones. The large primary tubercles enclosed by the peripetalous fasciole are more evenly distributed. *E. degrangei* Cotteau 1885, (Middle Eocene, Gironde, France) has more evenly distributed adapical primary tubercles enclosed by the peripetalous fasciole, which truncates the paired petals. *E. gibretensis* Cotteau 1885, (Middle Eocene, Landes, France) has four ambulacral plates adjacent to each side of the labral plate. It has an even distribution of large primary tubercles enclosed by the peripetalous fasciole.

Eupatagus (Eupatagus) excentricus (Gregory 1891) comb. nov.

(Text-figs. 7, 10, Pl.6, figs. 1a-g)

1891 *Euspatangus excentricus* Gregory: 26-28, text fig. 1.

Material: The holotype, BMNH 49820, probably from bed A3, judging from the matrix; also a specimen from the Barton Beds of Alum Bay, Isle of Wight, BMNH 39973. The description is that of the holotype.

Diagnosis: Test small, moderately inflated, broad, maximum width at middle of test; anterior as high as posterior; anteal sulcus very shallow and slightly angular; apical system eccentric, close to the anterior end of the test, about 68% along antero-posterior axis from posterior of test; petals do not reach ambitus.

Description

Shape: Heart-shaped, with shallow anteal sulcus; test at its broadest part is almost as wide as long; posterior end is a broad, rounded `V'- shape; anterior end has two rounded lobes with shallow anteal sulcus between them; oral surface gently rounded, with a slight bulge posteriorly beneath periproct.

Dimensions (in mm): length = 22.5; width = 21.0; height = 10.0; periproctal width = 3.0; periproctal height = 3.5; peristomial width = 3.5; peristomial length = 3.0. Angles between ambulacra: (in degrees) I and II = 80; II and III = 80; III and IV = 73; IV and V = 80; V and I = 47.

Apical system (Pl.6, fig. 1g): This is ethmolytic with four genital pores and is anteriorly eccentric.

Genital plates: Each has a large circular pore which is surrounded by a thick rim with occasional granular ornament on its top surface. Plates 1 and 4 are separated by a posterior, lanceolate extension of plate 2. This extension has a thick rim around its posterior margin.

Ocular plates: Small, approximately pentagonal, each with a pore.

Apical surface (Pl.6, figs. 1a, 1g).

Ambulacra: Ambulacra I, II, IV and V are petaloid over most of the apical surface. The petals are short, closed and are flush with the surface of the test. The posterior pair are only very slightly longer than the anterior pair. Pore-pair columns Ia, IIb, IVa and Va are curved convexly anteriorly. The pore-pairs are oblique, with the perradial pores more adapical than the adradial pores. The pores of the paired petals are tear-drop shaped, with the adradial pores longer than the perradial pores and each is surrounded by a thin, raised wall. A narrow neural canal is present at the perradial end of the adradial pore.

On each ambulacral plate adapical to the pore-pairs is a broad ridge which has about four secondary tubercles. The specimen has 18 pore-pairs in columns IIa and IVb, 17 in columns IIb and IVa, 23 in column Ia, 22 in column Vb and 32 in column Va. Ornament on the paired petals consists of a few primary tubercles which are present on the interporiferous zone and many smaller secondary tubercles.

Each primary tubercle is crenulate, with about nine coarse crenulations and perforate and its scrobicule is slightly sunken. A single primary tubercle is present on the interpore zone near the perradial pore of a pore-pair. Secondary tubercles form scrobicular circles around the primary tubercles and are also distributed randomly elsewhere on the interporiferous zone.

Ambulacrum III is non-petaloid and is situated in a shallow anteal sulcus. The plates are large, their height the same as their width. Each plate has ornament which consisting of a few primary and many secondary tubercles similar in structure to those of the paired petals. The pores of ambulacrum III are not very clearly defined, but appear to be recessed in a horse-shoe shaped depression with a low, narrow ridge between the pore-pairs. The pores are adradially adoral in position. There is one primary tubercle perradial to each pore-pair and others are distributed randomly. Secondary tubercles form scrobicular circles around the primaries and are also distributed randomly over the rest of the plates.

Interambulacra: Interambulacra 1-4 are broad and, adapical to the peripetalous fasciole, have ornament consisting of large primary tubercles with shallow, depressed scrobicules, smaller primary tubercles and secondary tubercles forming scrobicular circles. Secondary tubercles also occur over the remainder of the interambulacra. The large primary tubercles are present on interambulacra 1-4 adapical to the peripetalous fasciole. Most of the ornament on interambulacrum 5 has been eroded away. Three smaller primary tubercles are preserved near the apical disc and a few secondary tubercles mark the remains of scrobicular circles.

The smaller primary and the secondary tubercles are similar in structure to the primary and secondary tubercles of the ambulacra.

From the peripetalous fasciole to the ambitus, the interambulacra have ornament which consists of small primary tubercles and secondary tubercles. However, their distribution and detailed structure cannot be determined from the specimen.

Oral surface (Text-fig.10, Pl.6, figs.1b,1f):

Ambulacra: The posterior paired ambulacra are about 1.5 times the size of the anterior paired ambulacra, from the peristome to the ambitus. The ornament of I and V consists of widely spaced, small secondary tubercles giving the ambulacra a smooth appearance from the peristome to the ambitus. Ambulacra II and IV have similar ornament close to the peristome, but sub-ambitally, the ornament includes large primary tubercles. The primary tubercles each have approximately circular scrobicules whose antero-lateral rims are raised into flanges. The tubercles are inclined adorally. Widely spaced secondary tubercles form scrobicular circles. The ornament of ambulacrum III consists of a few large primary tubercles per plate, and widely spaced secondary tubercles whose exact disposition is unclear because of the preservation. No scrobicules are preserved in the specimen.

Ambulacral pores on the oral surface are much reduced. In the plates adjacent to the peristome they are key-hole shaped, with the long axis parallel to the perradius of each ambulacrum. The pores are situated in a slight depression, and are surrounded by a horse-shoe shaped raised rim. Paired pores are present in plates Ia, IIa, IIIb, IVa and Vb and single pores are present in plates Ib, IIb, IIIa, IVb and Va. Successively aboral plates have tiny, single, slit-shaped pores close to the adoral margin of each plate (text figure 10a).

Interambulacra: The plastron is probably ultramphisternous, but the sternal plates and the aboral portion of the labral plate are missing. Ornament on the interambulacra consists of large primary tubercles with flanged scrobicules, and small secondary tubercles. On interambulacra 1-4, each primary tubercle has a large scrobicule which is slightly elongated and inclined towards the peristome. They are all about the same size and are distributed evenly over interambulacra 1-4. Most of interambulacrum 5 is missing except for that which is enclosed by the sub-anal fasciole. Here, each of the primary tubercles are similar in structure to those of 1-4, except that the scrobicular flange is antero-median in position and the boss postero-lateral on the scrobicule. The tubercles decrease in size towards the fasciole.

Fascioles: There are two fascioles - peripetalous and sub-anal, neither are well preserved:

(i) Peripetalous fasciole. This lies midway between the ambitus and the apical disc and is 0.4mm. wide. It does not truncate the adoral ends of the paired petals and carries about four rows of tiny tubercles.

KEY:
Matrix and missing test:
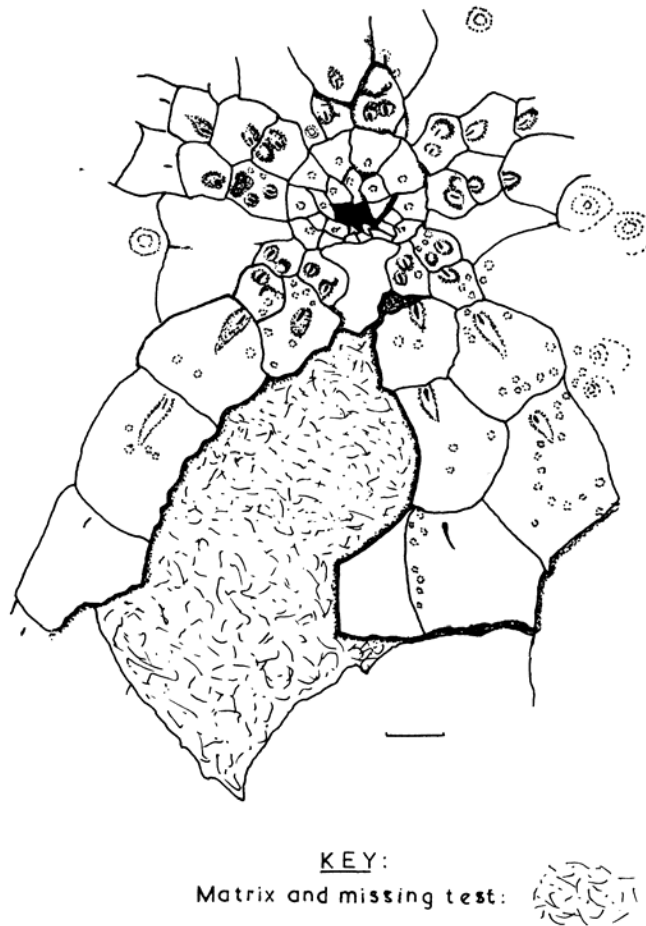
Text-fig. 10. Camera-lucida drawing of part of the oral surface of *Eupatagus* (*Eupatagus*) *excentricus* Gregory, 49820, the holotype. Some of the test on the oral surface is missing. Scale bar: 1mm.

(ii) Sub-anal fasciole. This has an approximately circular outline, is between 0.6 and 0.8mm. wide and has between 8-11 rows of very tiny tubercles. No ambulacral pores can be observed in the area enclosed by the fasciole.

Peristome (Pl.6, fig.1f): This is decagonal in outline and is slightly sunken into the test. The labrum is small, has a smooth, thin ridge around the margin, and does not overhang the peristome. The labral plate is not complete, only the part adjacent to the peristome being preserved. Most of the buccal plates are present *in situ* in the peristome, some of them broken and shattered, especially near the labrum. There is an outer series of large plates and an inner series of smaller ones, the outer ones wedge-shaped, with the narrow oral end truncated obliquely. They are situated at the ends of the ambulacral columns, are ambulacral in position, but have no pores, overlap the interradii slightly, and have two small tubercles on each plate. The inner series of plates are situated adjacent to the oblique ends of the outer plates and are irregular tapering polygons, each with a single small tubercle situated in the middle of the plate.

Periproct (Pl.6, fig.1d): This has a vertically elliptical outline and is slightly adapical to the ambitus, at the posterior margin of the test. Periproctal plates are present, mostly *in situ*, or only slightly displaced.

Comparisons

E. (E.) excentricus is easily distinguished from *E. (E.) hastingiae* and from other species by its much more anterior apical system. It also has a more developed anteal sulcus than does *E. (E.) hastingiae*.

Discussion

The holotype of *Eupatagus (Eupatagus) excentricus* is preserved in a matrix which consists of very sandy clay, similar to that found in the sandy shell drifts of bed A3. The molluscs of these shell drifts have a characteristic greyish-cream colour, similar to that of the echinoid specimen. Although Gregory did not give a precise location for the specimen, it is very likely that it came from this horizon.

The reason for the smoothness of the test is unknown but may indicate that it was rolled and abraded in the fine sandy matrix over a short period of time and was rapidly buried, so preserving intact the peristomial and periproctal plates. (Alternatively, the test may have suffered from over-enthusiastic cleaning after its discovery, but there is no obvious trace of this.)

Gregory, (1891) did not see either of the fascioles, but said "...The presence of a peripetalous fasciole is indicated by the structure of the test and distribution of the tubercles...". The specimen has since been removed from the matrix in which Gregory saw it and it has revealed traces of both peripetalous and sub-anal fascioles.

Another specimen, BMNH 39973, is recorded as coming from the Barton Beds of Alum Bay, Isle of Wight. It is approximately the same size as the holotype, is an internal cast in sandstone and is slightly distorted along the antero-posterior axis of the test, but the relative proportions are the same as for the holotype.

<div align="center">

Family   Spatangidae Gray 1825.

Genus   *Spatangus* Gray 1825.

Subgenus   (*Phymapatagus*) Lambert 1910.

</div>

Spatangus (Phymapatagus) grandituberculatus sp. nov.

<div align="center">

(Text-figs.11,12a-c, Pl.7, figs 1a-e,2a-c)

</div>

1852 *Spatangus Omalii* Galeotti; Forbes: 28, pl.3, figs.9a-c.
1891 *Maretia grignonensis* (Desmarest); Gregory: 26.
1933 *Maretia grignonensis* (Desmarest) (= *Spatangus omalii* Forbes); Burton: 152 (in faunal lists).

Type material: holotype - E 76821; paratypes - E 37320-3, E 76817-20 (from bed A3); E 76459 (from bed A2).

Other material: 49823, E 9588 (no horizon given); E 41506-9, E 76518-9 (from bed A3); GSM 118227-9 (no horizon). GSM 118227 was figured by Forbes (1852: pl.3, figs. 9a-c) as Spatangus omalii.

Derivation of name: species named for the large anterior primary interambulacral tubercles of the apical test.

Diagnosis: A small *Phymapatagus* with small, narrow, paired petals; periproct high up on truncated posterior end of test; large, very deeply inset tubercles on anterior half of adapical surface; plastron and periplastron naked except for a wedge-shaped area on the posterior of the plastron; anterior column of plates of anterior paired petals reduced in width, with pore-pairs much reduced in size in all these plates, but more so adapically; anterior margin deeply notched.
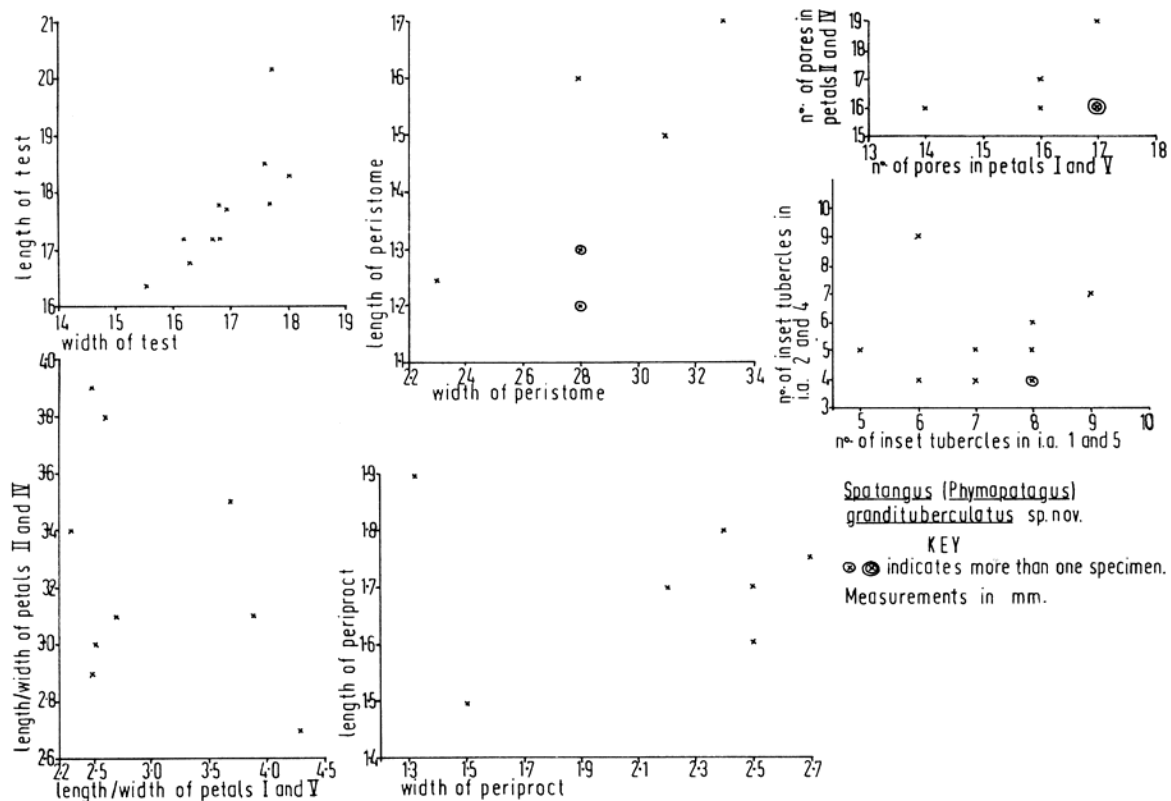
Text-fig. 11. Scatter diagrams of measurements taken from specimens of *Spatangus* (*Phymapatagus*) *grandituberculatus* sp. nov.

Description

Shape: (Text-fig.11) test heart-shaped, low, with deep anteal sulcus at ambitus, becoming shallower towards apical system; test truncated sharply at posterior end, highest just posterior to apical disc.

Apical system (Text-fig.12b, Pl.7, fig.2b): This is small, ethmolytic and has the outline of an indented pentagon. It is slightly anterior of the centre of the test, about 58% along the antero-posterior axis from the posterior of the test.

Genital plates: there are four gonopores, each with a raised rim on which lie several widely spaced perforate tubercles. Genital pores 2 and 3 are closer together than are pores 1 and 4. The madreporic part of plate 2 is perforated by several small pores along its posteriorwards extension.

Ocular plates: these are small, pentagonal and have elongated ocular pores.

Apical surface (Text-fig. 12c, Pl.7, figs. 1a, 2b, c). Ambulacra: Ambulacra I-IV are petaloid, slim and flush with the surface of the test. Ambulacrum III in the anteal sulcus has straight, almost parallel sides.

The petals are fairly long; II and IV extend 83% of the distance from the apical disc to the ambitus, whilst I and V extend about 66% of the distance.

The posterior columns of pores of the petaloid ambulacra extend one pair further towards the ambitus than do those of the anterior columns and the ends of the petals almost close.

In petals I and V, the pore-pairs of each column are oblique and tear-drop shaped and each has a low raised rim around it. The perradial pore is slightly more adapical than the adradial pore. Pore-pairs increase in size rapidly adorally and then diminish in size at the ends of the petals. Adoral to each pore-pair is a triangular depression and adapically there is a ridge with a row of about five small tubercles, usually three adapical to the perradial pore and two adapical to the adradial pore. The
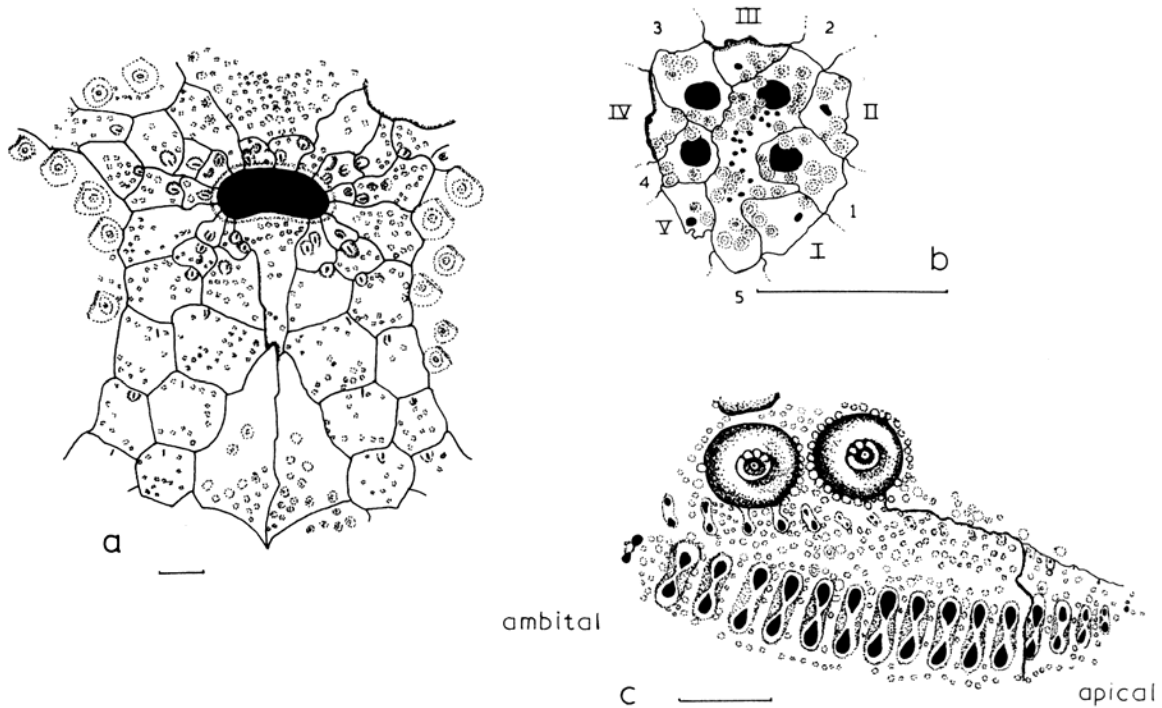
Text-fig. 12. Camera-lucida drawings of *Spatangus (Phymapatagus) grandituberculatus* sp. nov., showing: (a) part of the oral surface of E 37320. (b) apical disc of E 76820. (c) ambulacrum IV of E 37320, showing the reduction of the anterior pore-pairs adapically and next to the inset tubercles of interambulacrum 3b. Scale bars: 1mm.

interporiferous zone has ornament which consists of smaller secondary and larger primary tubercles. Each secondary tubercle has a circular convex boss with a small perforate mamelon, is tilted postero-medially and is present between the pore-pairs and over the interporiferous zone. Each primary tubercle has a convex boss with about 12 crenulations around the parapet, a small perforate, hemispherical mamelon and a narrow scrobicule which is tilted postero-medially. There is one primary tubercle situated near the adradial margin of the plate, one adapical to the perradial pore and usually one near the adapical perradial margin of the plate. The petals have between 17-20 pore-pairs and the height of a plate is about one quarter of its length.

In petals II and IV (Text-fig. 12c), the structure of the posterior columns of plates is similar to that of petals I and V, with the scrobicules of the larger tubercles tilted postero-medially. The structure of the anterior columns of plates is variable. Adapically, near the apical disc, the anterior plates are less than 50% of the width of the posterior plates. About halfway along the petal they are about 75% of the width of the posterior plates and near the adoral end of the petal they are about 70% of the width of the posterior plates. The height of both anterior and posterior plates is about equal.

The anterior pore-pairs are between 10% and 60% of the size of the posterior pore-pairs. They are similar, oval in outline and are close together, with a thin ridge between each pore of a pair and occupy a small portion of the adoral adradial part of each plate. The extent of the much reduced pore-pairs (i.e. those of up to 20% of the size of the posterior pore-pairs) varies from about 40% to about 70% of the total length of the petal, not depending on the size of the test. They occupy proportionally less of the whole area of the plate (about 4% less) than the less reduced pore-pairs adoral to them (i.e. those of about 60% of the size of the normal posterior pore-pairs). The less reduced pores occupy between 11%-25% of the whole area of the plate.

The pore-pairs of a normal posterior plate occupy about 31% of the total area of the plate.

Towards the adoral end of the petals, the anterior column of pore-pairs may be interrupted by the encroachment of a single, large, recessed interambulacral tubercle which truncates two adjacent ambulacral plates at the adradial margin, leaving only the perradial pore of a pair of one of the

ambulacral plates and causing the adradial pore of the other plate to form on the edge of the recess (Pl.7, fig.2b).

Ambulacrum III forms part of the anteal sulcus which is shallow near to the apical disc and deepens adorally, forming a deep notch at the ambitus. The sulcus is not particularly wide, the ambulacral part being about the same width as the widest part of one of the paired petals. The height of each plate is about three quarters of its length. The pores are very small and very oblique, with the adradial pore almost completely adapical to the perradial pore. Adapically, for the first five to seven plates, the pores are situated near to the adoral margin of the plate, about halfway between the perradius and the adradius, but adorally the pores are situated in the centre of the plate. Each of the pore-pairs has a small rim adapically perradial, with a stout, peg-like ridge separating each pore of a pair. The adradial pore is tear-drop shaped, with the long axis parallel to the axis of obliqueness and is about twice the size of the almost circular perradial pore.

Ornament consists of a few larger primary tubercles and many tiny secondary tubercles. There are between two and eight primary tubercles per plate, depending on the size of the plate and of the specimen. The secondary tubercles have a random distribution over the ambulacrum.

The sutures between the plates are faint and there are about 11 plates per column to the ambitus.

From the ends of the paired petal to the ambitus, the pore-pairs are reduced to minute pores. The ornament of the ambulacra here consists of widely spaced, tiny secondary tubercles about half the size of the secondary tubercles of the paired petals and larger primary tubercles about the same size as those on the petals.

Interambulacra: Interambulacra 1 and 4 are nearly twice as wide as 2 and 3 and interambulacrum 5 is about twice as wide as 2 and 3, measured between the adradii at the ends of the petals. All have ornament which consists of small secondary tubercles, both large and small scrobiculate tubercles and a very few extremely large primary tubercles recessed into the test.

The larger, unrecessed scrobiculate tubercles are about twice the size of the smaller ones and on interambulacra 1 and 4 their scrobicules are tilted posteriorly. There are few of them, randomly distributed. They have a similar distribution and alignment on interambulacra 2 and 3, except for two or three columns on each side of the anteal sulcus, where they are close together and have their scrobicules tilted towards the apical disc. On interambulacrum 5, they are sparsely and randomly distributed, usually over the whole of the interambulacrum, but sometimes as a regular but sparse column either side of interradius 5.

The largest tubercles (Pl.7, figs 2b,c) are each inset into the test in a deep circular pit and have faint camellae (small bulges on the inner surface of the test which accommodate the deep-set tubercles) developed on the inner surface of the test. The surface of the test directly adjacent to the pit is strongly undercut. These tubercles are confined to interambulacra 1-4. In 1 and 4 they are present mostly on the anterior half of the interambulacra, but one may be present near the interradius on the posterior half of the interambulacrum. In 2 and 3 they are present over both halves of the interambulacra. They have a thick parapet with three very coarse crenulations on the antero-lateral edge for about a quarter of its circumferance, the remainder of the parapet being smooth. Each tubercle is raised very slightly above the surface of the test (i.e. out of the deep pit) has a small, perforate, hemispherical mamelon with an undercut neck and is tilted very slightly posteriorly or postero-laterally. There are dense circles of secondary tubercles around the edge of the circular pit.

The number of the very large inset tubercles varies. On interambulacra 1 and 4 there are between seven and ten, usually the same number on each, but occasionally there is one more on one side than the other. There are also smooth patches which are approximately circular, which have no ornament and may represent unformed tubercles. On interambulacra 2 and 3 there are between four and seven tubercles and with equal numbers on each side. Sometimes the anterior column of pore-pairs of ambulacra II and IV is interrupted by one or more of the adjacent large tubercles of interambulacra 2 and 3 but none of the other ambulacra are interrupted by interambulacral tubercles. On larger specimens, at the extreme anterior ends of interambulacra 2 and 3, there may be a few tubercles incompletely recessed into the test.

Oral surface (Text-fig.12a, Pl.7, figs.1b,2a): This is holamphisternous and except for a triangular-shaped area posteriorly, the plastron and the periplastronal areas of the test are almost naked, having only sparse, very tiny tubercles. The phyllodes are weak.

The ornament consists of tubercles of three kinds: large, with prominent scrobicules, some of which are fairly deeply recessed into the test but which do not form camellae in the inner surface of the test; smaller tubercles with much less prominent scrobicules; and tiny tubercles.

Ambulacra I and V on the oral surface are about 30% longer than ambulacra II and IV. Their plates are about 40% larger than those of II and IV and all plates have curved margins. The pores of plates adjacent to the peristome are much reduced and are either paired or single. Paired pores are present on ambulacra Ia, IIa, IIIb, IVa and Vb and single pores are present on plates Ib, IIb, IIIa, IVb and Va and on all ambulacral plates aboral to those adjacent to the peristome.

The labral plate is broad at the peristome and protrudes into it only slightly. Posteriorly it is narrow, with strongly concave margins next to the adjacent first ambulacral plates and reaches about halfway along the third plates of ambulacra I and V.

The paired sternal plates posterior to the labral plate are large and very narrow at their anterior ends and expand gradually posteriorly into approximately triangular-shaped plates with indented adradial margins. Towards their posterior ends, the ornament includes the smaller primary tubercles which form part of the triangular area of coarser ornament on the plastron. A second pair of sternal plates bears the rest of the triangular area of this ornament, and also part of the sub-anal fasciole.

Sub-anal fasciole: This is bilobed and is about 40% of the maximum width of the test. It extends from just beneath the periproct to the adoral surface and is composed of several alternating rows of very tiny perforate tubercles. The widest part of the fasciole is just beneath the periproct, thickening adorally, where there are up to 15 rows. It is narrowest either side of the interradius on the oral surface, where there are about seven rows. Close to the narrowest part, there are two small raised portions of the test, one on either side of the interradius.

Within each lobe of the fasciole there are up to three large tubercles which usually have deeply inset scrobicules, many more smaller tubercles with circular scrobicules not inset and tiny tubercles about twice the size of those forming the fasciole, irregularly spaced along both the margins of the fasciole.

Just within the fasciole, at the outer edge of each lobe, there are three or four very small, very oblique pairs of elliptical pores, inset in shallow depressions. The long axis of the pores is from the periproct to the lateral margin of the test, with the adradial pores almost directly adapical to the perradial pores.

Peristome (Pl.7, fig.1b): This is small, about the same width as the anteal sulcus, is kidney-shaped and is situated at about 35% of the test length from the anterior of the test. It is slightly sunken into the test, with the labrum higher than the rest of the plates which surround the peristome and which each have a very narrow, rounded rim.

Periproct (Pl.7, fig.1d): This is small, transversely elliptical and is situated high up on the flat, vertical posterior end of the test. The height of the periproct is about 60% of the width.

Comparisons

Spatangus (Phymapatagus) grandituberculatus differs from S. (P.) omalii (Galeotti 1837) (Middle Eocene, France, Germany, Hungary, Belgium) by having a deeper anteal sulcus at the ambitus and by its much more reduced anterior pore-pairs and plates of the anterior paired petals. The test of S. (P.) omalii is higher anteriorly and the apical disc more anterior than in S. (P.) grandituberculatus. The interporiferous zones of the paired petals of S. (P.) omalii are wider than those of the Barton species and are also more petal-like in shape. The periproct of S. (P.) omalii is vertically elongated, not horizontally so as in the Barton species.

Although the anterior columns of pore-pairs of the paired petals are not reduced in Maretia, it is interesting to compare some of the species with S. (P.) grandituberculatus:

M. desmoulinsi (Cotteau 1863), (Upper Eocene, La Gourèpe, France) has a greater number of large inset tubercles and a shallow anteal sulcus. The posterior margin of the test is not vertical but slopes inwards and downwards. M. pellati (Cotteau 1863), (Upper Eocene, Biarritz, France) has a shallow anteal sulcus and very few large inset tubercles. M. heberti Cotteau 1885, (Middle Eocene, France) and M. calvimontana (Cotteau 1885), (Middle Eocene, Lower Calcaire Grossier, France) both have a circular outline, many more inset tubercles and a central apical disc.

Discussion

Spatangus (Phymapatagus) grandituberculatus has been recorded from two horizons in the Barton Beds. Most specimens and fragments are from bed A3 from one of the many sandy, lenticular shell-drifts. The complete specimens are fragile and are filled with clean sand and are sometimes so encrusted with sand grains as to give them a `sugary' appearance. They were probably not moved very far post mortem before burial as they are still intact and retain most of the fine detail of the test.

The other horizon in which the species has been found is bed A2. Specimen E 76459 from this bed is crushed, but the detail is well preserved in clay containing small amounts of glauconite. *S. (P.) grandituberculatus* was first described from the Barton Beds by Forbes (1852:28) who called it *Spatangus omalii* Galeotti. He figured a fragment of test - GSM 118227 - and stated that the fragments found by Mr. Edwards "...on comparison with an authentic example of *Spatangus Omalii* of Galeotti brought by Sir Charles Lyell from Eocene strata in Belgium, prove to be, almost beyond a doubt, identical with that species." Forbes also figured a restoration which he "...founded on the Belgian *Spatangus*...". Cotteau (1885:35) considered that *Spatangus omalii* was the same species as *Maretia grignonensis* and that *S. omalii* was a junior synonym of *Maretia grignonensis* because Desmoulins had listed the name in 1836 and Galeotti had described his species in 1837. As Desmoulins neither described nor figured the species, his name is a *nomen nudum* and the first valid name is that given by Galeotti, i.e. *Spatangus omalii*, for even though the figure is not recognizable as any particular species, his was the first description.

Gregory (1891:26) included the specimen figured by Forbes in his "Revision of the British Fossil Cainozoic Echinoidea", identifying it as *Maretia grignonensis* (Desmarest 1837). He reported that further fragments of the test had been found, but these were not sufficient to verify "...the accuracy of the specific determination.".

Burton (1933:152) in his faunal lists gave the species both names:- "...*Maretia grignonensis* (Desmarest) (= *Spatangus omalii* Forbes)..." and recorded them as being "common" in bed A3.Since the earlier descriptions were made of the fragments of test, several new and much more complete specimens have been found, especially by A. G. Davis, F. C. Stinton and W. J. Quayle and the species can now be assigned to *Spatangus (Phymapatagus)* based on the new information revealed by the tests. *Phymapatagus* Lambert (1910:2-4) is characterised by having only rudimentary pores in the adapical plates of the anterior pore-pairs of the anterior paired petals and by the lack of primary tubercles in the posterior interambulacrum. However, several other genera of spatangids also have a reduction of these anterior pore-pairs, (but differ in other respects) including: *Nacospatangus* and its sub-genera, which have three gonopores; *Hemimaretia*, which has three gonopores; *Paramaretia*, which has deep phyllodes and a very shallow, almost inconspicuous anteal sulcus. It is similar to *S. (P.) grandituberculatus* by having a plastron which is tuberculated only at the posterior end; *Semipetalion*, which has a tuberculated plastron and petals which are slightly depressed into the test. Specimens of *S. (P.) grandituberculatus* show slight variations which are not dependent on the size of the test. These include:

(i) The number of large, inset primary interambulacral tubercles on the anterior adapical half of the test is variable.

(ii) The anterior columns of plates on the anterior paired petals IIb and IVa.

(iii) the absence of some pores in IIb and IVa.

ECOLOGICAL IMPLICATIONS OF THE ECHINOIDS FROM THE BARTON BEDS.

Interpretations of living conditions.

The palaeoenvironment of the Barton Beds has been discussed in detail by several authors, but most recently by Murray & Wright (1974) and Hooker (1986), with comments by other authors, e.g. Curry (1981), Gardner *et al.* (1888).

Murray & Wright (1974:48-52), attempted by means of the foraminiferan fauna, to identify the conditions extant during deposition of the Barton Beds. They divided the lithostratigraphic units *sensu* Burton (1929,1933) into five faunules and using the foraminifera, described the prevalent conditions for sedimentation in terms of salinity, depth of water, local geographic features, etc.

In their discussion, Murray & Wright (1974:51) stated that the Barton Beds of the type locality "...represent a full marine cycle from continental deposits through marsh, inshore and offshore shelf and back to shallow water conditions...". The presence of "...few planktonic specimens..." of foraminifera "...suggest a restricted circulation...".

The water during this time was slightly hyposaline, influenced by freshwater from nearby rivers, with salinity down to 33% and was generally cool, with summer temperatures at the sea bottom between 10 and 18 degrees C., perhaps similar to the temperatures of the modern English Channel. Overall, the Barton Beds, with some exceptions, were deposited in slightly hyposaline, turbulent muddy waters, with a depth no greater than 100 metres and probably at about 50 metres for much of the period.

Curry (1981:31-32) however, disagreed with some of the conclusions drawn by Murray & Wright. He said that the presence of reptiles was inconsistent with their suggestions that the water temperatures of the Barton sea were perhaps similar to those of the modern English Channel. He thought that "...remains of stenohaline groups such as echinoderms and corals..." indicated "...deposition in a sea of near normal salinity. The occurrence of turtles (and of crocodiles in the succeeding Lower Headon Beds) suggests warm temperate to tropical conditions." The great variety of species from the Barton Beds may support the views of Curry. Murray & Wright in their summary (p. 114) indicated that there was some intermixing of faunas - "...cool-water fauna is of northern and the warm-water fauna of southern origin...", referring to the appropriate foraminifera, with the northern fauna dominant throughout the Palaeogene. The appearances of southern forms were brief though successful.

Hooker (1986) discusses the Barton Beds in terms of three sedimentary cycles (pp. 206-207) which indicated rapid transgressions, gradual regressions, "...ending in shoreface sands...". (For further discussion and details see Hooker 1986.)

The echinoids of the Barton Beds are not especially indicative of a particular type of environment. From the analysis of Murray & Wright, the fossil echinoids of beds A3 to basal F probably lived in waters no deeper than about 100 metres, and those from beds A2, top of F to the base of H, in waters no deeper than 50 metres, probably less. As the echinoids present were not specifically adapted to existence in a higher energy environment, the bathymetric zone was probably not littoral or tidal. Extant echinoids may show a considerable variation in the depths of water in which they live, so their use in correlating the depths at which their fossil relatives lived is very limited. Fossil echinoids therefore are not very useful as precise depth indicators.

Echinoids such as S. (H.) branderianus are useful as indicators of the general water temperature at the sea bottom - this species by having relatively fewer pore-pairs suggests a cooler environment. Other irregular echinoids of the Barton Beds also have relatively fewer pore-pairs, implying that the water in which they occurred was cooler.

Only within limits can they be used as indicators of normal salinity; a few echinoids can withstand salinity as low as 20% , others as much as 48% (Durham 1966:U258), but adapt less well to brackish water (see Hyman, 1955:564) than other marine invertebrates. The temperature of the water at the sea-bed may be indicated by the number of tube-feet possessed by an echinoid - many tube-feet indicate a higher metabolic rate, therefore higher respiratory rate and hence warmer waters and the converse is also true. Of course, warm water will probably contain less oxygen and this will be another reason for rapid respiration.

Work by Zoeke (1951) on species of Cretaceous Hemiaster of Europe and Africa showed that the European species of Hemiaster had fewer pore-pairs and a shallower ambulacrum III than African fossil species of Hemiaster which had many more pore-pairs and a deeper ambulacrum III. The irregular echinoids of the Barton Beds have relatively fewer pore-pairs, like the species of European Hemiaster discussed by Zoeke (1951), implying that the water in which they occurred was cooler.

Smith (1978) recognized a similar kind of correlation in the type of tube-feet of some regular echinoids, when he wrote "...echinoids inhabiting shallow warm waters have a greater oxygen consumption than those in colder waters. Echinoids inhabiting shallow tropical waters need the most efficient tube-feet..." (p.778). The cidarids with "...complex, flattened tube-feet specialized for gaseous interchange..." lived in shallow warm seas, whereas those with simple tube-feet lived in cold water (Smith 1984:140).

Reference to their modern counterparts can suggest a likely mode of life for fossil echinoids which may be correlated with other data to generate a picture of the palaeo-environment.

Regular echinoids

As the cidaroids of the Barton Beds are known only from their radioles, which are relatively short and robust, they are inconclusive as environmental indicators. Modern cidaroids occur in all depths of water from littoral to about 4000 metres (see Mortensen 1928:37) and on different bottoms. The cidaroid radioles from the Barton Beds are recorded from beds A3 to H.

Modern pedinids of the genus Caenopedina are normally found at depths of between 100-1200 metres, occasionally down to 2000 metres and were regarded by Mortensen (1940:73) as "...continental (archibenthal), not really deep sea forms...". He recorded one species - *Caenopedina mirabilis* (Döderlein 1885) from a depth of 20 metres. Modern pedinids are mostly found in the Indo-Pacific, with one species from the Atlantic (East Azores and Canaries) and one from the West coast of America (see Mortensen, 1940:96, key). Fell (1966:U345) thought them to be "...rare and solitary..." although fossil *Pedina* was "...occasionally gregarious...". The Barton pedinoid *Echinopedina paucituberculata* is certainly not a common species in the Barton Beds and was apparently not gregarious. It cannot be used as an indicator of the depth of water, but may indicate similar climatic conditions to those of the habitats of Recent forms.

The only known modern phymosomatid is *Glyptocidaris crenularis* Agassiz, recorded from northern Japan at depths of between 10-150 metres (see Mortensen, 1935:428-486). Mortensen thought that fossil phymosomatids lived at "...moderate depths..." from the evidence based on the Recent *Glyptocidaris*. The long thin radioles of the Barton species *Porosoma*? sp. may have served to support the test on a soft bottom, but the depth at which it lived cannot be determined. No information as to the respiratory requirements of this species can be obtained from the small portions of test preserved; whether the adoral pore zones were wider than elsewhere cannot be determined from the specimens.

Modern species of *Coelopleurus* are found at depths of between 100-500 metres, with one recorded from as low as 2380 metres (see Hyman, 1955:524; Mortensen, 1935:618) from as far north as Cape Hatteras, eastern U.S.A. to the Bass Straights in the south, with most occurring within 20 degrees north or south of the Equator (see Mortensen, 1935, for details). The only recorded specimens from the Barton Beds are from bed E, but whether from the upper or lower part is unknown. If the specimen came from the lower part - the `Earthy Bed' of Burton 1929:229 - then a slow rate of sedimentation probably accounts for the fragmentary nature of the material. Burton (1929) recorded the presence of much carbonaceous material which possibly formed some of the food supply of the *Coelopleurus*. Mortensen (1935:543) recorded that the food of some arbaciids (e.g. *Pygmaeocidaris*, p. 543) consists of algae and "...pieces of land plants...washed out to sea and sunk to the bottom...".

Glyphocyphids are known only as fossils, so that any discussion on their life styles has to be based on that of modern temnopleurids. Most modern temnopleurids are littoral or relatively shallow water forms, but a few are archibenthal or even upper abyssal (see Mortensen 1943:56; Hyman 1955:579). and are found in tropical and sub-tropical waters. Mortensen recorded that regenerated radioles were to be found on large and small specimens, but he did not believe that this was caused by rough seas, as the echinoids were not found in places exposed to rough waters. He supposed that predation was the cause. Glyphocyphids are found in rocks of Lower Cretaceous to Eocene age in India, North Africa and Europe, including Great Britain. The specimens of *Ambipleurus*? *quaylei* were found in bed A2 in a shelly drift which contained comminuted fragments of mollusc shells and whole gastropod shells, plus other faunal debris and carbonized wood.

Irregular echinoids

Modern species of the sub-genus *Hypselaster* are recorded from the littoral zone down to 1935 metres, from Japanese waters to Western Australia and like other spatangoids are burrowers. McNamara & Philip (1980) and Smith (1984) discussed the evolutionary trends from *Linthia* to *Schizaster* and concluded that there was a gradual adaptation from living in shallow burrows in coarse, loosely packed sediments to living in deeper burrows in fine cohesive sediments. McNamara & Philip indicated (1980:62) that morphological adaptations were required to "...produce more efficient current flow over the aboral surface of the test in a sediment of low permeability...". Water flow in Schizaster was restricted to that passing down the funnel constructed from the sediment-water interface to the echinoid, whereas in other spatangoids which inhabited coarser sediments the water flow could permeate through the sediment as well as down any constructed funnels. The specimens

of *Hypselaster* from the Barton Beds were probably adapted to life in fine-grained sediments - the labrum projects anteriorly to protect the mouth from underlying sediments and to direct water currents into the mouth; there are many tubercles and therefore radioles, on the plastron to assist in burrowing in a cohesive sediment; and ambulacrum III is long, with sufficient pore-pairs (therefore tube feet) for funnel construction by means of funnel-producing cilia (McNamara & Philip 1980:62).

Modern species of *Eupatagus* are restricted to the Indo-West Pacific (Mortensen, 1951:465), although many fossil species are recorded world-wide. They are found at depths of between 10-600 metres. There is little information available about the mode of life, but the type species of the genus - E. valenciennesi Agassiz - was collected from a depth of "...30-35 fathoms..." (55-64 metres) from "...mud..." (Agassiz, 1881:173).

Modern species of *Spatangus* are found from as far north as south Iceland, to New Zealand and South Africa, at depths from the lowermost tide limit to 1000 metres (see Mortensen, 1951). Two were studied in detail by Nichols (1959) - *Spatangus purpureus* and *S. raschi*, both found in British waters. *S. purpureus* came from shell gravel at a depth of 25 fathoms (45.75 metres), while S. raschi was collected from sandy mud at a depth of 120 fathoms (220 metres) and were recorded at depths of between 100-150 fathoms (183-275 metres) and also closer inshore. Nichols noted that S. raschi had a deeper, more angular anteal sulcus, a more conical test at the apex and a more tapered posterior test than *S. purpureus*.

The sub-anal fasciole of *S. purpureus* is bilobed and that of *S. raschi* almost circular. These features, Nichols argued, seem to reflect the different modes of life of the two species. *S. purpureus* burrows with its upper surface 5 cms below the surface of the substratum and has no direct connection (by tube) with the surface, but instead, draws water through the pore spaces of the shell gravel. A double sanitary tube is constructed from the bilobed sub-anal fasciole and waste material is removed into the pore spaces of the shell gravel or to the surface. S. raschi, on the other hand, although capable of burrowing to a depth of about 2.5cms, normally ploughs along the surface of the substratum with half of the test exposed. It constructs a single sanitary tube from its circular fasciole because its respiratory tube-feet are not confined to a burrow and so do not need a large drain. Nichols (p. 391) suggested a similarity between the interlocking characteristics of shell gravels and those of mud, which made it easier to build and maintain a funnel from the lower surface, around the anterior ambitus, to the upper surface. Only a relatively shallow anteal sulcus would be needed, whereas a sand or sandy-mud dweller would have to arch its anterior radioles over the anteal sulcus for protection when burrowing.

The species of *Phymapatagus* from the Barton Beds is in several respects more like *S. purpureus* than *S. raschi*. The Barton species S. (*P.*) *grandituberculatus* has a bilobed fasciole with large tubercles in each lobe, indicating that it made two sanitary drains; it also has a deep anteal sulcus at the ambitus and a test whose profile is closer to that of S. purpureus and which probably indicates a similar life-style. However, the depth of the anteal sulcus, especially at the ambitus, suggests that the echinoid burrowed in the sandy mud of the matrix which fills the fossil tests of specimens from bed A3. The specimen from bed A2 (E 76459) is flattened so that its original shape is not known, but the characters of the test are the same as those from bed A3 and so presumably was its mode of life.

Food

Because the gut contents of echinoids from the Barton Beds were not recognizably preserved, the feeding methods and types of food have to be evaluated by reference to their living relatives. Summaries of the types of food preferred by some kinds of echinoids are given by several authors, but notably by Eichelbaum (1910) and Lawrence (1975, regular echinoids only), who also cited the source works for his summaries. Hyman (1955) also gave an account of the feeding habits of several major groups of echinoids. The data were obtained by the various authors from the examination of the gut contents, faecal remains, or by direct observations of living animals. The faunal list of Burton (1933) contains a considerable number of plants and animals which probably served as food for the fossil echinoids.

Lawrence (1975), Mortensen (1935, 1943), Lewis (1963), included the following types of food in the diets of regular echinoids: bottom material, foraminifera, sponges, coelenterate polyps, hydroids, worms, bryozoans, various mollusc shells, ascidians, balanids, crustaceans, ophiuroids and plant remains, including algae and wood. Some of these echinoids are carnivorous, such as cidarids, which

will capture live animals which are sluggish or moribund (Hyman 1955:553), while other regular echinoids are scavengers. Lewis (1963:361) observed that a species of *Coelopleurus* had a marked preference for a telestid (octocoral). One fossil species - *Ambipleurus? quaylei* - was found in a shell drift of bed A2 in association with complete and comminuted shells, and a small log of carbonized wood. Mortensen (1943:298) recorded a specimen of *Asterechinus elegans* Mortensen as having an intestine "...full of small bits of (apparently) decayed wood...", so perhaps the specimens of *Ambipleurus? quaylei* were feeding upon the wood just before death.

The irregular echinoids of the Barton Beds being all spatangoids, probably fed while buried in the substratum, like their modern counterparts. Food was obtained direct from bottom sediments, including anything suitable which floated down and was gathered by the specialized tube-feet extending from around the mouth. (See Smith 1984, section 3.3.1-3, pages 51 - 55, for further descriptions of feeding in both regular and irregular echinoids). Eichelbaum (1910) examined the gut contents of several irregular echinoids (of which three belonged to the same families as the species from the Barton Beds). He found the following types of food in the diets of irregular echinoids: foraminifera, sponges, coelenterates, spirorbis, serpulids, polychaetes, terebellids, bryozoans, ascidians, young bivalves, pteropods, crustaceans, ostracods, small crabs, echinoderm remains, diatoms and algae. In summary, present day regular echinoids are (relatively) active feeders, hunting over the sea bed for any available food, either animal or plant, with preferences occasionally displayed for a particular food type. Food can be live, or it can be scavenged from dead or moribund material. Modern irregular echinoids feed on anything within the sediment. Generally, echinoids feed on whatever is available for their size and mode of feeding. Fossil echinoids from Barton probably fed like their nearest Recent relatives.

SUMMARY

Nine species of echinoids are herein recognized from the Barton Beds of the type locality. Some of them are known only from fragments of test and radioles, whilst others are more complete and so better known, but none are particularly common (compared with other fauna) and some are very rare.

They are of limited use as direct indicators of environment or depth of water because they can only be compared with their modern relatives and some of these show a considerable range of depth at which they can live. Indirectly, the fossil echinoids can demonstrate current activity by the distribution of their remains, either as fragments or as more complete tests. The habitats of the fossil echinoids can perhaps be suggested by the use of other more reliable indicators of the environment, such as the presence of different kinds of fossil foraminifera.

Further collecting needs to be carried out in the hope that more material may solve existing taxonomic problems.

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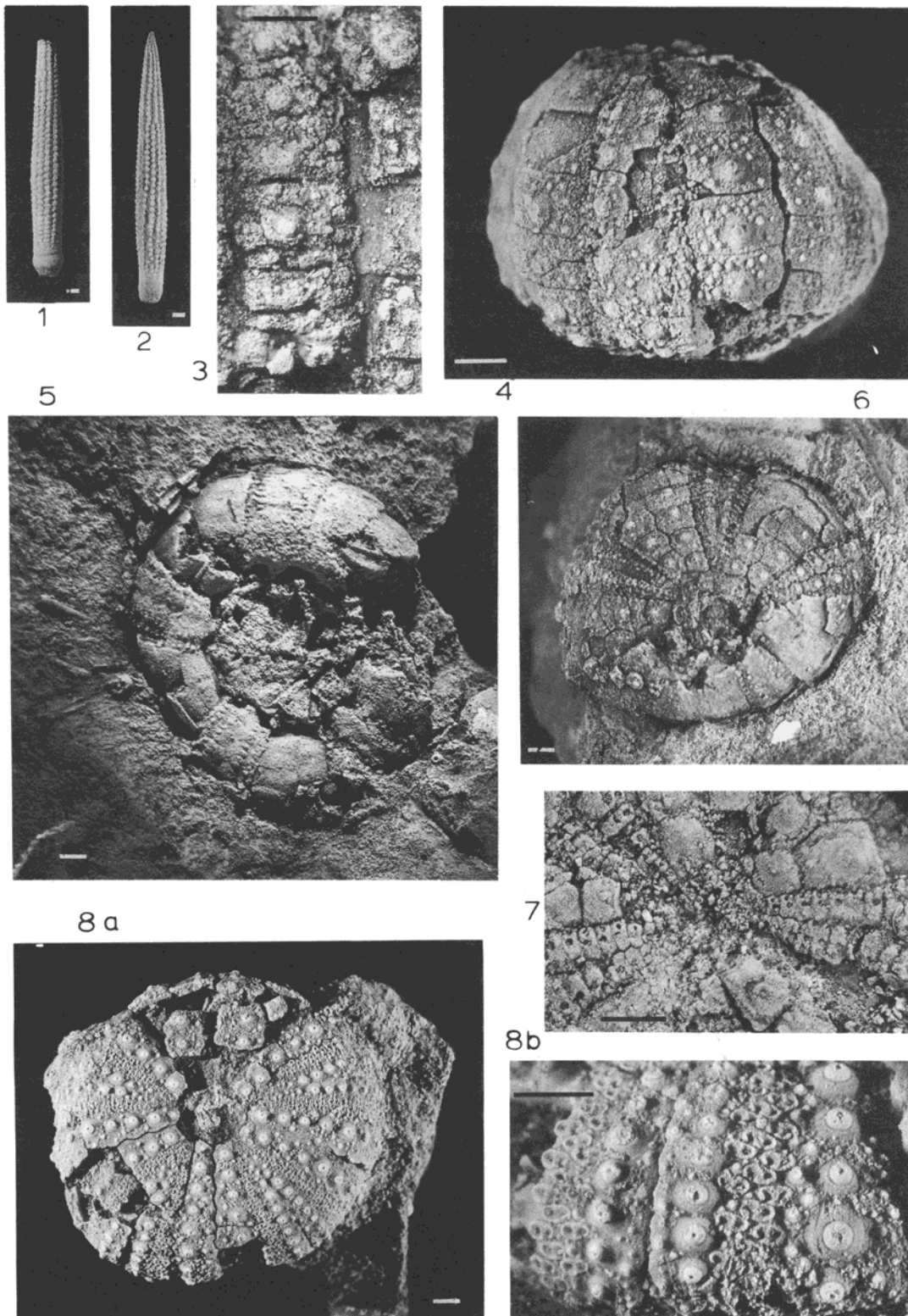
PLATE 1 Fig. 1 Indet. cidarid, lectotype of "*Cidaris*" *websteriana* Forbes, GSM 118221, radiole. Fig. 2 Indet. cidarid, E 17716, showing pointed distal end of radiole. Figs. 3-7 *Echinopedina paucituberculata* sp. nov; fig.3 paratype E 76577 from bed J, showing ambulacral plate-compounding and the heavily weathered surface of the test; fig. 4, the holotype, E 76581, from bed J. Side view; the smooth area on the extreme left of the test has been coated with 'Alvar' to enable the plate details to be seen under a microscope; fig. 5, paratype E76578, from bed J. Oral surface; the specimen is an internal cast and the matrix has several radioles embedded in it; fig. 6, paratype E 79701, from bed J. Apical surface; the test is heavily pyritized; fig 7, paratype E 76425, from bed J and showing plate compounding near the apical disc; the specimen is not pyritized. Fig. 8. *Leiopedina edwardsi* (Forbes); lectotype, GSM 59420, from Bracklesham; a, view of test from the apical surface to compare with *Echinopedina paucituberculata*; b, a close-up view of the compounding to show the three columns of pore-pairs. Compare this with fig. 3 All specimens coated with ammonium chloride sublimate. Scale bars: 1 mm.
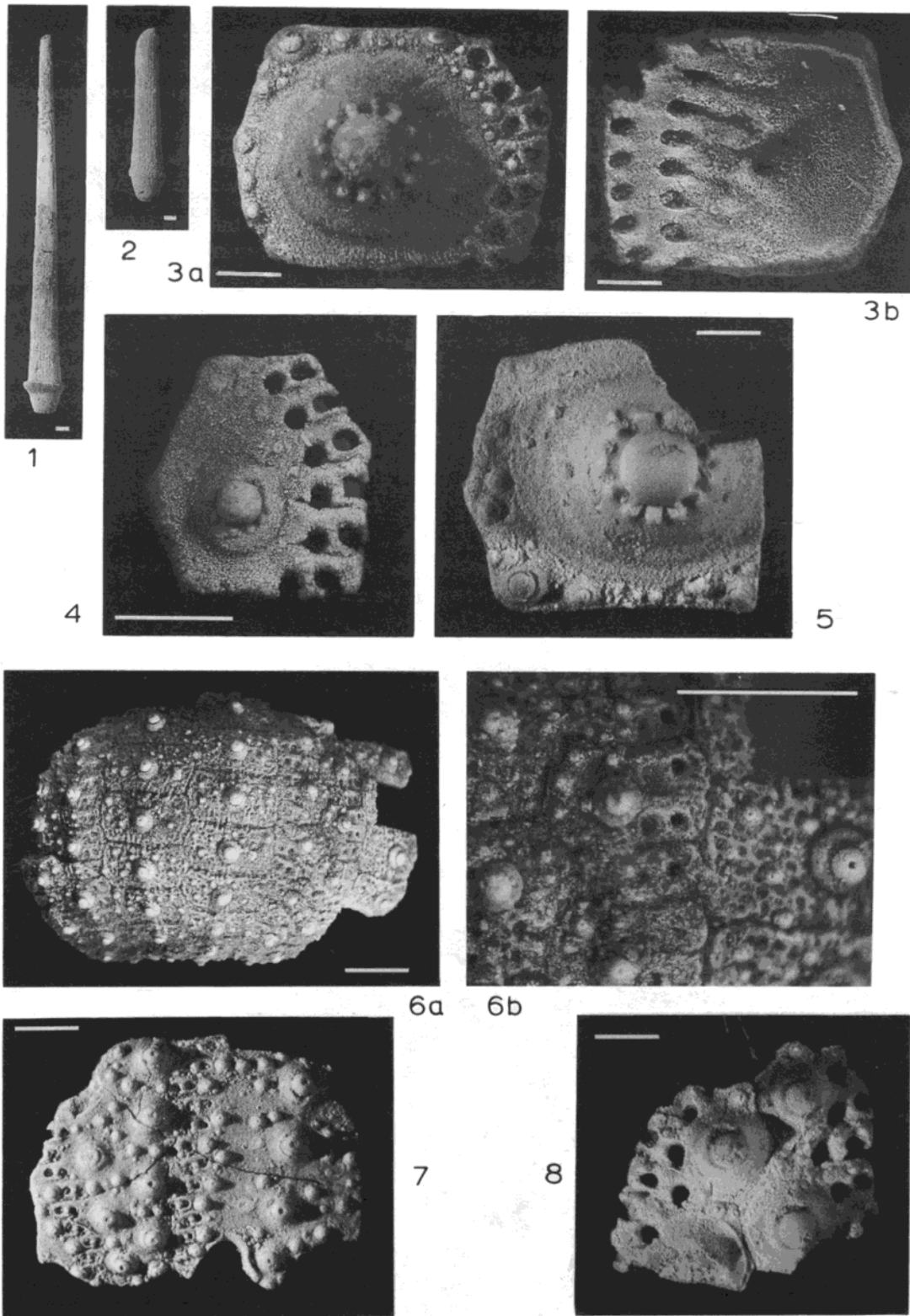
PLATE 2 Figs. 1-5 *Porosoma*? sp; fig.1 E 79781. Radiole; fig 2, holotype of "*Echinus*" *dixonianus*, GSM 118225, radiole; fig. 3a, E 76922, a single ambulacral plate seen from the outside; fig. 3b, the same specimen seen from the inside; fig 4, E 41522, an ambulacral plate from near the apical disc; fig. 5, E 41523, an interambulacral plate.

Figs. 6-7 *Ambipleurus*? *quaylei* sp. nov., fig. 6a, holotype, E 76822, from a shell drift in bed A2. Side view; fig. 6b, enlargement of part of an ambulacrum to show the compounding of the ambulacral plates; fig. 7, E 76923, from the same shell drift in bed A2. Fragment of test from close to the peristome, showing plate compounding and gill slits. The specimen has been hardened with `Alvar' so that some of the detail is slightly obscured when coated with ammonium chloride.

Fig. 8. *Coelopleurus* sp. E 76520, from bed E. Test fragment from near the apical disc.

All specimens coated with ammonium chloride sublimate. Scale bars: 1 mm.
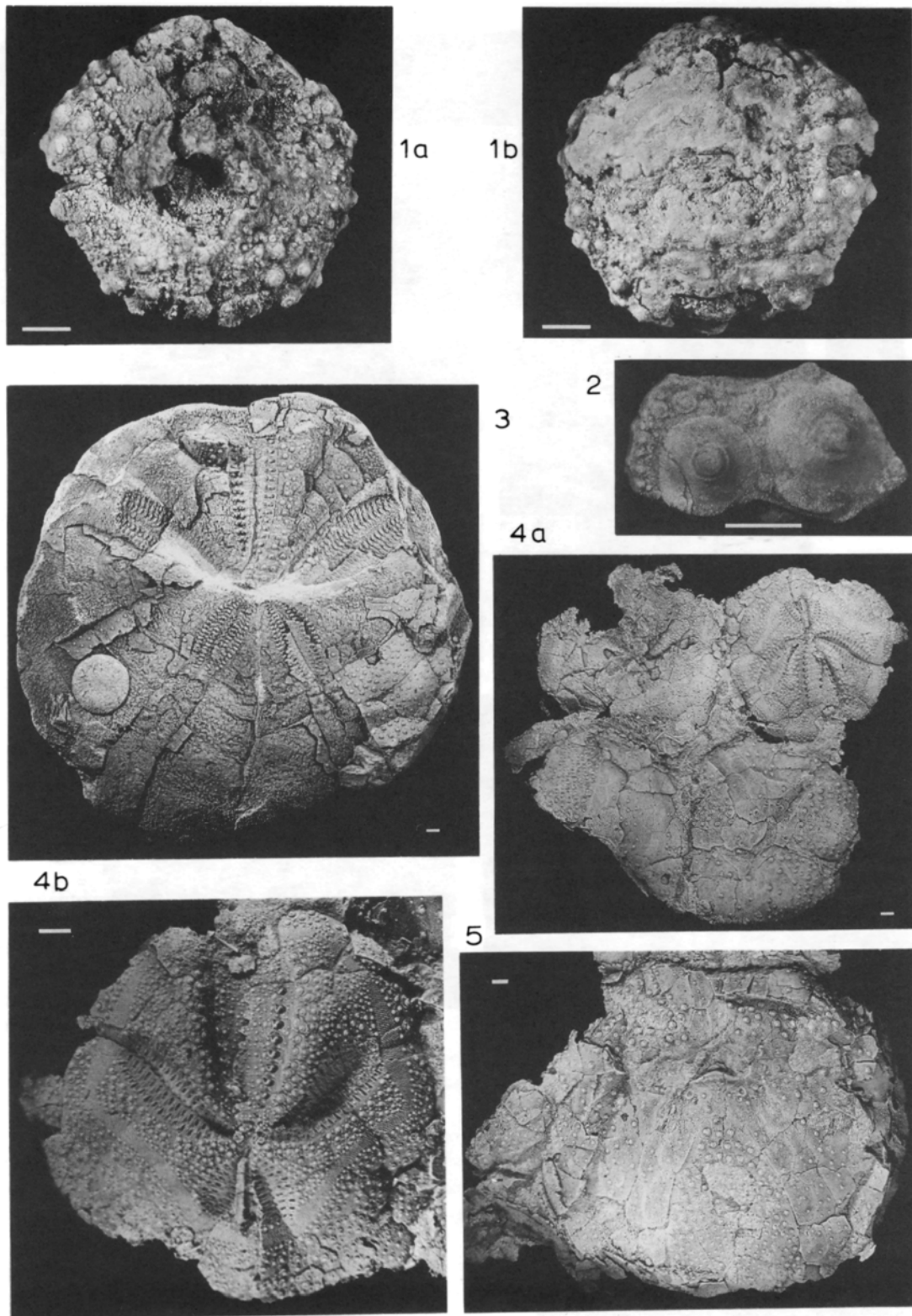
PLATE 3   Figs. 1-2 *Coelopleurus* sp , fig1a E, 76768, from bed E, apical view;   fig1b, oral view; fig 2, E 76522, from bed E, iInterambulacral plate.
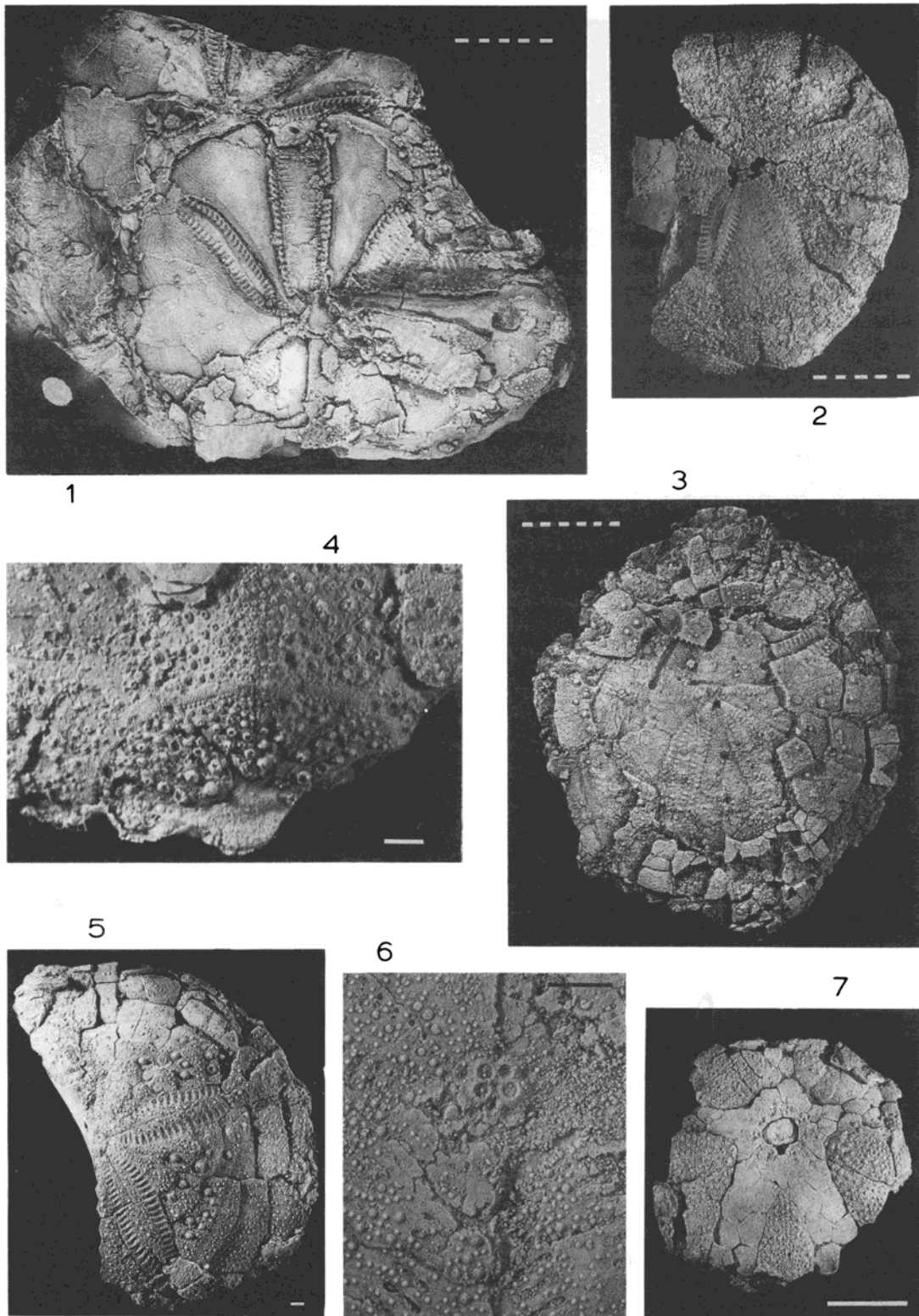
Figs. 3-5 *Schizaster (Hypselaster) branderianus* (Forbes), fig. 3 lectotype, GSM 118226, apical surface; fig4a, E 81679, from bed A3. A small group of specimens extracted from matrix by means of the transfer technique, showing very fine detail and radioles; fig. 4b, a single individual from the above group, showing details of the apical surface, including the well preserved peripetalous fasciole; fig. 5, E 81716, from bed A3, oral surface.

All specimens coated with ammonium chloride sublimate Scale bars: 1 mm
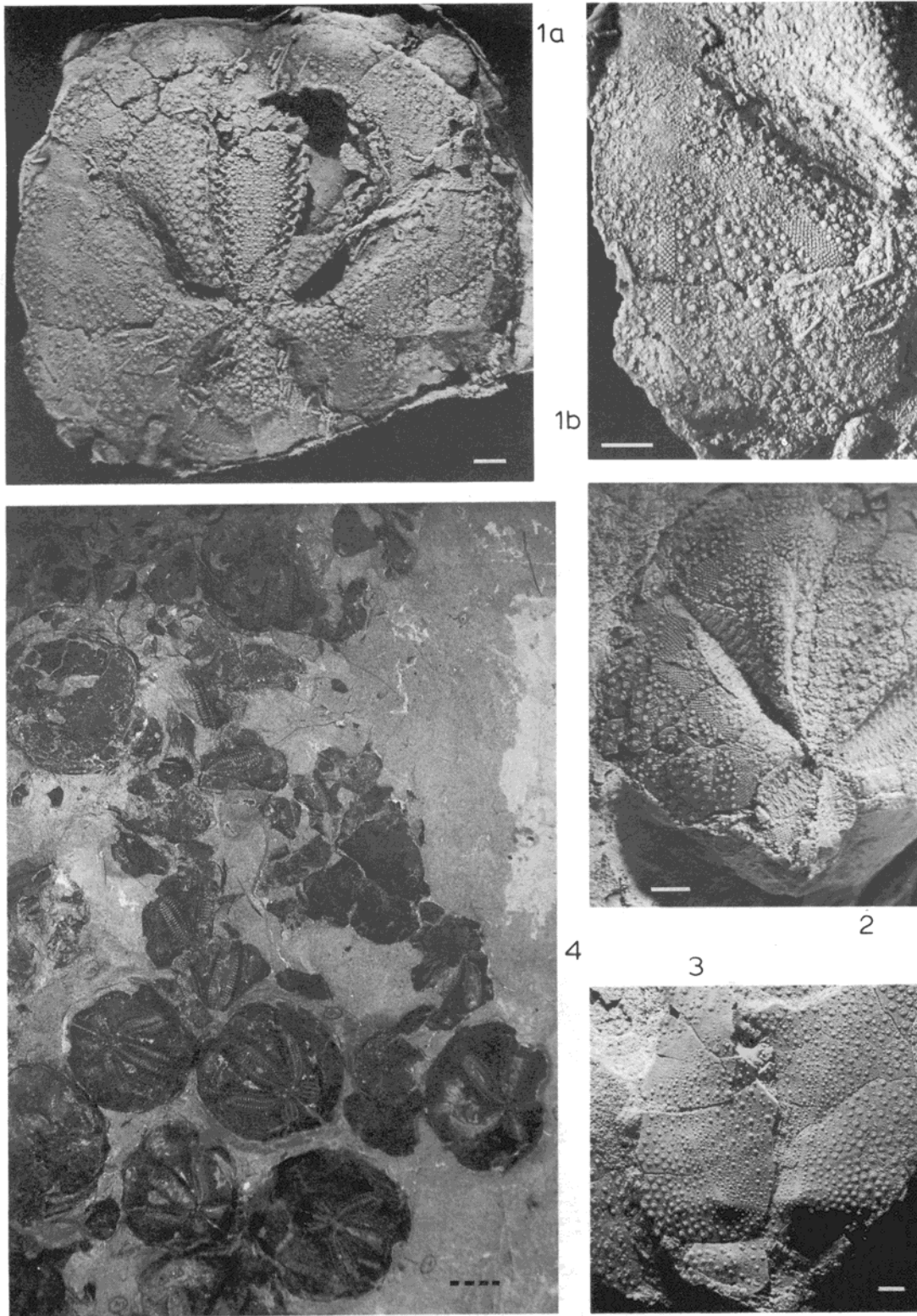
PLATE 4 Figs.1-4 *Schizaster (Hypselaster) branderianus* (Forbes), fig. 1a, E 76598b, from bed A3. Apical surface, showing fine detail, radioles and lateral fasciole; fig. 1b, close-up of the lateral fasciole; fig. 2, E 81673a, from bed A3, a smaller specimen than E 76598b, showing lateral fasciole; fig. 3, E 81684a, from bed A3, anal fasciole; fig. 4, 40373, a block of matrix containing many individuals, all of them internal casts. Specimens are frequently found with this kind of preservation.
All specimens except fig. 4 coated with ammonium chloride sublimate. Continuous scale bars: 1mm; broken scale bar: 10mm.

PLATE 5 Fig. 1 *Schizaster (Hypselaster) branderianus* (Forbes), 33395, the syntypes of *Schizaster durbani* Forbes, from the Barton Beds of Alum Bay, Isle of Wight

Fig. 2-7 *Eupatagus (Eupatagus) hastingiae* Forbes, fig. 2, E 76466, from bed F, apical surface of a test to show a typical mode of preservation; fig. 3, holotype, GSM 118232 Apical view; fig. 4, E 76463, from bed F, a latex rubber cast of an external mould in clay of sub-anal fasciole; fig. 5, E 76515, from bed F, apical surface of a specimen with good preservation; fig. 6, E 76589, from bed F, close-up of apical disc; fig. 7, E 76460, from bed F, oral surface.

All specimens coated with ammonium chloride sublimate. Continous scale bars: 1mm; full length of broken scale bars: 10mm.
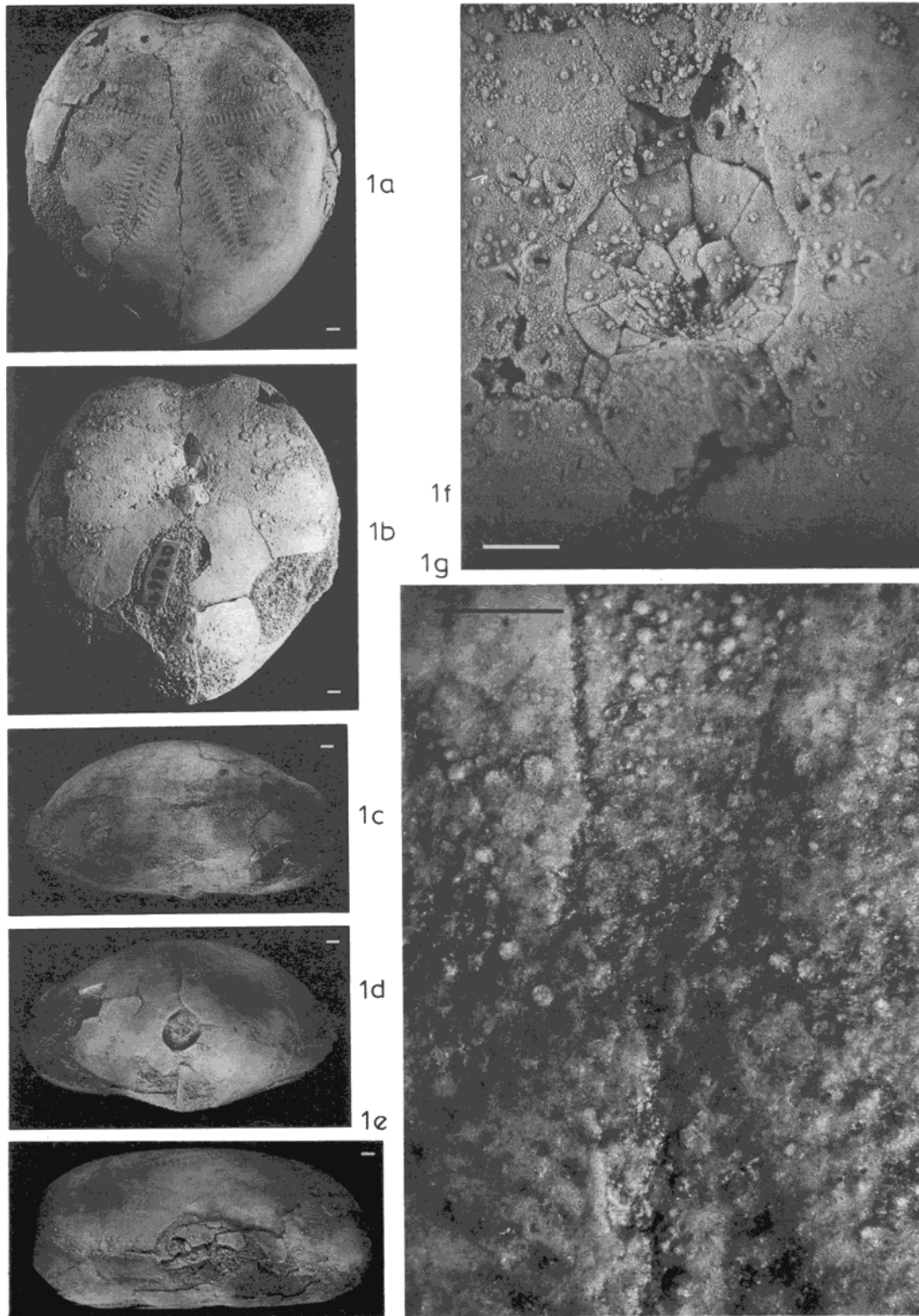
PLATE 6 Fig. 1 *Eupatagus (Eupatagus) excentricus* (Gregory), a, holotype, 49820, apical surface; b, oral surface; c, anterior view; d, pos terior view; e, side view; f, peristomial area, showing buccal plates; g, close-up of apical disc. Specimen coated with ammonium chloride sublimate, except in fig. 1g. Scale bars: 1 mm
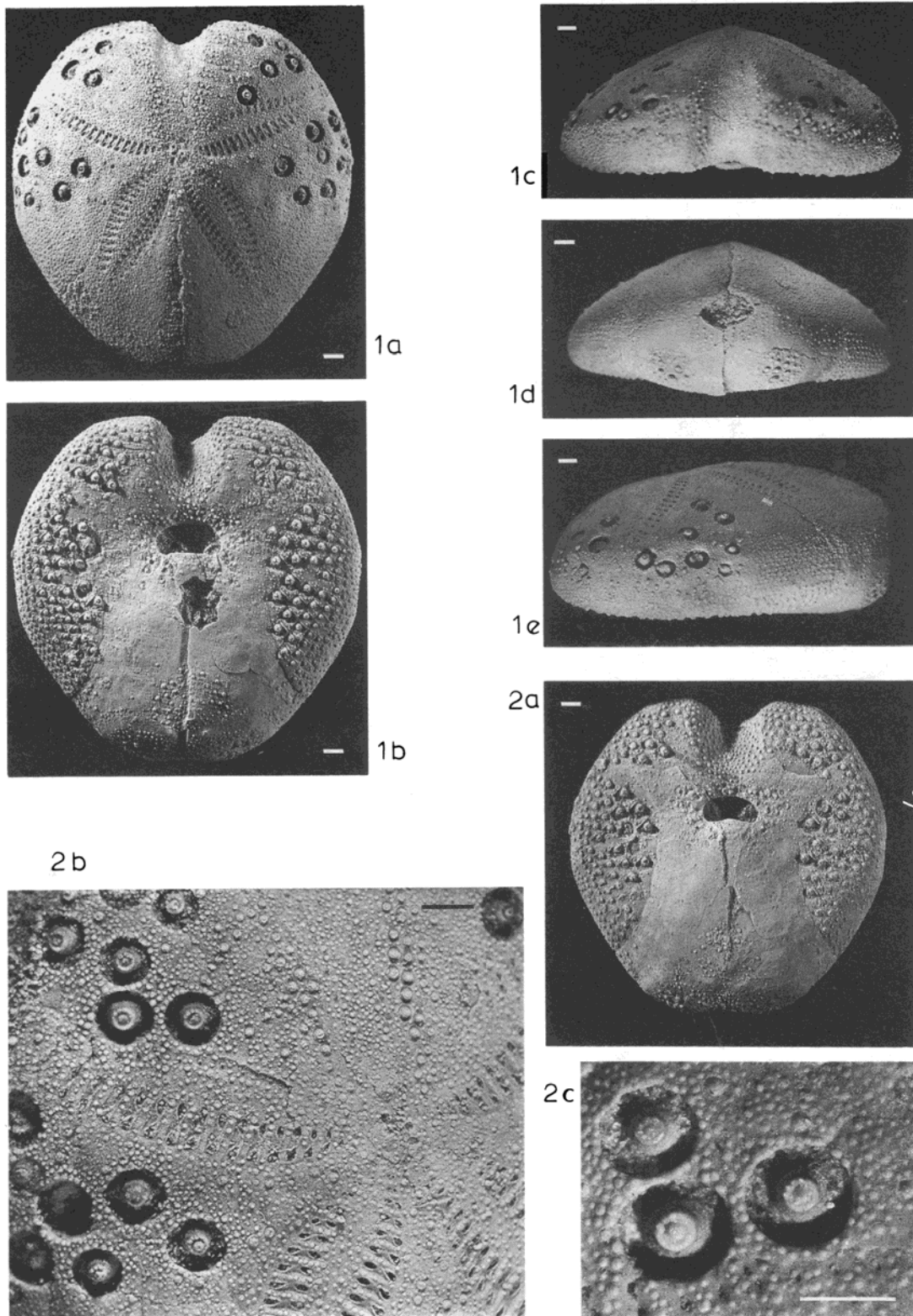
PLATE 7 Figs. 1-2 *Spatangus (Phymapatagus) grandituberculatus* sp. nov., fig. 1a, holotype, E 76821, from bed A3. Apical surface; fig. 1b, oral surface; fig. 1c, anterior view; fig. 1d, posterior view; fig. 1e, side view; fig. 2a, E 37320, from bed A3, a better preserved oral surface than in fig. 1b; fig. 2b, view of ambulacrum IV, showing reduced anterior plates, large inset primary tubercles and apical disc; fig. 2c, close-up of some large, inset tubercles.
Both specimens coated with ammonium chloride sublimate, except in fig. 2c. Scale bars: 1 mm.