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Pithonella ovalis from the early Cenomanian of England

ABSTRACT

The *Mantelliceras mantelli* Zone (early Cenomanian) of the Isle of Wight, southern England, provides the most northerly documented occurrence of *Pithonella ovalis* (Kaufmann). Stereoscan electron micrographs are presented of this abundant but enigmatic planktonic microorganism, and its nature and occurrence are briefly discussed.

INTRODUCTION

Culver Cliff, a promontory on the eastern seaboard of the Isle of Wight, Hampshire, southern England, consists of steeply dipping chalks in a nearly continuous sequence from the earliest Cenomanian to the late Campanian. The lithostratigraphy and a biostratigraphy based on macrofossils were first comprehensively described by Rowe (1908), but these have subsequently been, in part, refined. The Cenomanian, which lies directly upon the Albian Gault and Upper Greensand, has traditionally been considered to comprise a basal "Glaucconitic Marl", the overlying soft, creamy-buff-coloured "Chalk Marl", and finally the "Grey Chalk". This succession has been divided by Kennedy (1969) into 13 "bands", Band 1 being the Glaucconitic Marl and representing the lowest part of the *Mantelliceras mantelli* Zone, while Bands 2 to 11 represent the "Chalk Marl" and comprise the remainder of the *M. mantelli* Zone (early Cenomanian) and much of the *Acanthoceras rhotomagense* Zone (middle Cenomanian).

The material described in the present paper was collected from within the interval of Bands 2 and 3, and may be referred to the *M. mantelli* Zone. On disaggregation, the samples yielded infrequent *Hedbergella brittonensis* Loeblich and Tappan, *Hedbergella portsmouthensis* (Williams-Mitchell) and *Praeglobotruncana stephani* (Gandolfi), which is a typical Cenomanian planktonic foraminiferal assemblage (Bandy, 1967; Loeblich and Tappan, 1961), and an abundant benthonic foraminiferal assemblage which included *Arenobulimina (Columnella) anglica* (Cushman), *Ataxophragmium depressum* (Perner), *Eggerellina* cf. *murchisoni* (d'Orbigny), *Gyroidinoides* cf. *turgidus* (Hagenow), *Hagenowella obesa* (Reuss), *Marssonella oxycona* (Reuss), *Pseudotextulariella cretosa* (Cushman), *Spiroplectammina elongata* (Barnard) and "*Tritaxia*" *pyramidata* (Reuss). This dominantly agglutinated foraminiferal assemblage is also typical of the early Cenomanian of England (Barnard and Banner, 1953). However, thin sections of the rock disclosed that the most abundant organism of a size larger than that of nannofossils was *Pithonella ovalis* (Kaufmann), and that the Chalk Marl was crowded with it (plate 1, figures 1–2). Disaggregated material was coated with gold-palladium and photographed, with the use of the emissive mode of a Cambridge Mark IIA stereoscanning electron microscope at an acceleration voltage of 20 kV. The results are shown on plates 1 and 2.

This organism was first described from thin sections of Alpine Cretaceous limestones, when Kaufmann (in Heer, 1865) drew specimens and named them *Lagena ovalis*. Lorenz (1902) recognised that this generic

assignment could not be maintained and proposed the new monotypic genus *Pithonella* to contain them. Egger (1909) disregarded the priority of Lorenz's genus and placed these organisms in *Orbulinaria* Rhumbler, 1906, as Rhumbler had used that name for other minute, spherical objects found in thin sections of Cretaceous rocks. This allocation can not be correct, not only because of the seniority of *Pithonella* Lorenz, 1902, but also because the type species of *Orbulinaria* is a miliolid congeneric with (and possibly even conspecific with) the type species of *Keramosphaera* Brady, 1882 (see Loeblich and Tappan, 1964, p. 501). The nominal availability, as well as the seniority of *Pithonella* Lorenz was finally established in 1956, when Bonet formally designated *L. ovalis* Kaufmann as its type species.

THE NATURE OF *PITHONELLA OVALIS*

Bignot and Lezard (1964) most usefully summarized the observations that could be made with a light microscope. They photographed both thin sections and entire isolated individuals from the early Turonian of the Paris Basin and compared them with illustrations reproduced from the works of Kaufmann (in Heer, 1865) and others. The Cenomanian material from Culver Cliff confirms and amplifies their observations.

Individuals of *P. ovalis* vary from 55 to 60 microns in length and from 30 to 35 microns in breadth, with a maximum wall thickness in the equatorial section of 10 microns. In thin section (plate 1, figures 1–2, equatorial sections), traces of an original radial crystalline structure can be seen. The wall consists also of several (four or more) distinct lamellae, the innermost being clearest, as not only is it the thickest but also as traces of fibrous structure end at this innermost layer (black arrows, plate 1, figures 1–2); also Bignot and Lezard, 1964, (text-figs. 2, 4; pl. 2, fig. 4). This type of wall structure implies an initial secretion by the cell of a shell no thicker than about 2 microns and of uniform thickness over its entire area. Subsequent deposition of successive layers of fibrous calcium carbonate then built up the thickness of the shell, especially away from the polar regions. In rare instances, the later lamellae are incomplete. An example is shown in plate 1, figure 1 (white arrow), where only the basal layer remains entire, subsequent lamellae on one side of the test, between aperture and aboral pole, either not having been secreted or (which is more likely) having been detached by *post-mortem* damage before sedimentation and lithogenesis. Such "exfoliation" would emphasise the crystalline discontinuities that occur between successive lamellae. The fibrous structure is often wholly or partly obliterated. The crystals were probably originally aragonite but are now wholly or

partly recrystallised to calcite (plate 1, figure 5) in a sequence paralleling that documented in other microfossiliferous limestones (see Banner and Wood, 1964). Secondary crystalline calcite now occurs as characteristic overgrowths from the original shell surface (plate 1, figures 3–6, 8).

The surface of the test was photographed by Bignot and Lezard (1964, pl. 1, figs. 8–9), who interpreted their optical micrographs as showing longitudinal striae. The stereoscan electron micrographs (plate 2) show instead a reticulation, uniformly developed from pole to pole, produced by the intersection of relatively strong and continuous longitudinal ridges with relatively weak and discontinuous transverse ones. The longitudinal ridges are spaced at about 1-micron intervals, the transverse ridges at intervals of about 1.5 microns, producing a reticulate pattern of subrectangular pits about 1.3 microns deep (plate 2, figures 6–8). No perforations have been seen. The ridges are not smooth, but are weakly pustular or crenulate. Where the two sets intersect, individual transverse ridges may terminate, and the individual longitudinal ridges may be offset from their average direct course towards convergence at a pole.

The development of successive layers of shell material on the outside of the initial test lamella indicates that an external, extramural layer of cytoplasm must have been present, at least while additional lamellae were being deposited externally. The inner face of the extramural cytoplasm would have been in intimate contact with the reticulation of the shell surface. In some rotaline foraminifera, directional streaming in an analogous extramural cytoplasmic layer may be directly related to the orientation of test ridges and costae, but no homology is likely with *Pithonella*. In *P. ovalis*, the transverse ridges would be opposed to simple streaming longitudinally toward the aperture, and, in any case, *Pithonella* is unlikely to have been a foraminifer.

The test of *P. ovalis* is imperforate and is not rotaline in character. Wanner (1940) did consider *Pithonella* to be a foraminifer, but placed the genus in the Cadosinidae, a family that, though heterogeneous, was based on *Cadosina* Wanner, 1941, referred to the Tintinnida by Loeblich and Tappan (1964, p. 786), and that included *Calpionella* Lorenz, 1901, belonging also in the Tintinnida, according to Campbell (1954) and Loeblich and Tappan (1968). Although the lorica of Recent tintinnids is organic, in some fossil genera (*Pseudarcella* Spandel, *Remanellina* Tappan and Loeblich, *Tythyocorys* Tappan and Loeblich, *Yvonniellina* Tappan and Loeblich) it appears to have been primarily secreted as radial calcite (Tappan and Loeblich, 1968). These

Tertiary forms, grouped in the Codonellidae by Tappan and Loeblich (1968), were all, as were the calcitic tintinnids recorded by Hermes (1966) from the Silurian, much larger than *Pithonella*, and their wall structures do not agree well with those of that genus. None shows the multilamellar structure of *P. ovalis*, and it is difficult to see how a tintinnid could secrete external layers to its lorica. For this reason above all, the present writer would exclude *Pithonella* from the Tintinnida, although its other characteristics would not be wholly incompatible with such an assignment.

To refer *Pithonella* to an order that possessed cilia or flagellae would seem to be suitable. A planktonic organism with a test as dense and heavy as that preserved in *P. ovalis* would, by analogy with both the Tintinnida and the Coccolithophorida, benefit from the possession of a motile organelle to aid its suspension in the ocean. Otherwise, its systematic position remains uncertain.

THE DISTRIBUTION OF *PITHONELLA OVALIS*

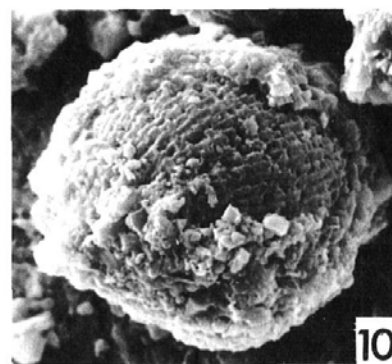
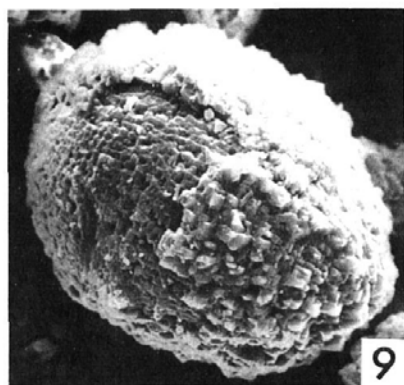
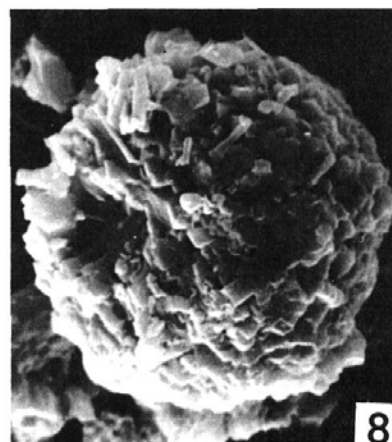
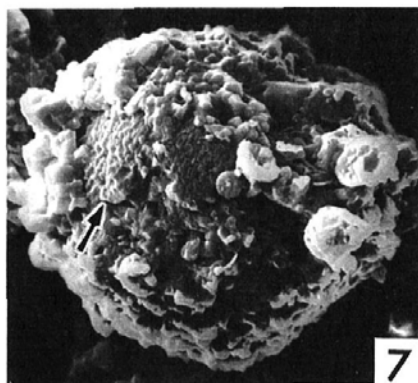
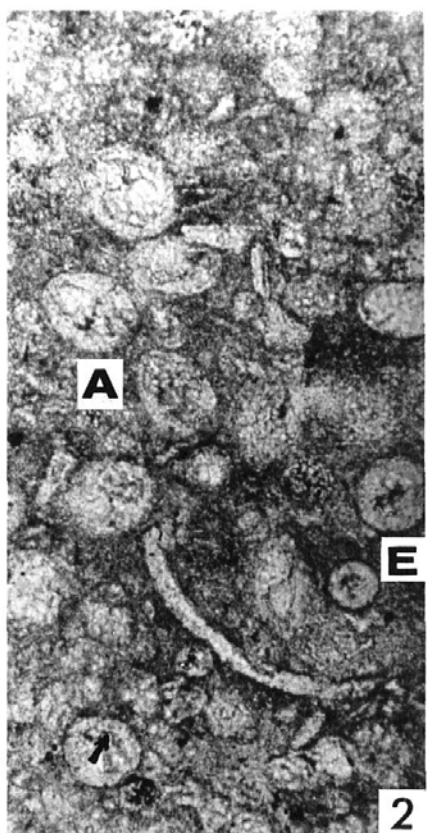
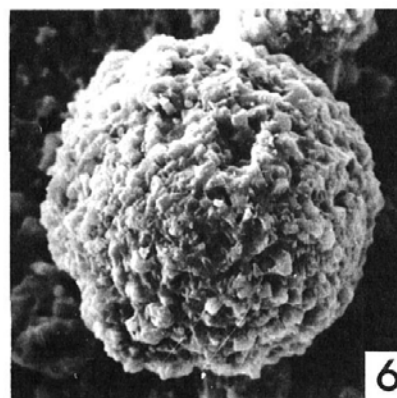
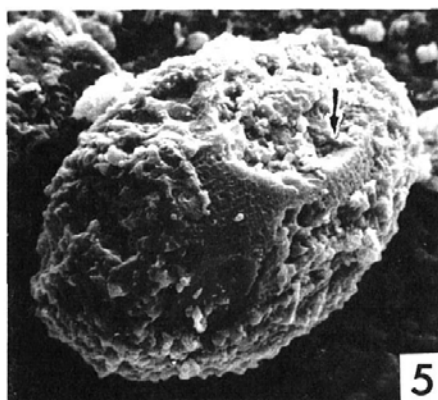
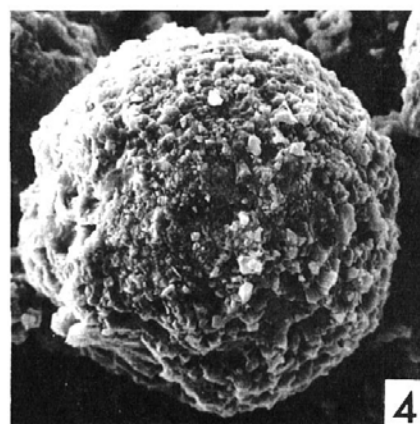
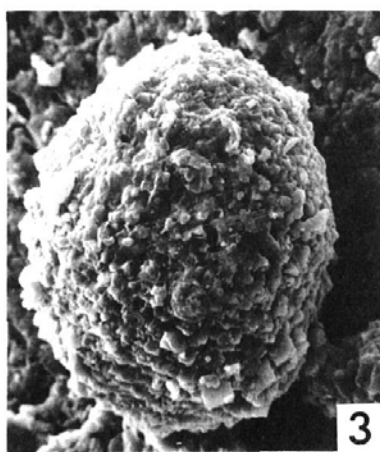
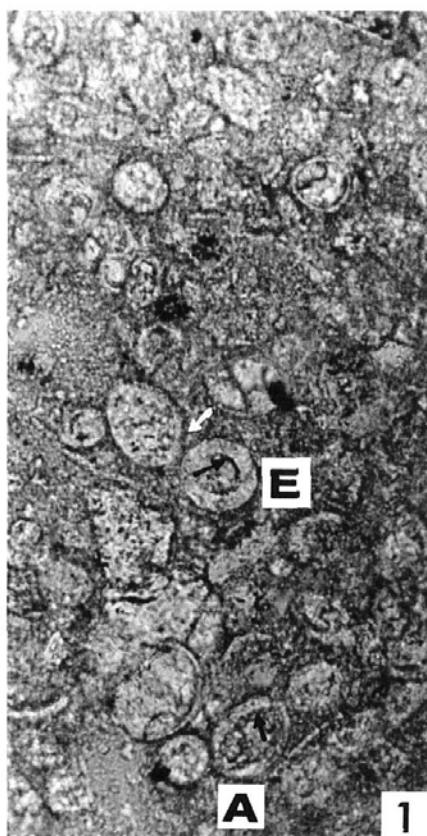
Pithonella ovalis has been recorded only where its remains are conspicuous by their abundance. With the limitation that records are almost wholly confined to bathyal limestones, where dilution of *Pithonella* tests by clasts of similar or greater size has been insignificant, the geographical distribution has been graphically summarised by Colom (1955, text-fig. 3) for the western Mediterranean and Atlantic areas; and other occurrences, from Indonesia to Texas, ranging in age from late Aptian to Santonian and Maestrichtian, were noted by Bignot and Lezard (1964). Since then, records from Israel (Cenomanian, Arkin and Hamaoui, 1967), Italy (Cenomanian, Andri, 1967; Cenomanian-Santonian, Crescenti, 1969) and Cuba (Campanian-Maestrichtian,

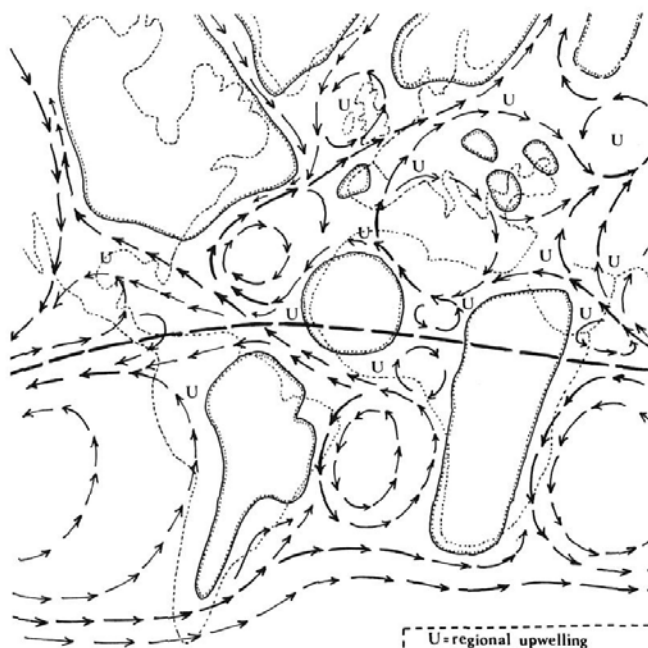
Ayala-Castañares and Seiglie, 1962) have been among those confirming the wide geographical distribution of this species in the Late Cretaceous. The concept of the spreading Atlantic floor (see, for example, Funnell and Smith, 1968) now requires a closer juxtaposition of the western microfossil localities than that assumed by Colom (1955), and his distribution map should be compared with that for "epicontinental" deposits of the mid-Cretaceous for a partly closed Atlantic given by Sutton (1968). The Culver Cliff early Cenomanian record given here provides a documentation for the most northerly known occurrence in either palaeogeography.

Jefferies (1962) has attempted to interpret the environment that existed in southern England during the deposition of the marls and marly chalks of the early Turonian. The lithology of these rocks is not unlike that of the early Cenomanian Chalk Marl of the same area, and the faunas have much in common. With the use of his criteria, during the deposition of the *Pithonella ovalis*-rich Chalk Marl, the bottom water would be deduced to have been at a temperature lower than 10°C. (below the equilibrium temperature of aragonite) and to have allowed slow deposition below depths of "significant" turbulence. This would be consistent with a bathyal sea floor in an area where, as now, drift currents transported plankton from the western boundary current of a subtropical, anticyclonic, mid-oceanic gyre. The inevitability of such a surface circulation, regardless of the relatively reduced size of the Cretaceous North Atlantic, results from the models described by Munk (1950) and Munk and Carrier (1950). Fell (1967) showed such a surface circulation, but for an Atlantic of present dimensions. If the Atlantic were

PLATE 1

- 1-2 Chalk Marl from Isle of Wight, Culver Cliff, *Mantelliceras mantelli* Zone; thin sections in transmitted light, both $\times 240$, showing presence of *Pithonella ovalis* (Kaufmann) in axial (A), equatorial (E), and abundant random sections.
- 3-10 *Pithonella ovalis* (Kaufmann) isolated from same sample as above; stereoscan electron micrographs, emissive mode
 - 3-4, 6, 8, uncleaned specimens, characteristically coated with secondary calcite; 3, axial view, $\times 870$; 4, equatorial view, $\times 840$; 6, equatorial view of much smaller specimen, $\times 2088$; 8, similar specimen, also $\times 2088$, showing radial disposition of the coating calcite crystals.
 - 5, 7, oblique axial views, $\times 870$ and $\times 1085$, respectively, of partly cleaned specimens, fractured areas of the test (arrowed) showing its blocky, non-fibrous, recrystallised calcitic structure and crystalline drusy calcite infilling.
 - 9-10, oblique axial views, $\times 930$ and $\times 1500$, respectively, revealing reticulate *Pithonella* outer surface below the secondary calcite coating.





TEXT-FIGURE 1

Suggested pattern of Late Cretaceous major geostrophic and drift surface currents, indicating probable areas of regional upwelling (and high productivity) due to cyclonic and other divergences. Because of the greater angular velocity of terrestrial rotation, the Coriolis effect would be stronger than that of today, and the sub-polar cyclonic gyres more intense. The equatorial gyres of Africa were, in contrast, probably weak and seasonal, and are depicted as for the northern winter. The heavy dashed line is the Late Cretaceous position of the equator. The fine dashed lines indicate land masses at the end of the Eocene. The solid lines with internal parallel dotted lines indicate Late Cretaceous land masses.

reduced to a size and shape like those suggested by Funnell and Smith (1968) for the Late Cretaceous, and if the cyclonic subpolar gyre (also inevitable in Munk's model) were to be introduced into a modification of

Fell's palaeoceanology, then it will be seen that the area now occupied by northwestern Europe would be dominated by a cyclonic gyre and consequent regional upwelling. Therefore, it is probable that the *Pithonella ovalis* populations would occur in abundance in such an area of nutrient-rich surface waters and high primary productivity, which would be supplied with planktonic populations expatriated by Tethyan equatorial and western boundary currents to this northerly area.

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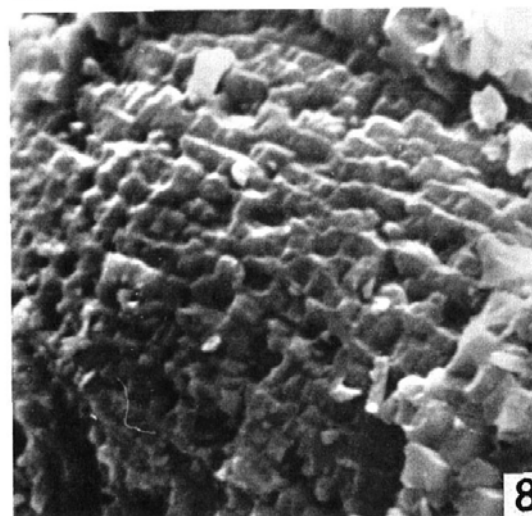
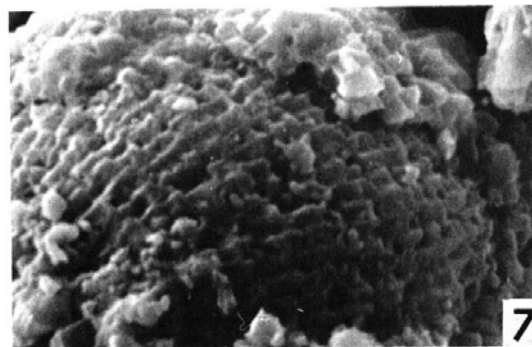
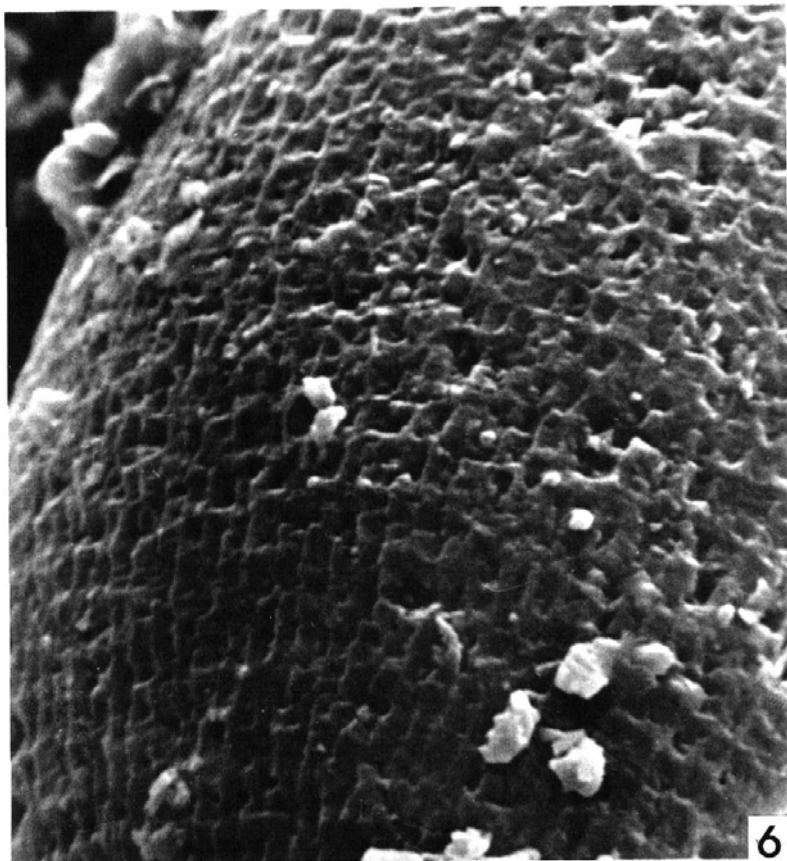
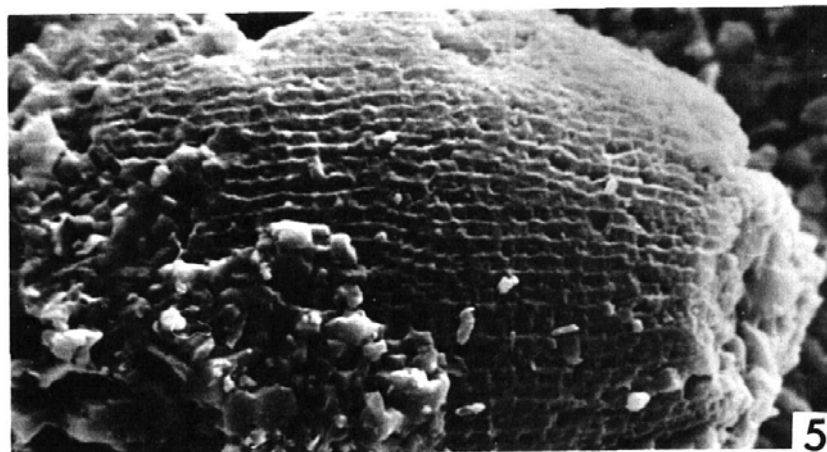
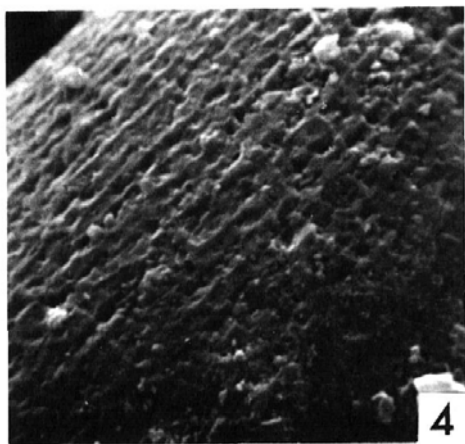
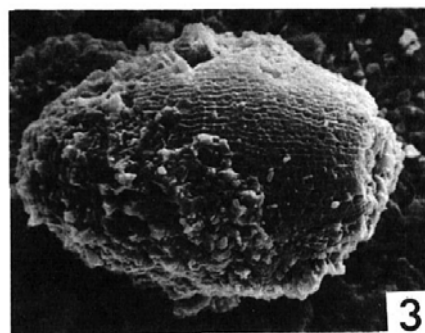
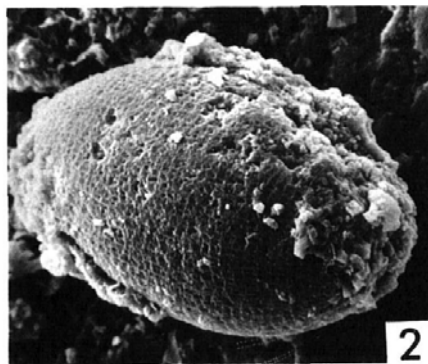
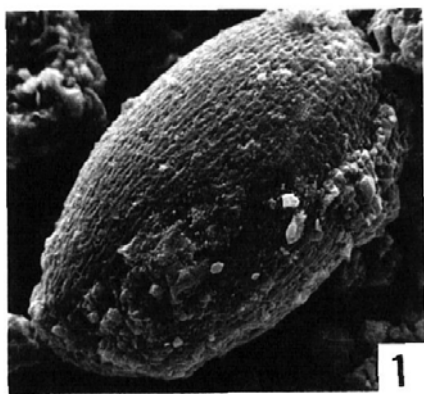
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PLATE 2

Pithonella ovalis (Kaufmann) from Isle of Wight, Culver Cliff, *Mantelliceras mantelli* Zone; stereoscan electron micrographs, emissive mode

1–3 Entire specimens, axial views.
1, $\times 1015$; 2, $\times 850$; 3, $\times 870$.

4–8 Details of the reticulate surface topography of the tests.
4, enlarged portion of figure 1, $\times 2785$; 5, enlarged portion of figure 3, apertural end, $\times 2320$; 6, enlarged portion of figure 2, $\times 4000$; 7, enlarged portion of plate 1, figure 10, $\times 860$; 8, enlarged portion of plate 1, figure 9, $\times 3000$.



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