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PIOTR MIERZEJEWSKI

PTEROBRANCHITES KOZŁOWSKI, 1967 — AN ABERRANT GRAPTOLITE?

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The periderm of Ordovician *Pterobranchites antiquus* Kozłowski, 1967 has been examined with SEM. Four components have been recognized within the thecal wall: outer lining, cortex, fusellum and inner lining. The cortex material is composed of thick, straight, unbranched fibrils arranged in several layers as in cortical layer of the graptolite periderm. *P. antiquus*, previously referred to cephalodiscid pterobranchs, is identified as an aberrant graptolite of uncertain taxonomic position.

Key words: graptolites, pterobranchs, ultrastructure, Ordovician, Poland.

Piotr Mierzejewski, Zakład Paleobiologii, Polska Akademia Nauk, ul. Newelska 6, 01-447 Warszawa, Poland. *Received: November, 1983.*

INTRODUCTION

Pre-Cenozoic cephalodiscid pterobranchs are known only from the Ordovician deposits of Poland. The first fossil cephalodiscid was described by Kozłowski (1949) from the Upper Tremadocian chalcedonites of Wysoczki (Holy Cross Mts.). This form, named *Eocephalodiscus polonicus* Kozłowski, is included to the extinct monotypic family Eocephalodiscidae (Kozłowski 1949, Bulman 1970). The second fossil form, *Pterobranchites antiquus* Kozłowski, was described from the Middle Ordovician of Krzyże 4 borehole in the north-eastern Poland (Kozłowski 1967). *Pterobranchites* has been assigned by Bulman (1970) to the living family Cephalodiscidae.

The primary aim of my work was to study the ultrastructure of the *Pterobranchites* periderm as well as to clarify the systematic position of this fossil. Using EM methods for the verification of *Pterobranchites* systematic position was fully justified because of sharp differences between skeletal tissues of graptolites and pterobranchs at the submicroscopic level (see Urbanek 1976).

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MATERIAL AND METHODS

The specimens studied and illustrated in the present paper were etched from bore core samples of the deep boring named Krzyże 4 (north-eastern Poland, region of Białowieża) from a depth 473 m (type locality). The stratigraphic division of Ordovician deposits from this boring was discussed by a few authors (e.g. Tomczykowa 1964, Bednarczyk 1966), and the type horizon of *Pterobranchites antiquus* Kozłowski was estimated as Middle Ordovician (Kozłowski 1967). The type horizon was determined more precisely on the basis of conodonts by Dr. Jerzy Dzik (oral information) as Llandeilo.

All specimen of *P. antiquus* found up to now are tiny fragments originated presumably from the single colony (Kozłowski 1967). They were found associated with the rich assemblage of various organic microfossils. Unsatisfactorily, these microfossils were almost completly unidentified up to now. Only Kozłowski (1967) mentioned the presence of graptolites *Bulmanicrusta latialata* Kozłowski and *Glyptograptus* sp., Górka (1969) recognized plant microfossil *Tasmanites huronensis* (Dawson) and Mierzejewski (in press) signalized hydroids *Rhabdohydra tridens* Kozłowski.

All electron micrographs were taken with the Coates and Welter scanning electron microscope.

RESULTS

Detailed morphological description, based on the material from the only locality hitherto recorded, was given by Kozłowski (1967). In supplementing the description, it should be noted that fuselli may vary from 8 to 35 μm in width (9.4—18 μm according to Kozłowski).

SEM studies showed that the wall of coenecium, 10—16 μm thick, is built of a periderm, in which the following layers may be traced: (1) outer lining, (2) cortex, (3) fusellum (i.e. fusellar layer) and (4) inner lining. The cortex and the outer lining are best developed here, whilst fusellum is usually underdeveloped. The inner lining may be sometimes missing.

1. Outer lining represents a layer 4.1—5.3 μm thick (pl. 20: 1—2, pl. 21; pl. 23). It is built of a system of fine fibrils. The arrangement of fibrils is relatively difficult to trace but it seems irregular in some pictures (pl. 23: 3) and perpendicular to the periderm surface in transversal fractures (pl. 23: 5). Transversally fractured periderm also display fairly clear lamination of the outer lining (pl. 21: 2). The outer surface of the lining is smooth (pl. 23: 1), except of occasional foreign bodies or perforations

(pl. 23: 4). Outer lining was covered with a thin membrane, small patches of which may be locally noted (pl. 23: 2).

2. Cortex is the best developed part of the periderm layers (pl. 20: 1—3, pl. 21, pl. 22: 1—3), varying from 5.7 to 8.0 μm in thickness. It is built of coarse, long fibrils arranged in over a dozen layers. Fibrils are subparallel within a given layer but those of adjoining layers are set oblique to one another (pl. 22: 2—3). The diameter of individual fibrils is markedly varying (0.11 to 0.41 μm), often even within a single fibril. It should be also noted that the fibrils display some periodicity, reflected by fairly irregularly distributed constrictions about (0.10 to 0.38 μm) (pl. 22: 4).

3. Fusellum is the most underdeveloped layer of the periderm, merely up to 0.4 μm thick (pl. 20: 1—3, pl. 21: 1), and is sometimes represented by irregular patches (pl. 22: 1). It is easy to identify thanks to sharp boundaries of fusell. Top parts (heads) of the latter are best preserved here. Inner surface of fusellar layer displays a lumpy character. The SEM studies failed to reveal details of ultrastructure of fuselli, except for some folding of the pellicle (pl. 21: 2).

4. Inner lining is sometimes fairly thick (up to 1.7 μm), clearly differing from the remaining layers of the periderm (pl. 20: 1—3, pl. 21: 1, pl. 22: 2), but it may be sometimes missing. It appears structureless, at least in SEM micrographs, and undoubtedly different in ultrastructure from both the cortex and the outer lining.

REMARKS

The data on ultrastructure of periderm in *Pterobranchites* raise serious doubts with reference to affiliation of that form to cephalodiscid pterobranchs. Periderm of *Pterobranchites* markedly differs in structure from that of modern cephalodiscids in number of layers and character of material. The comparison, given below, is based on results of electron microscope studies on periderm of *Cephalodiscus* (Urbanek 1976, Andres 1980, and unpublished observations of A. Urbanek, P. N. Dilly and P. Mierzejewski).

In *Cephalodiscus*, wall of zooidal tube is mainly built of fusellar layer, on which secondary layers are secreted. Both secondary layers, i.e. outer and inner, are built in the same way, of complexes of densely packed membranes. Straight, long fibrils built of the hitherto unidentified matter occur between individual membranes and in the fuselli. The fibrils are randomly distributed in all the three elements of the periderm.

The fusellar layer is the only fully comparable element of *Cephalodiscus* and *Pterobranchites*, despite of the fact that details of an ultrastructure are unknown in the latter. The periderm layers adjoining fusellum from both sides in *Pterobranchites* differ in ultrastructure from one another as well as secondary layers in *Cephalodiscus*.

The periderm of *Pterobranchites* appears much more similar to that of graptolites, especially those of the genus *Mastigograptus*. The periderm of the latter was studied in detail by Urbanek and Towe (1974). It is characterized by: (1) weak or, sometimes, even rudimentary development of the fusellar layer, (2) the presence of very well developed multilayer cortex, and (3) the presence of structureless inner lining, strewing fusellar layer from the inside. Cortex of *Mastigograptus*, similarly as the typical cortex of other graptolites, is built of several layers of straight, long fibrils 0.15 μm in diameter and arranged parallel to one another within a given layer and transversally in relation to those of the adjoining layer.

I regard the similarity in ultrastructure of periderm of *Pterobranchites* and *Mastigograptus* as simply striking. We may speak about a full analogy of the periderm of the latter and three inner layers in the periderm of the former. The similarity is further supported by an irregular development of fuselli in both forms (see Andres 1977: fig. 11 and Kozłowski 1967: fig. 12).

The periderm of *Mastigograptus* differs from that of *Pterobranchites* mainly in the lack of outer lining. However, I think that an equivalent of that layer may be found in other graptolites, especially in *Orthograptus gracilis* (Roemer). Urbanek and Mierzejewska (1978) recorded a layer built of a different tissue, called as a taeniocortex by them, at surface of the cortex of the dependent type according to the classification of Urbanek (1976) in the mentioned above graptolite. In comparison with the cortex with the normal structure, the taeniocortex is mainly built of a reticular material which resembles a fusellar one. Taking into account the differences in images obtained with the use of SEM and TEM methods, there may be noted some similarity in the ultrastructure of the outer lining of *Pterobranchites* and the taeniocortex of *Orthograptus gracilis*. The latter mainly differs from the former in the fact that it is secreted in the form of "bandages". Nevertheless, the outer lining of *Pterobranchites* displays some lamination which somewhat resembles boundaries between individual "bandages" of taeniocortex as seen in cross section (comp. pl. 21: 4 and Urbanek and Mierzejewska 1978: pl. 35). However, it is very important for this comparison that Crowther (1981) did not support the Urbanek and Mierzejewska's concept of the taeniocortex.

The results of the above comparisons make possible an attempt to correlate the components of the periderm in *Pterobranchites*, *Mastigograptus* and *Orthograptus* (fig. 1). This correlation should be treated as a tentative, requiring to be verified when results of TEM on the periderm of *Pterobranchites* are available. The studies should make it possible to state whether or not the similarities in the structure of the periderm in *Pterobranchites* and graptolites are homologous in character. The systematic position of *Pterobranchites* still remains disputable. On the one hand, all the features of morphological structure of its skeleton remains easily fall within the limits of variability of the Cephalodiscidae and on the other — the ultrastructure of periderm appears uncomparably closer to that of graptolites than pterobranchs. Therefore, one may even try to interpret *Pterobranchites* as an intermediate form between cephalodiscids and graptolites, at least from the point of view of the morphological and

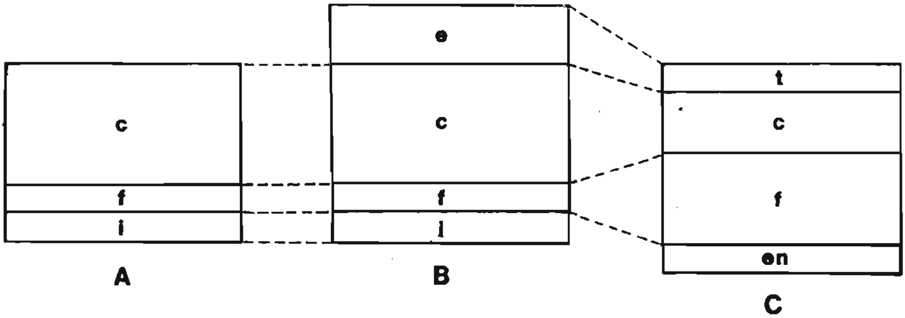

Fig. 1. Diagram to compare the structure of the periderm in *A Mastigograptus* sp. (according to Urbanek and Towe 1974), *B Pterobranchites antiquus* Kozłowski and *C Orthograptus gracilis* Roemer (according to Urbanek and Mierzejewska 1978). Abbreviations: *c* cortex, *e* outer lining, *f* fusellum, *en* endocortex, *i* inner lining.

histological structure of the skeleton. It is worth to note here that the skeleton of *Pterobranchites* is somewhat similar in morphology to rhabdosomes of some graptolites of the order Camaroidea (Kozłowski 1967). This similarity is connected with differentiation of coenecium of the former into tubes and vesicles which resemble necks and camarae of the autothecae of the Camaroidea. Therefore, in analysing systematic position of *Pterobranchites* it should be noted that it may represent:

(1) an unusual representative of the Pterobranchia, with some features of graptolites in the periderm ultrastructure, or

(2) a graptolite displaying and aberrant morphology of the rhabdosome.

Because there is a distinct difference between the pterobranch and graptolite periderm ultrastructure (Urbanek 1976), one may claim that *Pterobranchites* was a genuine graptolite. In may opinion, *Pterobranchites* represents an unknown group (family?) of aberrant graptolites of post--crustoid structural stage (see Urbanek and Mierzejewski 1984: 90).

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PTEROBRANCHITES KOZŁOWSKI, 1967 — ABERRANTNY GRAPTOLIT?

Streszczenie

Pterobranchites antiquus Kozłowski, 1967 był uważany dotąd za jednego z dwóch paleozoicznych przedstawicieli Cephalodiscida (Pterobranchia) (Kozłowski 1967, Bulman 1970). Badania elektronowo-mikroskopowe wykazały jednak, że periderma *P. antiquus* różni się zasadniczo od peridermy Cephalodiscida. Zbudowana jest ona z czterech warstw: powłoki zewnętrznej, korteksu, warstwy fuzellarnej i powłoki wewnętrznej. Najsilniej wykształcony jest korteks i powłoka zewnętrzna, najsłabiej warstwa fusellarna. Powłoki wewnętrznej niekiedy brakuje. Korteks zbudowany jest z grubych, długich włókien, leżących w kilkunastu warstwach. Włókna w każdej warstwie leżą w przybliżeniu równolegle do siebie, w stosunku zaś do włókien warstw sąsiednich, ukośnie. Obserwuje się wyraźną periodyzację włókien. Tak zbudowana tkanka kortykalna właściwa jest jedynie graptolitom, nie występuje nato-

miast u pióroskrzelnych (Urbanek 1976). Przeprowadzono homologizację warstw peridermy *P. antiquus* z warstwami peridermy *Mastigograptus* sp. i *Orthograptus gracilis* (Roemer). Wyrażono pogląd, że *Pterobranchites* był aberrantnym graptolitem reprezentującym post-krustoidowe stadium strukturalne.

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EXPLANATIONS OF THE PLATES 20—23

All micrographs taken with a Coates and Welter field emission electron microscope. Abbreviations: *c* cortex, *e* outer lining, *f* fusellum, *i* inner lining, *m* membrane.

Plate 20

Pterobranchites antiquus Kozłowski, 1967

1—3. Fragments of the rhabdosome, ×400, ×675, ×675.

Plate 21

Pterobranchites antiquus Kozłowski, 1967

1. Components of the periderm, ×2250.
2. Details of three periderm components, ×7300.

Plate 22

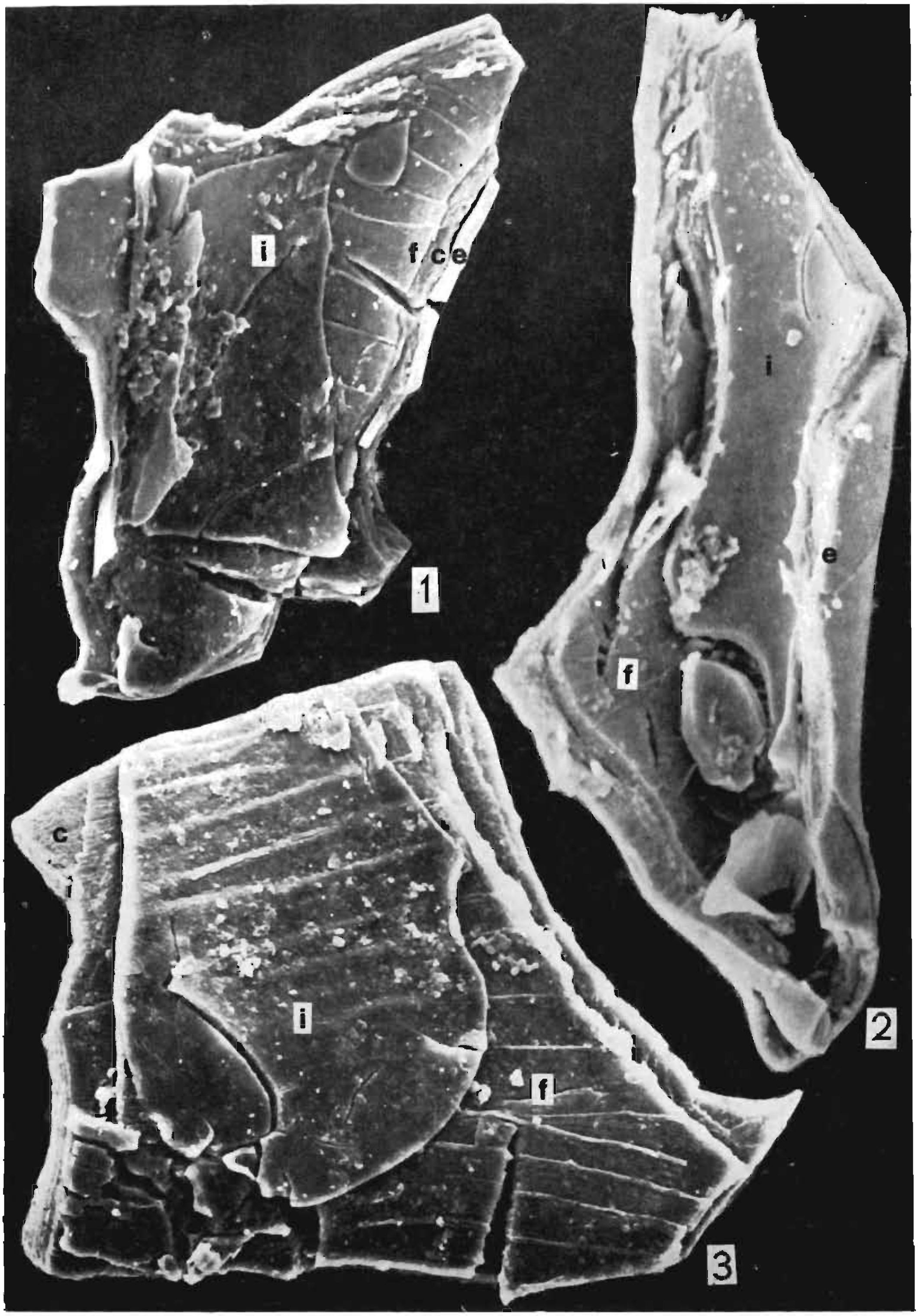
Pterobranchites antiquus Kozłowski, 1967

1. Inner surface of the periderm fragment, ×2000.
2. Layering of the cortex, ×4500.
3. Details of the cortex layering, ×12400.
4. Morphology of the cortex fibrils, ×17000.

Plate 23

Pterobranchites antiquus Kozłowski, 1967

1. Outer surface of the periderm, ×1820.
2. Remnants of the membrane covering the outer lining, ×10000.
3. Details of the outer lining fibrils, ×14000.
4. Circular perforations in the periderm, ×12000.
5. Transversally fractured outer lining, ×9700.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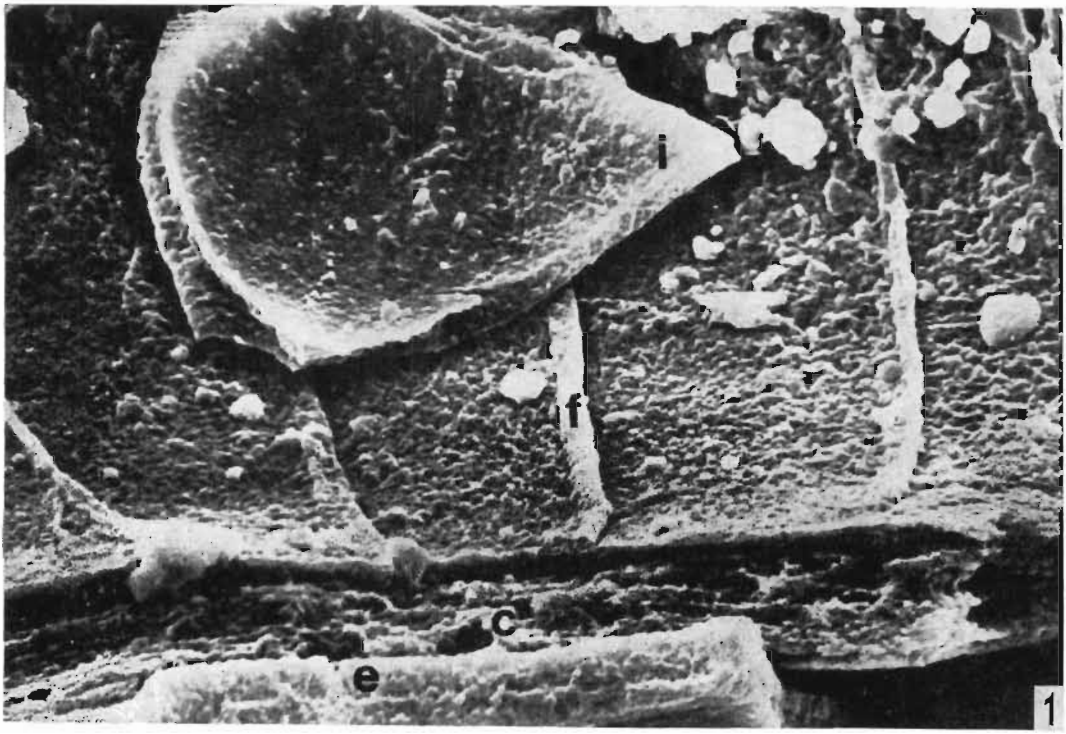

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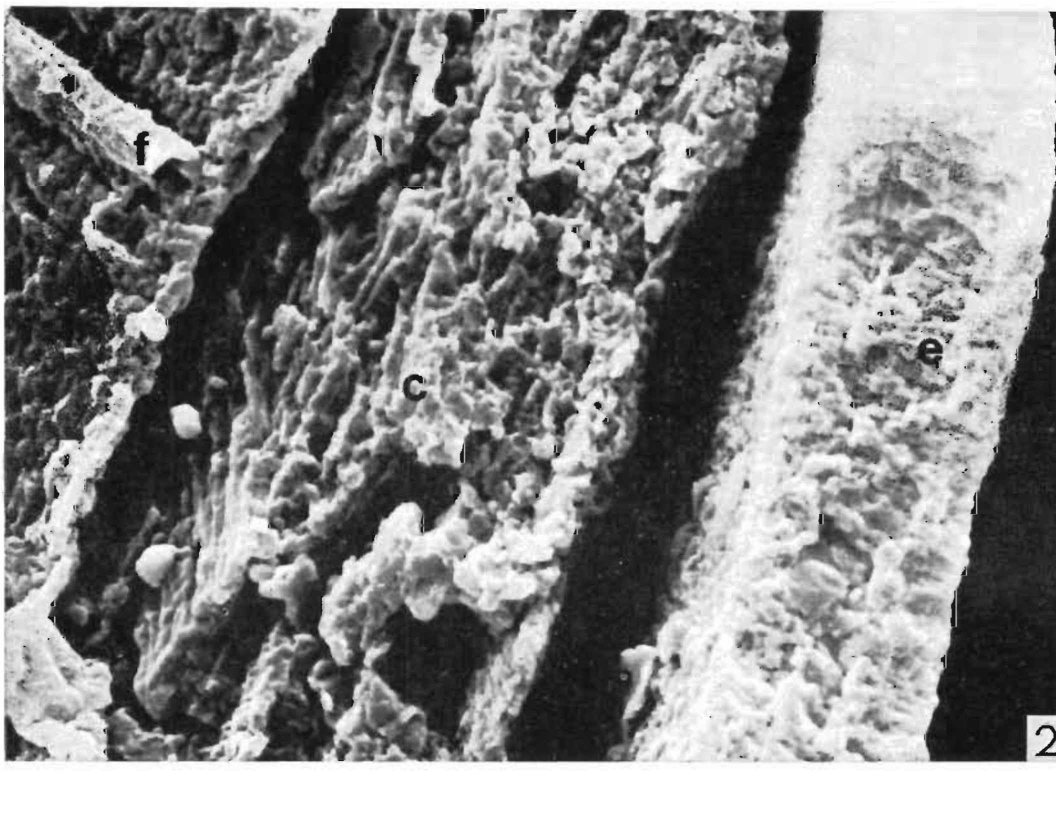

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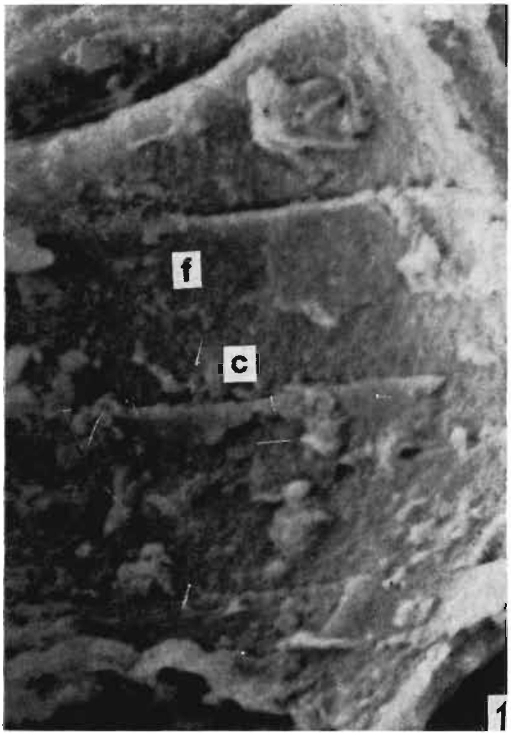
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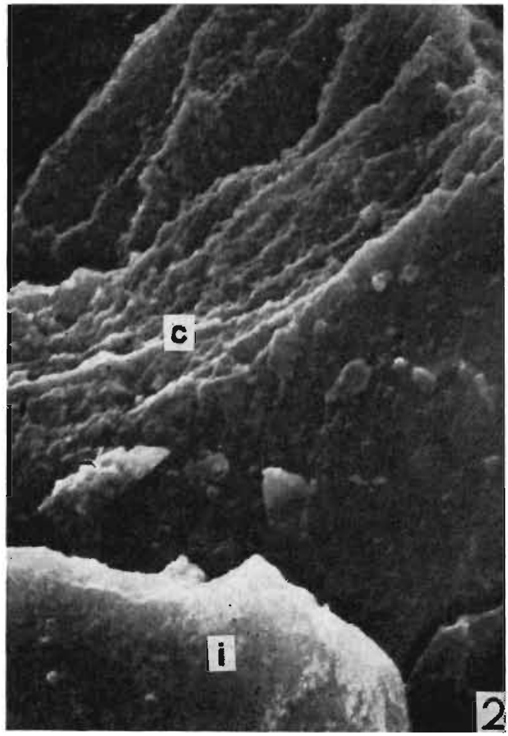
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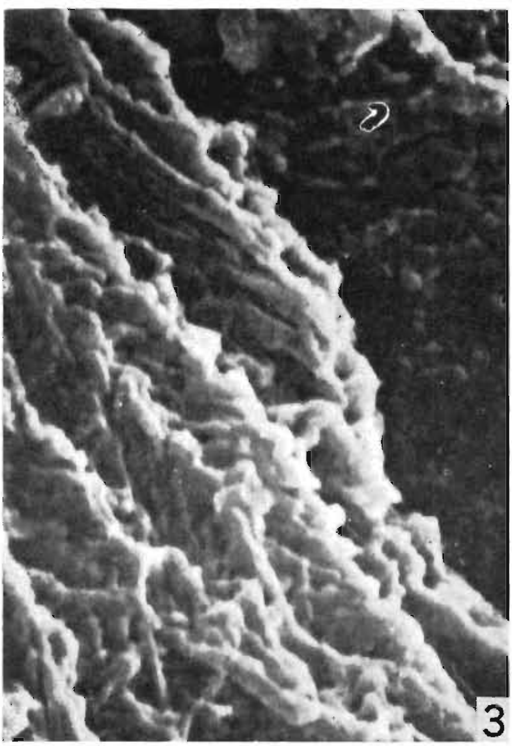
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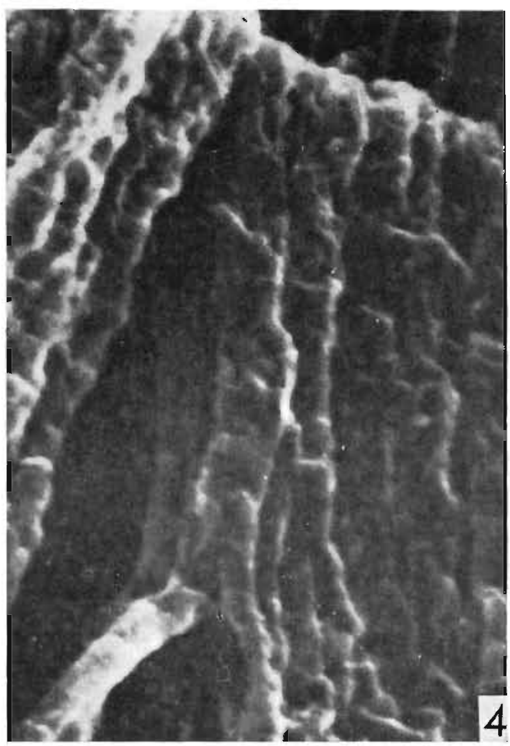
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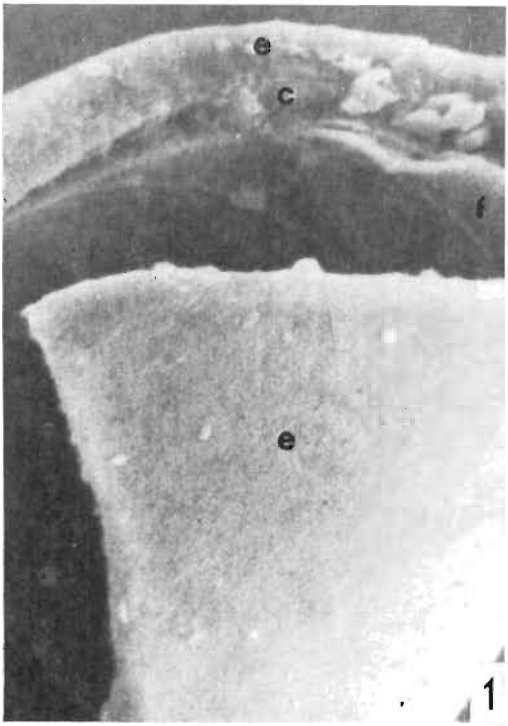
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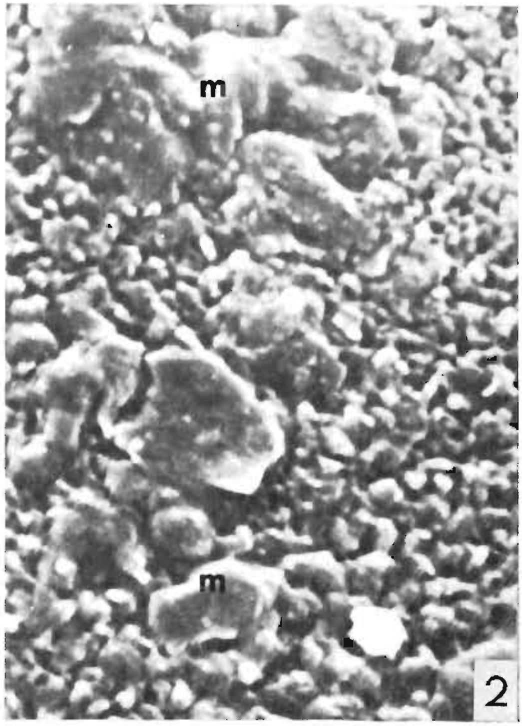
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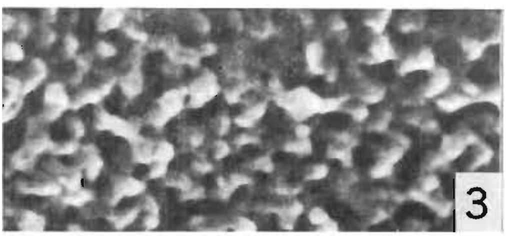
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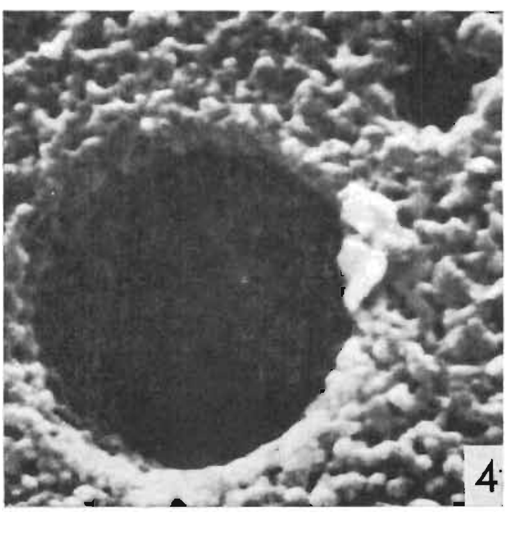
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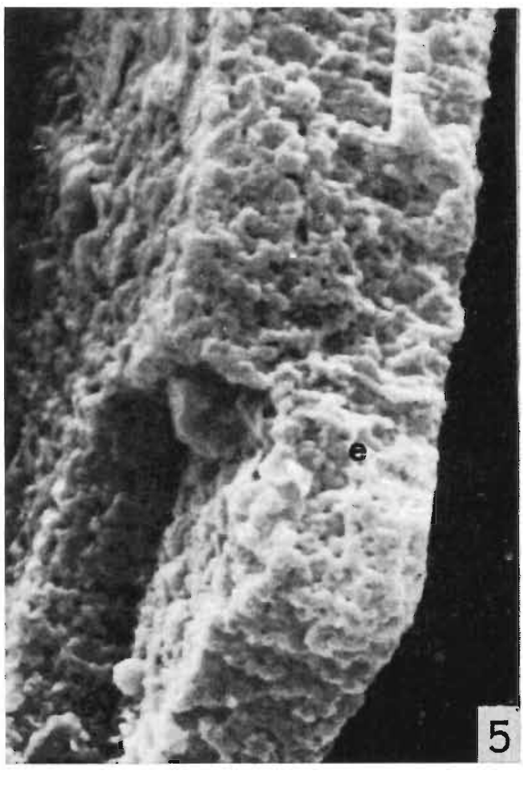
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