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Scanning Electron Microscopic Aspect of the Retral Process in Some Elphidiids (Foraminiferida)

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Introduction

Shell structures of species belonging to *Elphidium* and related genera are rather complicated as those of the so-called smaller Foraminifera, so that they have been a subject of detailed anatomical study since the 19th century (e.g., CARPENTER, 1862). In his splendid book, as fine as an art book, CARPENTER disclosed essential features of shell construction, such as canal system and retral process, using two species, *Polystomella* [=*Elphidium*] *crispa* LINNÉ and *P. craticulata* FICHTEL and MOLL.

Afterwards, the excellent work of HOFKER (1929) was succeeded by many studies on the shell structures of elphidiids to be published one after another in the latter half of the 1950's, as represented by SMOUT (1955), HOFKER (1956), UJIIÉ (1956), WADE (1957), VOLOSHINOVA (1958), REISS (1958) and REISS & MERLING (1958). Although these authors based their work mainly on the observation of thin sections and consequent interpretation, they scarcely referred to the results of others because of the roughly contemporaneous publication of those papers.

It is considerably difficult to restore a three-dimensional shell structure from thin sections which are essentially two-dimensional, although it is possible for us to assume three-dimensional features if a thin section has some thickness and is still available for optical microscopic observation, by shifting a focus from the section's top plane to the bottom plane.

In the latter half of the 1960's, a scanning electron microscope was employed in the study of Foraminifera, and some authors (e.g., MARSZLEK et al., 1969; HANSEN & REISS, 1971; HAYNES, 1973) showed the scanning electron micrographs of several elphidiid species. These authors, however, apparently overlooked the previous investigations cited above, and so they failed to draw more realistic figures of the shell structures.

On the basis of many scanning electron micrographs of efficiently dissected specimens together with thin sections, I would like to show in this paper the actual nature of the retral process relating to the canal system, both being most important characteristics of elphidiids. It may turn out to be a combination of the ideas of REISS (1958) and WADE (1957), and yet it may present a clearer view on the genesis of the retral process. The knowledge gained in the present study shows that WADE's criticism of my previous study (Ujiié, 1956, my first work on Foraminifera) was correct.

Nature of Retral Process

The family Elphidiidae Galloway under the superfamily Rotaliacea is unique in having septal canal system which opens into single or double rows along the intercameral suture, according to Loeblich & Tappan (1964) who published one of most modern taxonomic syntheses. Concerning this canal system, almost all the authors seem to have the same idea, but I hold a somewhat different opinion about the umbilical canal system and its connection to the septal one, particularly against the views of Wade (1957) and Loeblich & Tappan (1964). I am inclined to believe that every genus of the family Elphidiidae is provided with the umbilical canal system of essentially the same scheme, as will be discussed later.

Unlike the case of the canal system, the concept of retral process has been diverse among the authors, who nevertheless regarded the retral process as one of the critical features distinguishing some genera from the others in the family Elphidiidae. To avoid futile confusion, therefore, we should be mindful of Carpenter's (1862) original definition of the retral process, stated by Reiss (1963) as follows*: "retral processes are 'a set of processes of the sarcode' extending from the margins of 'each segment of the sarcode body' and upon the surface of which the 'spiral lamina which forms the outer wall modelled' ". The modelled wall represents an undulating outer surface of wall, ridges of which run approximately parallel to the equatorial margin of test. Just beneath each ridge, a short tubular and backward prolongation of chamber lumen is located, at least in elphidiid species provided with well-developed ridges on the wall surface. Accordingly, so far as the taxonomy of Foraminifera is dependent mainly upon the shell morphology, the term retral process must be used for this peculiar morphology of shell, apart from the problem whether a protoplasmic mass is housed in the tubular projection throughout the life or not; hence a slight modification of the original sense is needed.

In order to know the genetic development of the retral process which must be reflected on the internal structure, I chose the following four taxa**:

Elphidium crispum (Linné) (from the beach at Arasaki, Nagai-machi, Miura City, Kanagawa Prefecture). Most popular and typical species of *Elphidium* provided with well-developed retral processes, many of which run across almost the whole length of chamber.

Elphidium cf. *macellum limbatum* (Chapman) (from a drilling core in the offing southwest of Yamakawa, Motobu-machi, Okinawa-jima, Okinawa Prefecture; . . . 8 m below the bottom surface of 38.5 m water depth). The specimens have difinite retral processes which terminate at the middle of chamber length.

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* Clauses in '- - - - -' cited from Carpenter (1862).

** Specimens of the first taxon were supplied by Mr. T. Samata, the next two by Dr. Y. Kuwano, both of our museum, and the last one by Dr. M. Wade of the University of Adelaide, Australia.

Cellanthus craticulatus (FICHTEL and MOLL) (from the same core sample as *E.* cf. *macellum limbatum*). Not full-grown specimens, so that they do not have any diverged outlets of septal canal but have one row of outlets along the suture. Although LOEBLICH & TAPPAN (1964) described that "surface [of wall] not highly ornamented as in *Elphidium*, but only with perforations of canal system", the "retral process" is certainly developed though weakly.

Parrellina craticulatiformis WADE (Lower Miocene topotypic materials collected by WADE from a cliff, 90 feet above sea level, on the bank of the River Murray at Blanchetown, South Australia). Species has innumerable but not prominent ridges across the whole length of chambers, so WADE (1957) considered that the ridges were not accompanied by the tubular projections beneath them.

WADE (1957) in her study also used the three species, *E. crispum*, *C. craticulatus* and *P. craticulatiformis*. Her work gave most useful results on the shell structures of elphidiids, compared with the previous studies, and was adopted in a textbook by LOEBLICH & TAPPAN (1964). To ascertain or to modify WADE's results, therefore, re-examination of these species becomes necessary.

Unfortunately, however, WADE's work was carried out before the concept of lamellar wall structure in Foraminifera was introduced by REISS (1958 et seq.). As has been generally accepted, most fundamental morphology of Foraminifera of rotaliid group, for example, superfamily Rotaliaceae of LOEBLICH & TAPPAN (1964), must be the rotaliid wall that is a double wall consisting of a normal chamber wall lamella lined with another lamella. Elphidiids, constituents of the Rotaliaceae, also have such inner lamellae though their development is limited, occurring only around the intercameral septum, as shown here in the equatorial sections of *Cellanthus craticulatus* (see Plate 7). This feature indicates that the inner lamella should be called a septal flap.

The scanning electron micrographs of many dissected specimens of the above-mentioned elphidiid taxa revealed the actual nature of the septal flap and its relationship to the retral process and to the septal canal system. The following conclusive observation can be applied to every taxon treated here, and very probably to other taxa of the Elphidiidae.

As a rule the septal flap lines nearly all over the intercameral wall, differing from the observation by WADE (1957) and REISS (1958, 1963), and its proximal end terminates at the base of septum or around the margin of basal foramen (particularly see Plate 7, fig. 2), while its distal end turns inwards and then thins out as if it was fused into the spirothecal wall for a short distance from the intercameral suture. Beneath the retral process, however, the proximal margin of the septal flap thins out at the half height of the septum, never attaining to the base of the latter.

Around the retral process the septal flap is always strongly indented. More precisely speaking, a short tubular indentation of the septal flap makes itself a retral process. The short tube attached to the intercameral wall forms a circle, inside of which no septal flap exists. Although REISS (1963) was the first to mention the role of septal flap in the formation of retral process, he thought that the distal roof of retral process was made of a spirothecal wall, not a flap. But, in fact, the spirothecal wall merely rests upon the roof made essentially of the septal flap, thus accentuating the ridge-like relief on the surface of test.

In my previous paper (UJIIÉ, 1956) I considered erroneously that the short tube of retral process is penetrating the intercameral wall and proposed a new term to replace the retral process. As pointed out by WADE (1957) and REISS (1963), this idea should be suppressed, although there is a fact that the intercameral wall is occasionally hollow at the base of this short tube even between the last and the penultimate chambers (refer to Plate 3, fig. 2).

It must be noted here in addition that every part of the septel flap is perforated just like the other wall at least in typical *Elphidium*. Mainly on the basis of the imperforate septal flap, HOFKER (1956 et seq.) assigned its origin to a kind of tooth plate.

Between the septal flap and the intercameral wall which was the former apertural face, there is left a considerably open passage, i.e., the septal canal system. The system is fundamentally made of a broad arched canal, which is much broader than mentioned before (UJIIÉ, 1956). Running below the retral processes, this arched canal branches off into funnel-shaped outlets between two adjacent retral processes since no septal flap is developed around the retral process. In this sense, whenever the divergence of the arched septal canal occurs near the chamber periphery, the species has a potential to develop the retral process. It can be presumed that the retral process is represented by a small solid node of indented septal flap in the most primitive stage, then enlarging its diameter it finally becomes hollow, as seen typically in *Elphidium crispum*.

The proximal end of every arched septal canal connects with a spiral canal in a transparent umbilical plug. From the random position of this spiral canal, a few radial canals extend straight toward the outside of test. This fundamental scheme of the umbilical canal system was introduced first by CARPENTER (1862) and was later substantiated by HOFKER (1929 et seq.) and myself (UJIIÉ, 1956), despite of some doubt expressed by other authors (e.g., WADE, 1957; REISS, 1963).

WADE (1957) emended the genus *Parellina* using *P. craticulatiformis* instead of the type species *P. imperatrix* (BRADY). She illustrated the anastomosing umbilical canal system as a most critical feature of the genus. However, so far as the topotypes sent from her are concerned, all the specimens were coated with secondary shell substance in the process of diagenesis, as is recognized in their thin sections and SEM pictures. Although it is very much difficult to show the true nature of the umbilical canal, particularly by observation of canada balsam sections, because of the diagenetic alteration, a vertical section suggests a normal type of the system. At least the illustrations of anastomosing canal by WADE are quite inadequate.

As a summary of the observation mentioned heretofore, I figure here once again a model of mold for *Elphidium crispum* (Plate 1) to replace the previous one (UJIIÉ, 1956, Text-fig. 2).

Taxonomic Significance of Retral Process

If the presumable step of development of the retral process in relation to the septal canal system is taken into account for the classification of *Elphidium* and related genera, the following lines may be strongly suggestive.

The only essential difference between *Elphidium* DE MONTFORT, 1808, and *Cribrononion* THALMANN, 1947, is the absence of retral process in the latter. In a description of genus *Cribrononion*, however, LOEBLICH & TAPPAN (1964) stated that "no retral process, but solid and imperforate septal bridges may occur". Putting aside the probably incorrect expression of "imperforate", their additional note implies that species with sprout of retral process are included in their *Cribrononion*. Scanning electron micrographs of *Elphidium exoticum* seem to show this primitive stage of retral process as seen in the original description by HAYNES (1973), who did not distinguish between the two genera. More intermediate forms can be recognized in *Elphidium advenum* (CUSHMAN) and its subspecies, whose vertical sections through near the intercameral septa indicate clearly a series of nodes along the test periphery (see UJIIÉ, 1956, Plate 15). Nevertheless, any of these nodes are not hollow, unlike the well-developed retral process. Thus, discrimination of the two "genera" depends upon rather qualitative evaluation of development of the retral process. *Cribrononion* might be placed in the subgeneric rank of the genus *Elphidium* as was done by the original author (THALMANN, 1947).

Similar gradational development of retral process can be recognized from *Elphidiella* CUSHMAN, 1936, through *Cellanthus* DE MONTFORT, 1808, to *Elphidium*, although the first two genera are different from *Elphidium* in having typically double rows of outlets of septal canal. Particularly, the specimens of *Cellanthus craticulatus* treated here often possess some thinly hollowed nodes of septal flap indentation. Such primitive status of retral process would be expected from the schematic figures of shell structure of *C. craticulatus* shown by WADE (1957), who nevertheless did not discriminate *Cellanthus* from *Elphidium*. On the other hand, *Elphidiella* does not develop the retral process and, moreover, hardly shows any distinct node resembling sprout of retral process (ANGELL, 1975). Besides, most species of *Elphidiella* and many *"Cribrononion"* show no, or very poor, development of the umbilical canal system, implying that the two genera are more primitive elphidiids. In fact, one of the geologically earliest records is *Elphidiella prima* (TEN DAM) from the Dutch Paleocene (TEN DAM, 1944) and from the Swedish Danian (BROTZEN, 1948).

Concerning *Parrellina craticulatiformis* WADE, I could not recognize such features as anastomosing umbilical canal and dendroid septal canal, which were pointed out by WADE (1957) to serve as the criteria for emendation of the genus, because of the secondarily deposited shell substance thickly coating the wall of the topotypes. So far as my observation of the specimens goes, the shell structures are similar to thoes of *Cellanthus*. As described by LOEBLICH & TAPPAN (1964) for the genus, *"P." craticulatiformis* is provided with "ridges across chambers between sutures" on test surface. Differing from the definition, however, the ridges never anastomose from one another. And some ridges seem to be hollow with a thin tube-like passage inside, resembling primitive retral process. Careful examination of the type species, *Polystomella imperatrix* BRADY, is still required before emendation of the genus is done if necessary.

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Postscript: After the manuscript was submitted for publication, I have found a paper which should have been referred to: VOLOSHINOVA, N. A., V. N. KUZNETZOVA & L. S. LEONENKO, 1970. Foraminifera from the Neogene formations in Sakhalin. *Trudy Vsesoyuznogo neftyanogo nauchno-issledovatel' skogo, geologorazvedornogo instituta*, (284): 1–303, 51 pls. [in Russian]. They read correctly the previous authors' papers concerning the shell structures of elphidiids cited here too, and on the basis of their own experience (VOLOSHINOVA, 1958; VOLOSHINOVA & KUZNETZOVA, 1964) they formed almost the same opinion as mine, even though they illustrated there dissected specimens merely by several sketches. Figure 25 seems to summarize their idea; this schematic diagram indicates a space interrelationship between the infraseptal canal and the retral process in *Elphidium crispum*, and this relation is completely analogous to the corresponding part of a mould model shown here in Plate 1. Besides, they agreed with a current opinion of many authors (e.g., HOFKER, 1956; REISS, 1963) that the "septal flap" leaving the intraseptal canal between it and the primary septal wall may have been originated from a tooth plate. As shown here, however, the septal flap, at least in *Elphidium* (s.s.), is clearly porous and indicates the same nature as the primary septal wall. Genus *Retroelphidium* VOLOSHINOVA proposed in their paper may represent such an intermediate stage of retral process development between typical *Elphidium* and *Cribrononion* THALMANN as seen in *E. advenum* (CUSHMAN) and its subspecies (see my discussion in p. 121). I am greatly indebted to Dr. Yukio KUWANO of our Department who translated the Russian paper for me.

Explanation of Plates

Plate 1

A model of mold for *Elphidium crispum* (LINNÉ)

Plate 2

Figs. 1–3. *Elphidium crispum* (LINNÉ). Micropaleontology Collection Natl. Sci. Mus., 909.

1. Distal portion of intercameral septum, showing floor of the tubular prolongation of chamber lumen, which consists of a part of septal flap bent backward and perpendicular to the plane of septum. Roof and lateral walls of the tubular prolongation were lost by dissection using a point of glass fibre. It can be seen that a passage remains between the bent septal flap and the normal septal wall, as a part of arched septal canal. The septal flap is normally perforate, as seen also in the other specimens of the species shown here. ×800.
2. Proximal portion of two intercameral septa, showing somewhat broken outlets of a septal canal and floor parts of the tubular prolongations of chamber lumen (i. e., retral processes) located between two outlets. On the proximal extension of the septal canal, an outlet of radial canal of the umbilical canal system is observed, suggesting a direct connection between septal canal and umbilical one. ×800.
3. A whole view of the dissected specimen, parts of which are magnified in figs. 1 and 2. ×80.

Figs. 4, 5. *Elphidium* cf. *macellum limbatum* (CHAPMAN). Micropal. Coll. N. S. M. 916.

4. Septum between last and penultimate chambers; its double wall was partially taken away below a row of retral processes, in order to show an inner view of alternate arrangement of typical tubular indentations of septal flap and of canal outlets between the adjoining tubes. Septal flap much thinner than normal septal wall fuses completely into the spirothecal wall of the last chamber without any distinct boundary. ×800.
5. The same specimen as in fig. 4, similarly oriented but at lower magnification, indicating the position of the figure. ×240.

Plate 3

Figs. 1–3. *Elphidium crispum* (LINNÉ). Micropal. Coll. N. S. M. 910.

1. Lateral view of the last three chambers dissected through their distal parts. ×240.
2. Enlarged fig. 1, focused on the distal end of last septal wall, particularly indicating two types of the base of tubular prolongation, i. e., retral process. Two bases are closed with normal septal wall, whereas another type is accompanied by a hole of smaller diameter probably because of subsequent? absorption even in the last chamber. This essentially blind base of the tubular retral process supports the opinions of WADE (1957) and REISS (1958, 1963) against my previous work (1956). The present indented mode of septal flap as tubular prolongation bears an exact resemblance to that of *Elphidium* cf. *macellum limbatum* (for example Pl. 2, fig. 4). ×800.
3. Another view of the same specimen but opposite to fig. 1. Comparison of the two pictures leads us to understand a close correspondence between the hollowed internal structure of retral process and the ridge of test surface. ×240.

Fig. 4. *Elphidium crispum* (LINNÉ). Micropal. Coll. N. S. M. 911.
External aspect of remarkable ridges, particularly showing their truncated anterior end and the posterior part being never superimposed upon the intercameral suture. ×800.

Figs. 5, 6. *Elphidium crispum* (LINNÉ).
Whole views of two dissected specimens, parts of which are enlarged in Plate 4. Micropal. Coll. N. S. M. 912 and 913, respectively. Both ×120.

Plate 4

Figs. 1–4. *Elphidium crispum* (LINNÉ).

1. Dissected portion, particularly indicating a connection between thick umbilical canal and septal canal; cover of septal flap was mostly taken away. It clearly shows that the lower margin of the septal flap runs roughly parallel to the peripheral margin of septum at about the middle height of the septum, while septal flap may extend further downward. ×240.
2. A part of fig. 1 enlarged, giving an external view of efficiently dissected retral processes on the left-hand side of this picture and, at the same time, an inner view of two retral processes where septal flap is partly absent. ×800.
3. A part of Plate 3, fig. 6 enlarged. ×240.
4. A part of fig. 3 enlarged, revealing the spatical relationship between short tubes of retral process and outlets of septal canal. ×800.

Plate 5

Figs. 1–3. *Cellanthus craticulatus* (FICHTEL and MOLL). Micropal. Coll. N. S. M. 917.

1. A whole view of a not fully grown specimen, last five chambers of which were dissected. ×80.
2. Enlarged proximal parts of septal canal, effectively suggesting connection between double-walled septum and outlets of the canal. ×240.
3. Enlarged distal portion of a septum shown in fig. 1, indicating short tubular backward prolongations of chamber lumen though with smaller diameter than that of typical *Elphidium*. This picutre also clarifies the situation of septal passage surrounding a trubular prolongation. The surface of septal flap is finely striated, as seen in fig. 6 also, differing from that of *Elphidium* species treated here. ×800.

Figs. 4–6. *Cellanthus craticulatus* (FICHTEL and MOLL). Micropal. Coll. N. S. M. 918.

4. Low-magnified view of a dissected specimen. ×80.
5. A part of fig. 4 enlarged, showing a well-developed septal passage attaining almost to the base of septum at the middle of picture and an alternate arrangement of rather weakly developed retral processes and outlets of septal passage (canal) in the lower right corner of picture. ×240.
6. Enlarged distal portion of the septum indicated in fig. 5. A thick-walled tubular prolongation of chamber lumen, i. e., half-developed retral process, is underlain by septal canal. ×800.

Plate 6

Fig. 1. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 924.
Test surface was coated with secondary deposit of carbonate substance and also partially dissolved so that many ridges across the whole length of chamber have their crestal parts hollowed out. Umbilical canal system also is somewhat exposed by this natural? dissolution. ×36.

Fig. 2. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 931.
Specimen less dissolved than the above-mentioned one. ×36.

Fig. 3. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 932.
Ridges on test surface run parallel to one another, never anastomosing. Due to dissolution, many ridges disclose their inside, leaving groove-like open space; this suggests that they may enclose tubular passages similar to those of retral processes. ×240.

Fig. 4. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 924.
Specimen dissected through its umbilical region to a considerable extent, indicating the same pattern of umbilical canals as that of their outlets shown in fig. 2. This fact implies that radial canals extend rather straight toward the exterior, unlike the anastomosing manner as presumed by WADE (1957). ×80.

Plate 7

Figs. 1, 2. *Cellanthus craticulatus* (FICHTEL and MOLL). Micropal. Coll. N. S. M. 929.

1. Thin section tangential to the shell and parallel to the equatorial plane, giving a general aspect of wall structure. It is noticeable that a spiral canal of the umbilical canal system branches off into septal canals. ×100.
2. A part of fig. 1 enlarged, particularly showing structures of septal wall and its adjacent areas. We can see the well-developed septal flap, the connection of umbilical canal to septal one, the remarkably perforate spirothecal wall, and so on. ×200.

Fig. 3. *Cellanthus craticulatus* (FICHTEL and MOLL). Micropal. Coll. N. S. M. 928.
Part of an equatorial section revealing the characteristic indentation of septal flap that produces the passage of septal canal between the flap and the essential septal wall, and also the backward bending of the flap, which results in retral process between it and spirothecal wall near the septum. ×200.

Figs. 4, 5 *Cellanthus craticulatus* (FICHTEL and MOLL). Micropal. Coll. N. S. M. 930.

4. Vertical section through the huge protoconch, giving a general aspect of wall structure in different angle from figs. 1 and 3. Umbilical canals extending straight outward are much impressive here. ×100.
5. A part of fig. 4 enlarged to show the pattern of a septal canal branching off from the umbilical canal system, and the details of a series of nodes near and along the intercameral suture. Some nodes are pierced at their basal portion by a fine pore which must correspond to a tubular space of the undeveloped retral process. ×200.

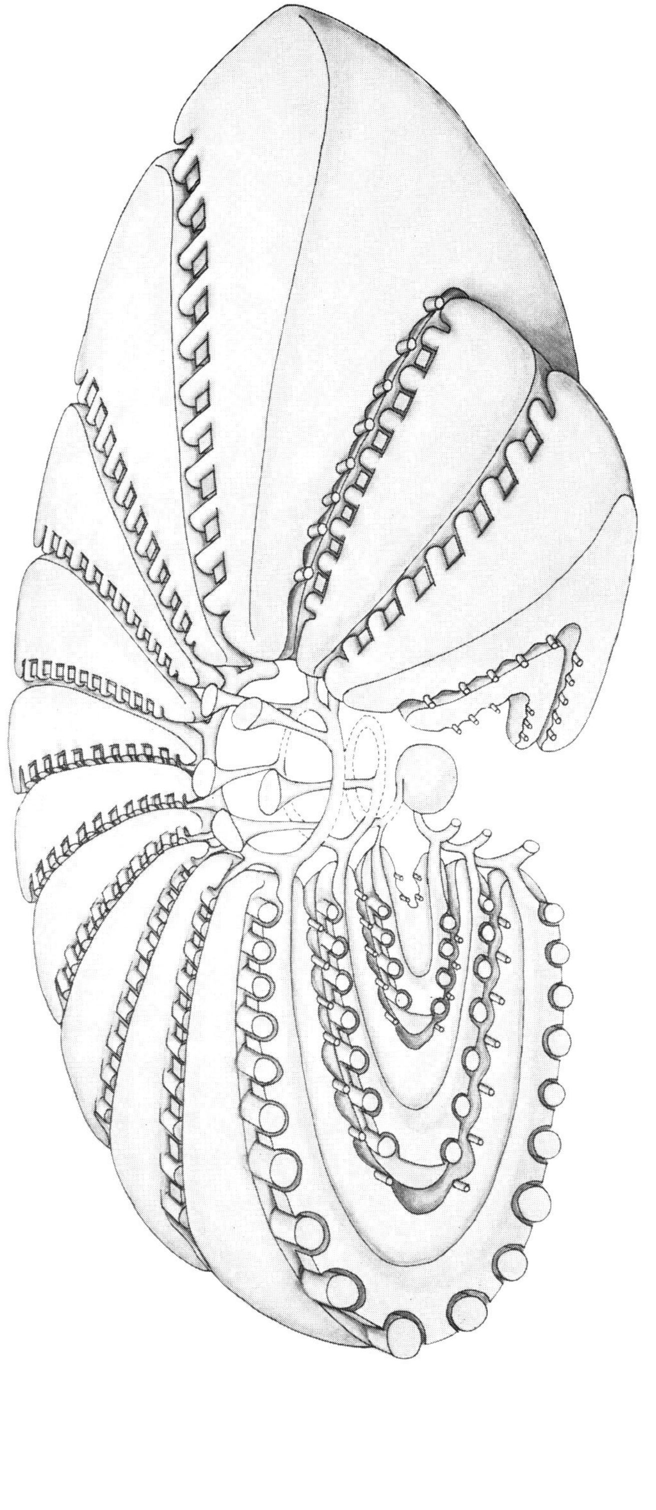
Plate 8

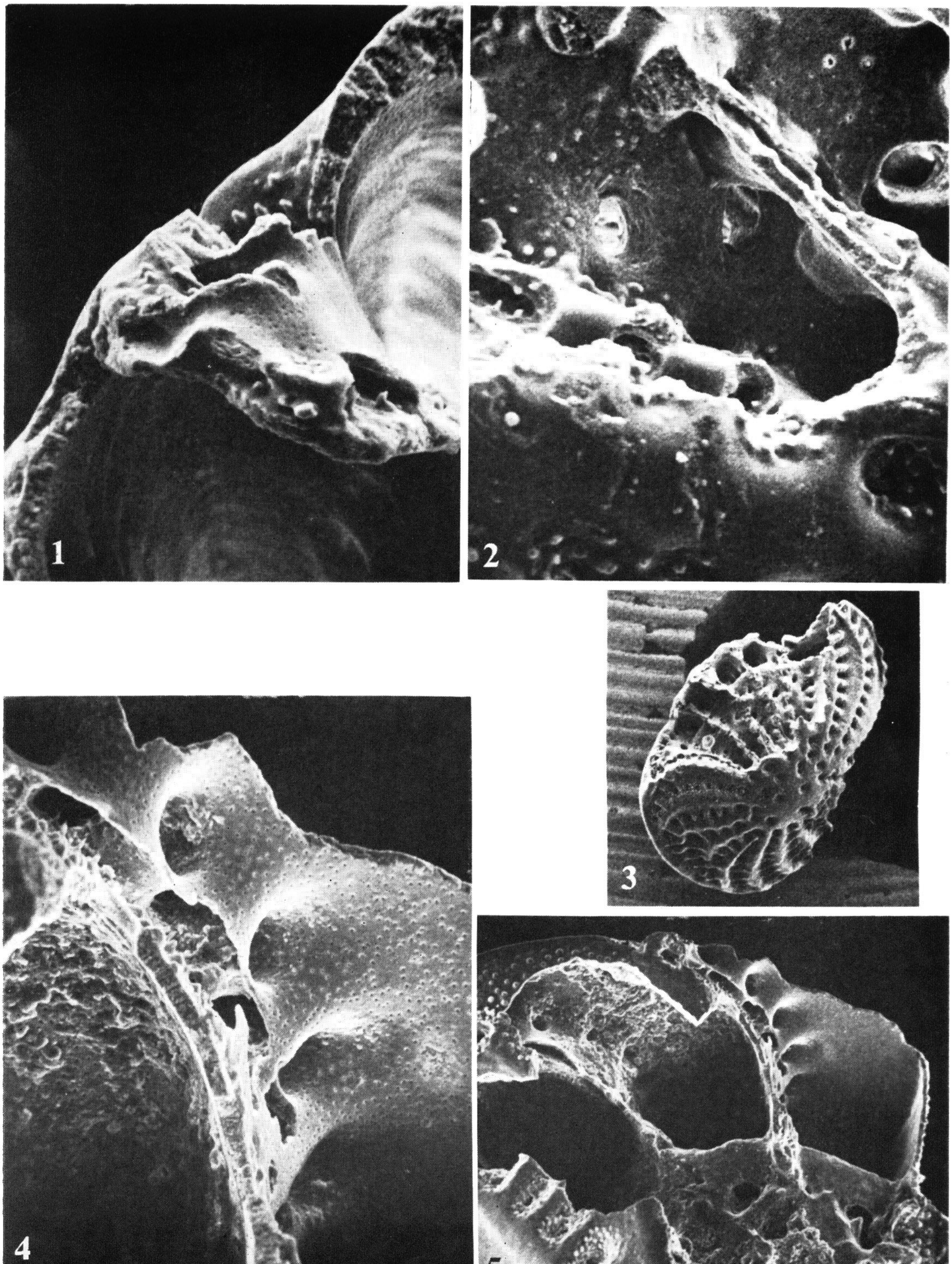
Figs. 1, 2. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 931.

1. Approximately equatorial section giving a general aspect of wall structure, though it may be somewhat obscure due to secondary coating. Septal canal sealed by septal flap is developed well. Most remarkable things are that very thick spirothecal wall is recognized throughout and that it is penetrated with radial thick perforation; no anastomosing canal is observed, different from the illustrations by WADE (1957). ×100.
2. A part of fig. 2 enlarged, showing the details of structures of doubled septal wall and spirothecal wall. ×200.

Figs. 3, 4. "*Parellina*" *craticulatiformis* WADE. Micropal. Coll. N. S. M. 932.

3. Vertical section, giving a general aspect of shell structure, in which anastomosing umbilical canals cannot be recognized. ×100.
4. A part of fig. 3 enlarged, particularly indicating the nature of nodes along the test periphery. The upper part of some nodes is pierced by a pore, which corresponds to a groove in such ridge as shown in Plate 6, fig. 3, and probably to a hollow of retral process even though its roof was broken away by dissolution. ×200.

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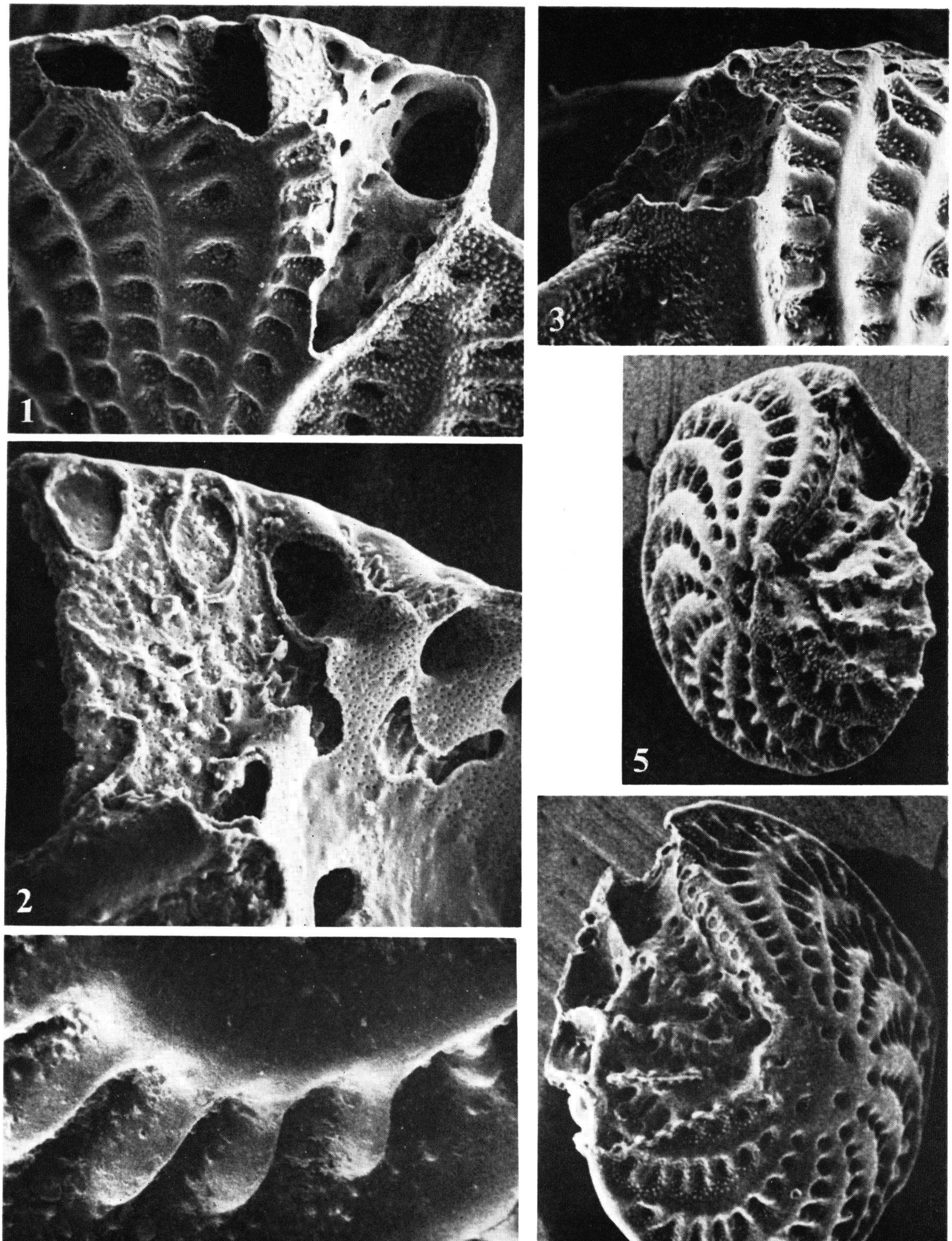

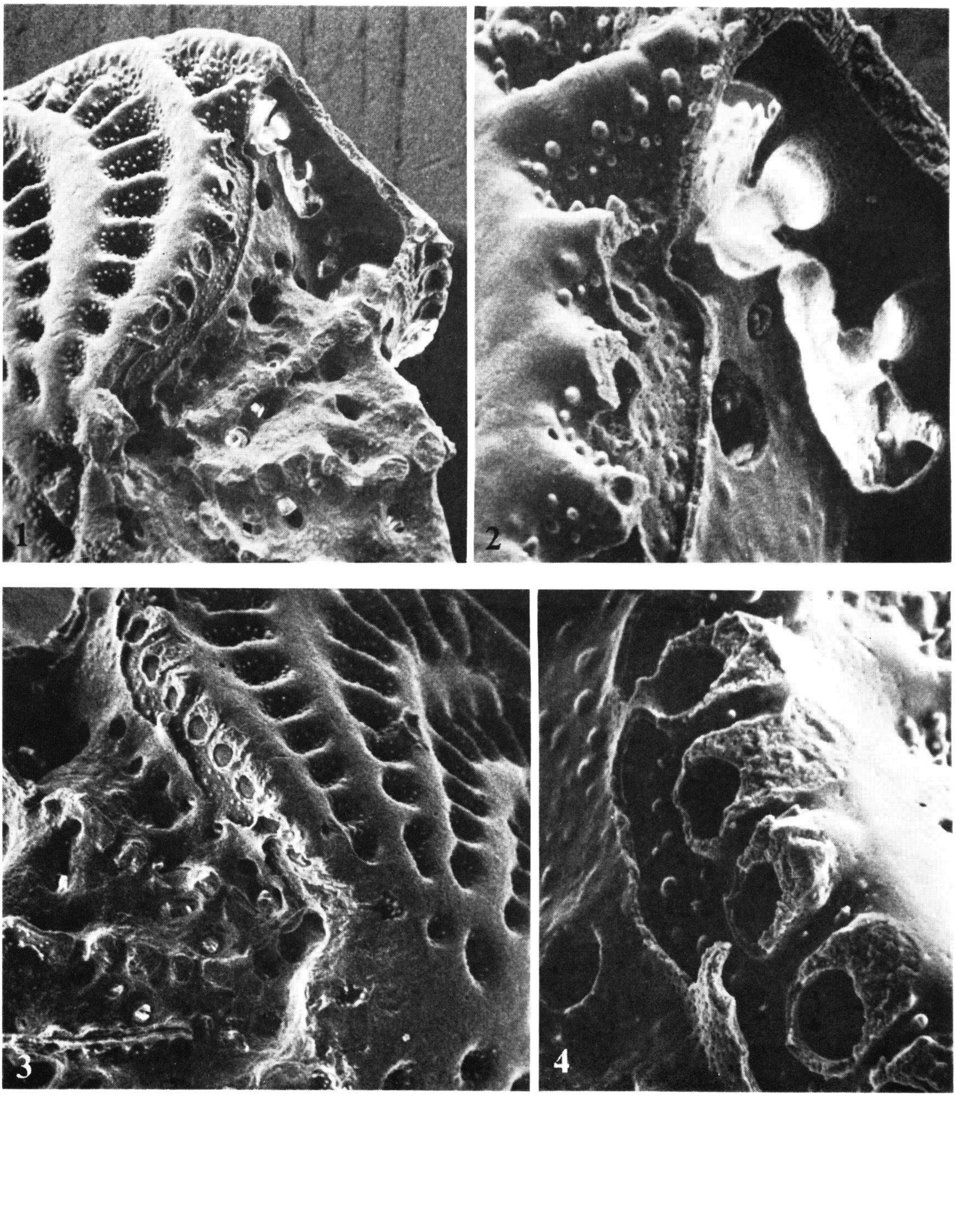
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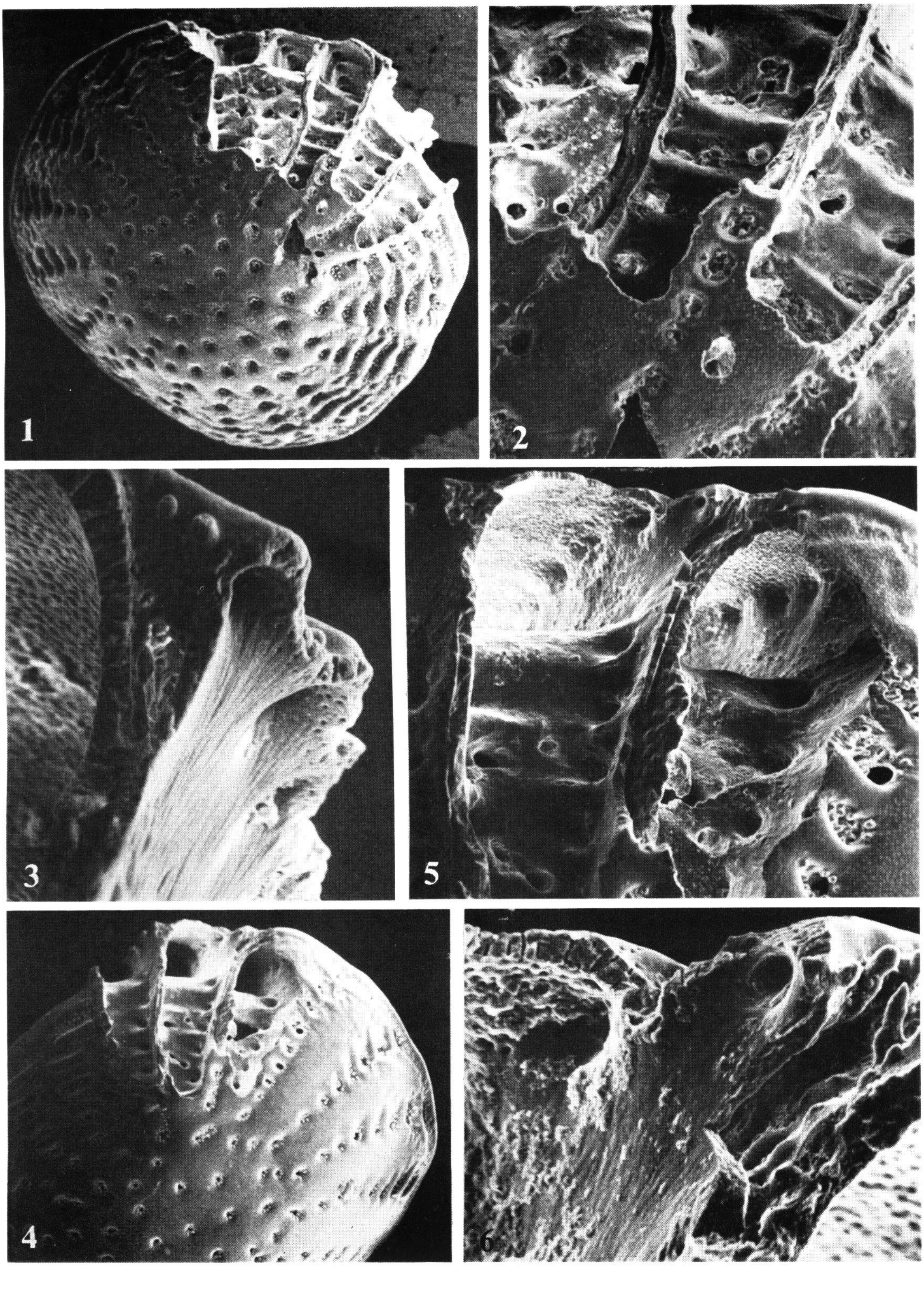
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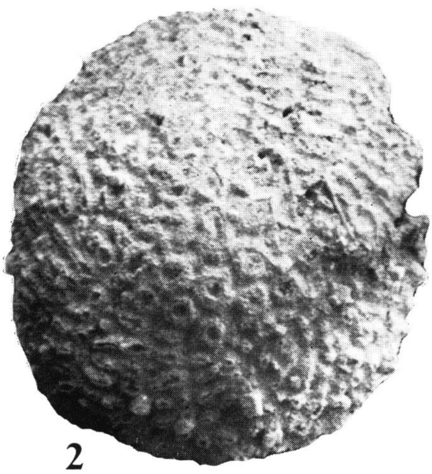

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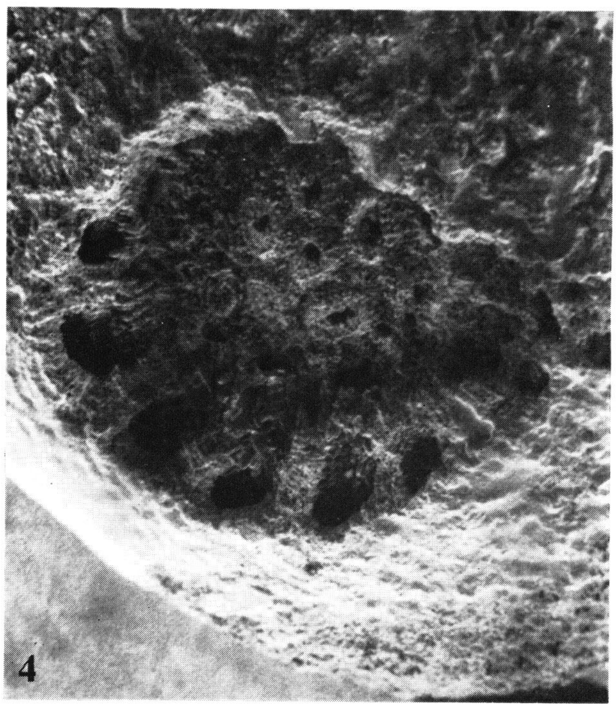

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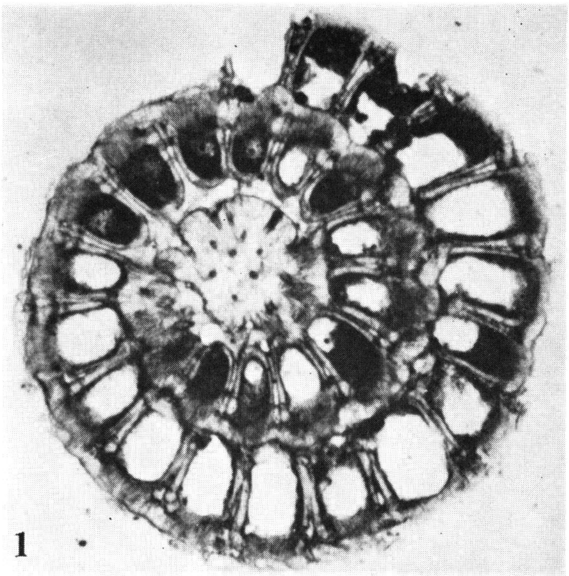
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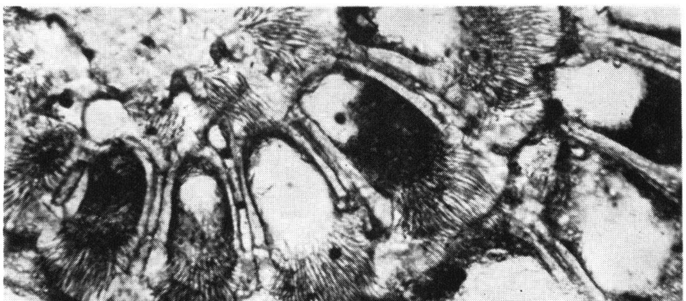
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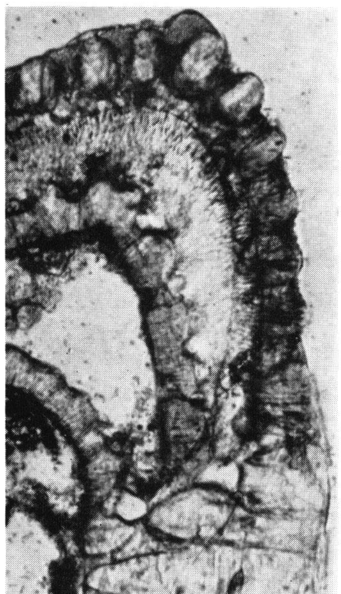
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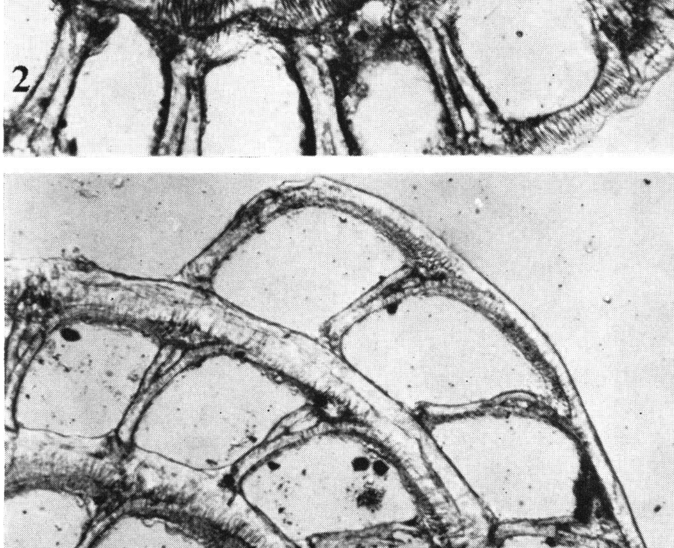
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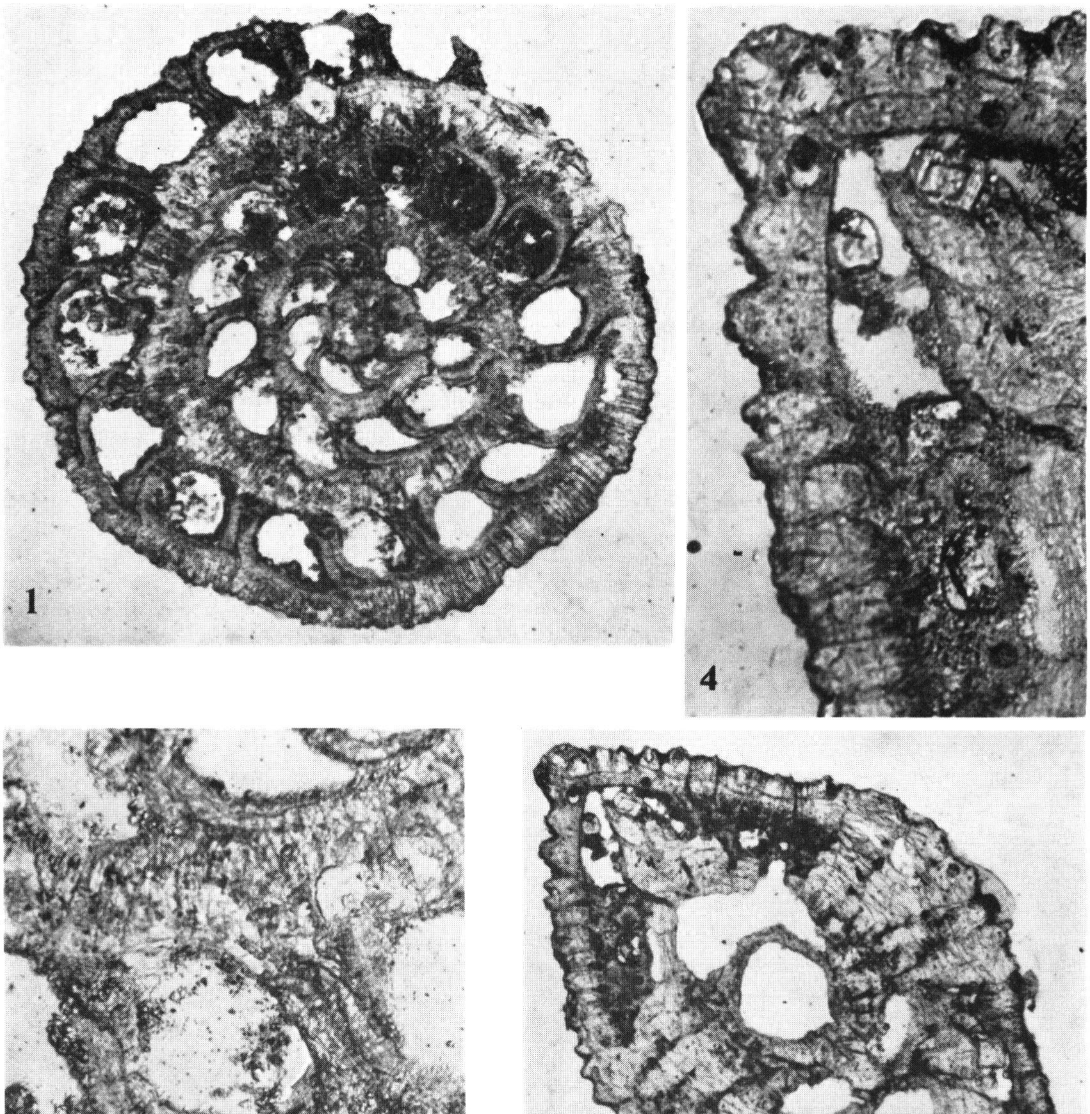
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