Anker Weidick

ELECTRON MICROSCOPY OF ROTALIACEAN WALL STRUCTURES

HANS JØRGEN HANSEN AND ZEEV REISS

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Representative species of the rotaliacean genera *Ammonia, Pseudorotalia, Pararotalia, Calcarina, Operculina, Elphidium, Cellanthus, Asterorotalia,* and *Rotalia* were studied by aid of the scanning electron microscope. All were shown to build their primary chamber walls according to the "bilamellar" pattern and to possess an inner lining and an outer lamella composed of stacked calcite platelets, and a median layer composed of paired calcite crystals in an organic matrix. The walls of all species examined are optically "radiate". All Rotaliacea possess a septal flap producing with the preceding septal face an interlocular space, which may be closed off partly at its border either primarily or by secondary lamination. Foraminal plates extending from the flap are present in all genera mentioned, except in *Rotalia.* An umbilical coverplate extending from the foraminal plate into the previous chamber (where it is attached to the previous foraminal plate) occurs in *Ammonia, Pseudorotalia, Pararotalia, Asterorotalia,* and in the early ontogenetic stages of *Calcarina.* Secondary lamination covers exposed surfaces of earlier chambers, as well as the sides of the interlocular spaces where individual lamellae thin out considerably. Thinning out of secondary lamellae is also observed in the electron microscope on the sides of ornamentational features which are all inflational and produced by outer lamellae only. 121 scanning electron micrographs illustrate the features described.

Since Smout's (1954, 1955) work, the Rotaliacea have been separated from other groups of perforate and lamellar foraminiferids mainly by the presence of a septal flap which was described as forming secondarily doubled septa with intraseptal passages communicating with a canal system. These features were believed to distinguish the "monolamellar" Rotaliacea from "bilamellar" groups, like e.g. the Orbitoidacea, where primary double septa and intraseptal passages without any true canal system were described (see Reiss, 1963 and references therein). Lately, the true structure of the bilamellar walls was clarified by Hansen, Reiss & Schneidermann (1969). They showed that the so-called "passage" in bilamellar forms is in fact an organic median layer containing, at least in some genera, euhedral calcite crystals and separating an outer lamella from an inner lining. This layer, therefore, can-not at all be compared with the true spaces formed between septal face and septal flap in the Rotaliacea. Moreover, it was shown that in some bilamellar groups the inner lining does extend as a septal flap covering a previous septal face (McGowran, 1966; Reiss & Schneidermann, 1969; Hansen, Reiss & Schneidermann, 1969). Finally, in thin sections of various rotaliaceans, examined under the light microscope, a kind of parting line within the primary wall of the septal face in the final chamber can be observed and traced over some distance. Such a parting line can be observed also in what was described as toothplates in such genera as *Ammonia* and *Pseudorotalia*.

In view of these findings the present authors examined by means of scanning electron microscopy the wall structure of representative species belonging to genera *Rotalia, Pararotalia, Ammonia, Pseudorotalia, Asterorotalia, Calcarina, Operculina, Elphidium* and *Cellanthus*. The results of the detailed ultrastructural study of these species lead also to a clarification of certain of their morphological features repeatedly discussed by various authors.

It should, however, be emphasized that the aim of the present paper is to describe mainly the primary wall structure and only some of the more important morphological features – which need clarification – of the genera mentioned, and by no means a complete redescription of the latter.

The material studied originates from the A. Nørvang and J. Hofker collection from the Indopacific region, originally sampled by T. Mortensen and deposited in the Mineralogical Museum of the University of Copenhagen, and from the micropalaeontological collection of the Department of Geology, The Hebrew University, Jerusalem. Special thanks are due to Prof. C. W. Drooger, Geological Institute, University of Utrecht, for putting at the authors' disposal specimens of *Rotalia trochidiformis* from Grignon and of species of *Pararotalia* described from the Aquitaine Basin.

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Techniques

Both whole and fractured specimens, as well as half sections and thin sections, etched or unetched, were examined in a "Stereoscan" Mk IIa scanning electron microscope. The preparation of the specimens for electron microscopy was made according to the methods described by Hansen (1968, 1969) and by Hansen, Reiss & Schneidermann (1969).

The nearly 200 specimens studied and partly figured here are deposited in the collections of the Mineralogical Museum of the University of Copenhagen, under registration number MMH no. 11164 (with subcode R1 – R153).

Ammonia beccarii (Linné)

Since the characteristics of the rotaliacean wall structure are well represented in the genus *Ammonia,* its type species, *A. beccarii* (Linné) will be considered first.

The primary chamber wall of *Ammonia* is composed of an inner and an outer layer, referred to here as the "inner lining" and the "outer lamella" respectively, and built of stacked calcite platelets. These two layers are separated from each other by a very thin third layer, built of relatively large calcite crystals, enveloped in organic material, arranged in pairs on both sides of a thin, organic sheet. Adjacent pairs of crystals may touch each other or they may be separated for a short distance, giving this third separating layer a beaded appearance in section. This layer will be referred to here as the "median layer" (pl. 1, figs 1–2).

The stacks of platelets composing the outer lamella and the inner lining are arranged normal to the median layer and to the test surface, although the platelets themselves lie at an angle with them. The orientation of the platelets within each individual stack remains generally constant. However, the platelets of each stack are seen in transverse section to be oriented with respect to those of adjacent stacks at an angle of about 110°, thus producing a "herringbone pattern" (pl. 1, fig. 2) ("chevron-shaped pattern" of Towe & Cifelli, 1967). Individual stacks of platelets may correspond to crystal units as defined by Hansen (1970). Thin sections through the walls of *Ammonia* examined under the optical microscope between crossed nicols exhibit an extinction pattern indicative of the "radiate" wall-structure in the sense of Wood (1949). Within the limits of accuracy of the light microscope the orientation of the c-axes of the platelets in the stacks is interpreted as normal to the test surface.

In those instances where the angle between crystal faces could be measured on electron micrographs of the median layer, it indicates a crystallographical orientation with the c-axis normal to the test surface. The orientation of the platelets in each stack appears to conform to that of a crystal face in the median layer (pl. 1, fig. 2).

In both inner lining and outer lamella so-called primary lamination is observable, marked by local changes in orientation and even size of the platelets. In places, the outermost part of the outer lamella shows a structure different from the stacked platelets: there, thin rod-like crystals about 0.3 μ long occur, arranged normal to the test surface. This part of the wall (pl. 1, fig. 3) corresponds to the "veneer" described by Towe & Cifelli (1967). No. such veneer was observed in transverse sections through secondarily laminated walls beyond the third or fourth outer lamella.

This structural pattern of the primary wall of *Ammonia,* i.e. inner lining, outer lamella, and median layer, is identical with that found in the "bilamellar" *Cibicides lobatulus* (Walker & Jacob). In the latter species, which is optically radiate or indistinctly so, outer and inner layers are also composed of stacks of platelets in a herringbone pattern, and are separated from each other by a median layer with paired calcite crystals (pl. 1, figs 4–6; pl. 2, fig. 1). On the other hand, in the bilamellar, but optically granulate genus *Heterolepa,* the median layer contains euhedral crystals, heterogenous in size, and which have not been observed to be arranged in pairs (pl. 2, fig. 2). The outer and inner layers of this latter genus are also composed of stacks of calcite platelets (Hansen, 1970; Hansen, Reiss & Schneidermann, 1969). It may be noteworthy that walls constructed of stacks of calcitic platelets occur also in such radiate nodosariaceans as *Lenticulina calcar* (Linné) (Towe & Cifelli, 1967) and *Lenticulina orbicularis* (d'Orbigny) examined by the present authors (pl. 2, fig. 3). In these latter species, however, the angle between adjacent stacks of platelets seems to be lower than in either *Ammonia* or *Cibicides,* viz. about 75°.

The disposition of the different primary layers in the wall of *Ammonia* differs considerably in the various parts of the test.

The inner lining forms the lateral (spiral and umbilical) chamber walls, including the lip. Furthermore, the inner lining continues in order to form a posterior wall of the chamber, covering the septal face of the preceding chamber and being glued to it in places (pl. 2, figs 4–5). This is always the case along the foraminal border. This posterior wall is the "septal flap" of Smout (1954) and other authors. In those places where the septal flap is not glued to the previous septal face a space is formed, referred to earlier as "fissure" or "intraseptal passage", and considered here to be an interlocular space in the sense of Reiss (1957). Thus, the "fissure" becomes in fact a deeply sunken suture on the umbilical side. At the umbilical border of the partly resorbed foramen, near the axial chamber wall (previous coil), the inner lining forms a plate-like extension, folded along an axis running towards the spiral side. This plate is glued to the umbilical wall of the adjacent previous coil at its end near the spiral wall and appears in section as a hook-like structure. This plate is referred to here as the "foraminal plate" and is present in all chambers, including the last formed one. It is in fact part of the "toothplate" of Hofker (1951), of Reiss & Merling (1958), of Reiss (1963), and of Ujiié (1965), as well as part of the "axial plate", as well as the "apertural lip" as shown on plate 21 in Cifelli's (1962) paper. In addition to forming the septal flap and the foraminal plate, the inner lining extends from the foraminal plate into the previous chamber where it forms an umbilical "coverplate", glued to the axial wall (previous coil), to the lip, as well as to the foraminal plate – below the fold – of that chamber. The coverplate leaves a communication open to the chamber interior corresponding to part of the posterior labial aperture. The accompanying figures (pl. 2, fig. 6; pl. 3, figs 1–6; pl. 4, fig. 1) illustrate these features. The coverplate is in fact part of the "toothplate" of Hofker; Reiss & Merling; Reiss; and Ujiié (opp.cit.) and corresponds to part of the "axial plate" of Cifelli (1962). Chamber wall, septal flap, foraminal plate, and coverplate in a previous chamber, are formed by the inner lining as one continuous structure.

The outer lamella covers the inner lining in the septal and lateral chamber walls, including the lip, as well as the septal flap wherever the latter is not glued to a previous septal face. Furthermore, the outer lamella covers the inner lining of the foraminal plate and of the coverplate. It covers outer lamellae of exposed earlier formed parts of the test, thereby producing the typical "lamellar" pattern. The outer lamellae of consecutive chambers cover the side walls of the interlocular spaces with secondary lamination. There, however, like on foraminal and coverplates, the individual outer lamellae become extremely thin in comparison with their thickness on lateral chamber walls and at the bottom of the interlocular space (see pl. 4, figs 2–6; pl. 5, fig. 1). Since the consecutive outer lamellae forming the thin secondary lamination on the sides of the interlocular spaces are less than about 0.5μ thick they are beyond the resolution of the light microscope, and for this reason earlier workers were led to the belief that lamination is interrupted ("incised") along the "fissure" (Smout, 1954, Reiss, 1963, etc.). All ornamentational features, like pustules, granules, knobs, etc. are formed exclusively by local thickenings of the outer lamella and are further thickened secondarily by subsequent outer lamellae.

Whereever the outer lamella is in contact with the inner lining, the median layer separates them, thus enabling the observer to follow the distribution of the inner and outer layers as seen in section. The median layer was not found to be present at the contact between outer and outer, or between inner and inner layers, and not present at the contact between an inner lining and the outer lamella of a preceding chamber. The latter case is clearly demonstrated in those parts of the test where the inner lining forms the septal flap and is glued to the preceding outer lamella (pl. 2, figs 4–5; pl. 5, fig. 1).

Except for the lip, only lateral chamber walls are perforate; all other structures mentioned lack pores. This is also true of all ornamentational features (Reiss, 1963). The organic pore-linings show a distinct constriction both at the junction with the median layer and at the boundaries between consecutive secondary lamellae, where thin sheets of organic material are present (pl. 1, fig. 1; pl. 4, figs 5–6).

The imperforate septal face of *A. beccarii* bears rather small rounded pustules, as well as low, elongated ridges running from the interior marginal border to the cameral edge (Reiss, 1963). At the junction between septal face and lateral wall, as well as between lateral wall and septal flap elongated pustules, formed by local thickenings of the outer lamella, are present. Inflational knobs are present in the central umbilical area (pl. 5, figs 2–3, 5–6). In *A. beccarii* lips of consecutive chambers are fused near their umbilical tips (pl. 5, fig. 3). In *A. batava* (Hofker) the lips are shorter and are not fused at their umbilical tips (pl. 5, figs 5–6). An inframarginal sulcus is present in the species of *Ammonia* examined, producing an infold of the apertural face at the spiral end of the aperture (pl. 5, figs 3 and 6). No interlocular space is formed on the spiral side (pl. 5, fig. 4) between consecutive chambers. On the other hand, the inner lining is drawn inwards along the spiral suture, being glued to the axial wall (former coil) some distance away from this suture. Thus, a very shallow interlocular space is formed along the spiral suture (pl. 5, fig. 6).

Pseudorotalia schroeteriana (Carpenter, Parker & Jones)

The wall structure of this species (which is the type species of the genus *Pseudorotalia*) is identical with that of *Ammonia* (pl. 6, figs. 1–4) and so is its basic morphology (pl. 6, fig. 5; pl. 7, figs 1–6; pl. 8, fig. 1).

Unlike in *Ammonia,* where no interlocular space is formed between consecutive chambers on the spiral side, a deep interlocular space is present in *Pseudorotalia* on both sides of the test. The septal flap is glued only to the axial wall (previous coil) and to the former septal face along the foraminal border. At the edge of the septal face a string of imperforate pustules, formed by local thickenings of the outer lamella, is present in the newly formed chamber at the junction between lateral wall and septal face, as well as between lateral wall and septal flap. These pustules are locally restricting, but not closing, the interlocular space (pl. 8, fig. 2). This situation is very similar to that in *Ammonia,* where, however, the interlocular space is broader, and the thickenings of adjacent chambers along this space are neither so strongly projecting, nor so near to each other.

In *Pseudorotalia,* with further secondary lamination, the opposing rows of pustules along the edges of the interlocular space become more and more thickened until they coalesce completely after 3–4 instars, leaving rounded to oval communications open into the interlocular space (pl. 8, figs 3–4). These openings are the "canals" of Reiss & Merling (1958) and of Reiss (1963) as well as the "toothplate foramina" of Hofker (1968). This is unlike *Ammonia* where the rows of pustules do not meet. In *Pseudorotalia,* the coalescence may be regular, whereby bridges parallel to the periphery are formed, with the sutural openings running in one line, or irregular, whereby bridges oblique to the sutures are formed with irregularly alternating rows of openings in between.

Although only as a matter of degree, another difference between *Ammonia* and *Pseudorotalia* may be noted, viz. the degree of distal folding of the foraminal plate which in *Pseudorotalia* is much stronger than in *Ammonia* (pl. 8, fig. 5).

Pararotalia

The following species of *Pararotalia* were examined: *P. inermis* (Terquem) from the Lutetian of Grignon, France (type species of *Pararotalia*); *P. mexicana mecatapecensis* (Nuttall) from the Lower Miocene of Australia; *P. calcar* (d'Orbigny) from Recent sediments of the Gulf of Elat, Israel; *Pararotalia* sp. from the Oligocene of Gaas, France.

The wall structure could be observed in *P. inermis* and *P. calcar* only, while it was obscured by recrystallisation in the other species examined. The original wall structure of *P. inermis* and *P. calcar* is identical with that of *Ammonia* and *Pseudorotalia* (pl. 8, fig. 6; pl. 9, fig. 1).

All the species of *Pararotalia* examined possess deep interlocular spaces on the umbilical side, formed by the septal flap and a preceding septal face; a rather slightly folded foraminal plate, extending from the septal flap and protruding into the chamber (including the last formed one); an umbilical coverplate (Loeblich & Tappan, 1957) extending from the foraminal plate into the preceding chamber and being attached there to the (preceding) foraminal plate (pl. 9, figs 2–6; pl. 10, figs 1–3).

The aperture in all species examined is interio-marginally drawn out into the apertural face in a kind of comma-shape. The distal border of the aperture is provided with thickenings forming an "apertural rim". The apertural face in the species examined is strongly pustulated, a feature which can also be observed in section (pl. 10, fig. 4). In *P. calcar* and in *P. mexicana* ridge-like thickenings running obliquely from the suture line in peripheral direction originate both from the junction septal face – lateral wall and from that of the lateral wall with the septal flap. They parallel roughly the chamber form. At the periphery of *P. calcar* these ridges coalesce with the inflational, "feathery" spines of the chambers. Secondary lamination thickens the ridges, whereby the interlocular spaces are bridged over and cavities are trapped. These communicate with the outside through narrow canals leading into the peripheral spines (pl. 10, figs 5–6).

Labial apertures are present in all species and they remain open after the formation of the coverplates (pl. 10, figs 3 and 5).

Calcarina spengleri (Gmelin)

Sections through the primary chamber wall of this species show the inner lining and the outer lamella, with the median layer between them, as in the other rotaliaceans mentioned. However, the platelets seem to be thicker than e.g. in *Ammonia* or in *Pseudorotalia* (pl. 11, figs 1–3). Strong primary lamination is present in both outer and inner layers (pl. 11, fig. 2). The crystals in the median layer are not as prominent in *Calcarina,* since the platelets of the adjacent layers of the primary wall are thicker and larger with respect to the crystal pairs in the median layer as compared to other rotaliaceans.

The apertures of adult chambers are multiple, rounded, interio-areal openings arranged in several rows. Each aperture is surrounded by a prominent collar-like rim (pl. 11, figs 4–5). In the earlier chambers of the test the cameral aperture appears to be single, and interio-marginal like in *Pararotalia* (pl. 11, fig. 6). When converted into foramina all apertures retain their original shape.

In the earlier parts of the test (in both mega- and microspheric forms) a foraminal plate is present, as well as a coverplate extending into a preceding chamber, again like in *Pararotalia.* In the adult chambers of the test, where multiple apertures occur, no coverplate is present any more and neither is a distinct foraminal plate recognizable, except a short forward extension of the septal flap at the umbilical tip of the chambers.

The apertural face is imperforate and covered by prominent elongated ridges running from the interior margin in a general peripheral direction (pl. 12, fig. 1).

Elongated thickenings are present both on the anterior and on the posterior edges of the lateral chamber wall, running into a general peripheral direction where part of them extends into the radial spines. The interlocular space communicates with the exterior through openings left between incompletely coalescing thickenings of adjacent chambers. Canals also continue into the complicated pathways of the inflational spines (pl. 12, figs 3 and 5). As secondary lamination covers the test, intramural cavities are formed (pl. 12, fig. 4). All ornamentational features are extremely complex, as can be seen on the accompanying figures. The system of coalescense along the suture line, as well as the "marginal cord"-like ridge-and-groove pattern present in the spines and its communication with the interlocular spaces, are all strongly reminiscent of the construction of *Operculina* (see below).

Operculina sp.

Specimens of *Operculina* collected in living state from the Gulf of Elat, were examined. Since the recent *Operculina* from the Gulf of Elat are at present under revision by Prof. L. Hottinger, Univ. of Basel, no species name is used here.

The wall structure of the specimens examined is identical with that of the other rotaliaceans described showing the herringbone pattern in both outer lamella and inner lining which are separated by the characteristically beaded, median layer. Both outer lamella and inner lining show primary lamination (pl. 12, fig. 6; pl. 13, figs 1–3).

The apertures are multiple, an interio-areal row of rounded openings surrounded by thickened rims (pl. 13, fig. 4). The apertural area is resorbed into an interio-marginal slit at the conversion of apertures into foramina (pl. 13, fig. 5). The septal face appears to be imperforate. It is covered by elongated thickenings running in an anastomosing pattern from the base of the septal face (interior margin) towards the periphery of the chamber (pl. 13, fig. 4) where they continue and form the islands of the "marginal cord".

Both at the junction between lateral wall and septal face, and between lateral wall and septal flap, rather irregular, imperforate, rounded thickenings are present on the final chamber (pl. 13, fig. 6). With the addition of a new chamber the thickenings coalesce along the border of the interlocular space leaving very narrow and scattered openings (canals) as communications of the latter with the outside of the test (pl. 14, fig. 1). This situation is in fact very similar to that in *Pseudorotalia* where, however, the residual openings are much larger. Unlike in *Pseudorotalia* no secondary lamination is present on the walls of the interlocular space in *Operculina* (pl. 14, fig. 2); this may be due to the relatively small size of the residual openings left in the latter. Secondary lamination thickens the island-like ridges of the marginal cord at the periphery, being very thin on the sides of these ridges (pl. 14, fig. 3). The grooves between the ridges of the marginal cord communicate with the interlocular spaces at the periphery. Moreover, scattered, radially directed canals lead from the interlocular space into the secondarily thickened marginal cord (radial canals).

The septal flap is imperforate, glued to the ridges of the apertural face, and reflecting them in elongated corrugations (pl. 14, fig. 5). The actual spaces between flap and previous septal face are, therefore, elongated and narrow (pl. 14, fig. 2). Rounded foramina are found scattered on the area of the septal flap (pl. 14, fig. 5).

In each chamber, including the last formed one, two folded extensions of the septal flap are found at its interior margin on both sides of the (resorbed) foramen (pl. 13, fig. 5). They run towards the septal wall of the respective chamber with which they are fused and they are also glued to the axial wall (former coil), together with which they form tube-like spaces (pl. 14, fig. 6). These plates appear in section as hook-like structures attached to the previous coil (Reiss, 1963). Position and structural relationship of these folded plates indicate that they are foraminal plates. They correspond to part of the toothplates of Hofker (see 1968) and to the toothplate of Reiss (1963) and other authors, while the spaces formed by them correspond to the so-called umbilical canals of authors. They seem to open frontally. No umbilical coverplate extends into an earlier chamber, thus emphasizing the individuality of the foraminal plate.

Elphidium macellum (Fichtel & Moll) and *Cellanthus craticulatus* (Fichtel & Moll)

The wall structure of the type species of *Elphidium* and *Cellanthus* (see Loeblich & Tappan, 1964) is identical with that of the other rotaliaceans described above. A columnar veneer has been observed in the outermost part of the outer lamella (pl. 15, figs 1–5; pl. 16, fig. 4). Both species are optically "radiate" or indistinctly so (Wood, 1949; Krasheninnikov, 1960). Secondary lamination penetrates through the fossettes deeply into the interlocular spaces, coating both walls in *Elphidium* and mainly the septal flap in *Cellanthus*.

The spines along the fossettes shown by Marszalek et al. (1969) are seen in section to be inflational features (pl. 15, fig. 4). Secondary lamination thins out strongly on the side-walls of the fossettes (pl. 15, fig. 4). It is absent inside the retral processes (pl. 16, fig. 1).

Lakeside-infilled preparations of *Cellanthus* show in vertical section the "umbilico-spiral canals" which are in fact the tubular spaces formed by the foraminal plates with the adjacent coil and opening frontally, like in *Operculina* (cf. Hofker; Reiss & Merling; Reiss, opp.cit., as well as Wade, 1957) (pl. 16, figs 2–3). These spaces lead into the "vertical canals" of the laminated umbonal knobs. No coverplates are present. Spinose projections are found on the walls of the vertical canals, similar to those in the fossettes (pl. 16, fig. 5).

Asterorotalia pulchella (d'Orbigny)

Like in *Ammonia* and the other rotaliaceans described three layers compose the primary chamber wall of the type species of *Asterorotalia,* viz. an inner lining and an outer lamella exhibiting the characteristic herringbone pattern of stacked platelets, and a beaded median layer in between (pl. 17, fig. 1).

The pustulated and imperforate septal face is strongly bent inward and backward, particularly in the umbilical region where it joins a large, perforate extension (lip?) of the umbilico-lateral chamber wall (pl. 17, figs 2–3). This extension continues into a posterior and peripheral direction forming a "suprasutural" cover over most of the interlocular space on the umbilical side (pl. 17, fig. 4). The suprasutural extension (which is probably homologous with part of a lip, although it is largely perforate) is glued to the former chamber, while its anterior part forms an elongated opening between itself and the wall of its own chamber, leading into the interlocular space (pl. 17, fig. 5). The interlocular space is also present on the periphery and for some distance on the spiral side, without being covered by the extension (pl. 17, fig. 4).

The cameral aperture is comma-shaped, interio-marginal and reminiscent of that in *Pararotalia* (pl. 17, figs 2 and 6). At the infold of the septal face (part of "lip" of Reiss & Merling, 1958; "toothplate" of Hofker, 1968) the aperture is strongly narrowed and may even become interio-areal (pl. 18, fig. 1). The apertural rim is strongly projecting and forms a kind of collar around the aperture (pl. 17, figs 2 and 6; pl. 18, fig. 1).

The septal flap is glued to the previous septal face only in that part which lies near the spiral side, as well as to the outer border of the foramen (pl. 18, fig. 2). Where the flap is not glued to the previous septal face a wide interlocular space is formed (pl. 18, fig. 3).

The septal flap extends into a foraminal plate, which is distally strongly folded backwards, like in *Pseudorotalia.* The foraminal plate continues into an umbilical coverplate in the preceding chamber, where it is attached to the foraminal plate of that chamber (pl. 18, fig. 4).

The spines originate from the peripheral parts of the interlocular spaces; they are hollow and secondarily laminated (pl. 18, figs 4–5). Secondary lamination is present on the walls of the interlocular space also where it is covered by the suprasutural extension (pl. 18, fig. 6).

Rotalia trochidiformis Lamarck

Specimens of the type species of *Rotalia* from the type locality Grignon were examined. Despite the fact that diagenetic processes have affected most of the material, the herringbone arrangement of the platelets in both outer lamella and inner lining can still be recognized, while the median, beaded layer can be observed in places (pl. 19, figs 1–2). Like in all other rotaliaceans mentioned, the pores of *Rotalia* are larger and more distinctly hexagonal in outline on the inside of the primary chamber wall than on the outside surface, where they are smaller and rounded to oval in shape (pl. 19, fig. 3).

Despite its basically simple architecture, the morphology of the test of *Rotalia* appears highly complex in sections. This is due to chamber form and lip attachement.

A marginal prolongation and an inframarginal sulcus are present whereby the septal face is strongly drawn backward between periphery and umbilicus (pl. 19, fig. 4). Along the interio-marginal aperture, near the periphery on the umbilical side, the distal wall turns inward sharply with the sulcus, forming a deeply penetrating extension which is attached to the axial wall (adjacent previous coil) (pl. 19, fig. 5).

The posterior wall of the chamber is formed by a septal flap which together with the preceding septal face delimit a wide interlocular space (pl. 19, fig. 6; pl. 20, fig. 1; pl. 21, figs 3–6).

Along the aperture a thickened rim is present extending into a broad, triangular, imperforate umbilical lip (pl. 19, fig. 4). This lip is usually fused with its umbilical tip both to the preceding lip of the same coil and to the inflational pustules in the umbilical area of the previous coil. Thus, an anterior and a posterior labial aperture are formed (Reiss & Merling, 1958; Reiss, 1963) (pl. 19, fig. 4; pl. 20, fig. 2; pl. 21, figs 2–3, 5–6). Almost at the border between septal face and lateral chamber wall the lip becomes separated from the latter (pl. 19, figs 4 and 6; pl. 20, fig. 2; pl. 21, figs 4–5). The lip is drawn out backwards towards the suture into a peripheral direction becoming attached to the lateral wall of the respective chamber (pl. 19, fig. 6). The line of attachment runs from the border between lateral wall and septal flap in an oblique anterior direction. Both lateral chamber wall and lip are strongly curved inwards along this line of attachment (pl. 20, fig. 3), thus forming what appears as the structure referred to as "astral furrow" or "toothplate" by various authors (cf. Davies, 1932, Reiss & Merling; Reiss, Hofker; Smout, opp.cit.). The attachment of the lip to the lateral chamber wall is, however, incomplete and an open umbilical, "labial" aperture is thus formed between them (Smout, 1954; Reiss & Merling, 1958) (pl. 20, fig. 4; pl. 21, figs 1–6). The shape of chamber wall and lip along the line of attachment produces the cornet-shaped infold described by Davies (opp. cit.) as the "puckering up" of the umbilical wall along the "astral lobe" (i.e. the lip).

The septal flap is attached to the preceding septal face along the border of the (partially resorbed at its inner margin) foramen and to the spiral wall of the chamber. The axial wall of the chamber (former coil) is seen to be largely covered by wall material of the respective chamber. This material coalesces with both the septal flap and the septal face of the same chamber (pl. 20, fig. 2). The state of preservation of the specimens examined precludes a determination of the nature of the axial cover (inner lining?).

Neither a foraminal plate, nor a coverplate, like those found e.g. in *Ammonia,* occur in *Rotalia.*

The illusion of a toothplate is created particularly in sections by the shape of the septal wall (compare e.g. *Neoeponides* or *Alabamina;* Reiss, 1960), as well as by the shape of lateral wall and lip at their attachment (pl. 20, fig. 5).

Imperforate, elongated thickenings occur both at the border between septal face and lateral chamber wall, as well as between the latter and the septal flap. Moreover, thickenings are present along the umbilical labial aperture and at the borders of the lip. These knobs and ridges are inflationally thickened by secondary lamination in later instars.

Discussion

All species of rotaliaceans examined by the present authors possess the same primary wall structure, viz. an inner lining and an outer lamella composed of stacked calcite platelets, and in between a median layer composed of paired calcite crystals enveloped in organic material. While the inner lining forms the interior part of the chamber wall, the septal flap, the foraminal plate, and the coverplate (wherever present), the outer lamella coates the inner lining on exposed surfaces and wherever a connection with extralocular cytoplasm is possible. Furthermore, the outer lamella covers surfaces of earlier formed chambers where such surfaces are in contact with extralocular cytoplasm, resulting in secondary lamination.

The wall structure of the rotaliaceans is, therefore, in principle identical with that of the "bilamellar" groups of foraminiferids, viz. Robertinacea, Globigerinacea, Orbitoidacea, Anomalinacea and Cassidulinacea (part) (Loeblich & Tappan, 1964).

While in these latter groups both optically radiate and granulate walls built of calcite platelets occur, as well as walls built of either morphologically granular calcite (optically radiate or granulate), or of prismatic aragonite all Rotaliacea seem to have their inner lining and outer lamella composed of stacks of calcite platelets which produce optically radiate extinction. The crystals of the median layer are paired in all rotaliaceans and in optically radiate, platy orbitoidacean genera, like *Cibicides,* but heterogenous in size, rather irregularly distributed, and apparently not paired in such optically granulate, though platy, genera as *Heterolepa.* No crystals have hitherto been found in the organic median layer of the planktonic Globigerinacea. The amount of organic material in the median layer seems to be larger in bilamellar forms other than rotaliaceans, thus showing up in the former group more distinctly as a "dark line" in sections observed under the light microscope. This difference in amount of organic material in the median layer is also evident in the electron microscope, both transmission and scanning (compare Hansen, Reiss & Schneidermann, 1969; Hansen, 1970).

The difference in wall structure between the rotaliaceans and other platy, optically, radiate, bilamellar foraminiferids is one of degree and not of kind. The Rotaliacea can be separated from other calcitic groups by the presence of a septal flap, as proposed originally by Smout (1954). The victoriellids and their allies may have to be transferred again to the Rotaliacea (Loeblich & Tappan, 1964), although they possess a "murus reflectus", absent in the rotaliaceans (Reiss, 1967). The bilamellar Robertinacea which possess a septal flap are clearly separated from the Rotaliacea by their aragonitic walls. The similarity between Rotaliacea and Robertinacea has been noted by Hofker and by Reiss (opp. cit.).

The interlocular space in the Rotaliacea seems to contain actively streaming, extralocular cytoplasm (cf. Reiss, 1963), as indicated by the thickenings at its borders and formation of openings between these thickenings wherever they coalesce, either primarily or secondarily; by the communication of the interlocular space with such structures as marginal cord, or inflational, canaliculate spines; by the formation of trapped intramural cavities communicating with the interlocular spaces; as well as by the thinning out of secondary lamellae within these spaces.

Whether or not the folded foraminal plate of the rotaliaceans is homologous with a true toothplate, like in the Buliminacea, remains questionable. It is certainly not characteristic of all rotaliaceans. An umbilical coverplate may or may not be present in the Rotaliacea.

All ornamentational features are in fact inflational, imperforate and produced by outer lamellae (Reiss, 1963). Thinning out of secondary lamination, which can hardly be resolved under the light microscope, led to the belief that these ornamentational features are in part incisional, in the sense of Smout (1954).

The present investigation clarifies certain confusing statements by earlier authors concerning the morphology of the rotaliaceans studied and reconciles various divergent views on their structure.

The structure of *Pararotalia* as described by Loeblich & Tappan (1957) is confirmed, although the latter authors did not distinguish between foraminal and umbilical coverplates (cf. also Ujiié, 1966). Cifelli's (1962) description of the morphology of *Ammonia* is correct in showing the relationship between foraminal and coverplates (collectively referred to by him as the "axial plate"), but confuses (opp.cit., pl. 21) the foraminal plate with the "apertural lip". This latter description also erroneously states that the foraminal plate is absent in the final chamber and that the septa of *Ammonia* are simple (cf. Wood, Haynes & Adams, 1963). Hofker; Reiss & Merling, and Reiss (opp.cit.) have evidently confused the foraminal plate in *Ammonia, Pseudorotalia* and *Pararotalia* with the coverplate extending into a previous chamber and believed both structures to be formed within one and the same chamber (cf. also Ujiié, 1965). However, these authors have correctly recognized the relationship between foraminal plate and septal flap. Hofker; Reiss & Merling; and Reiss (opp.cit.) have erroneously described toothplates in *Rotalia.* Smout's (1954) emendation of Davies' description of *Rotalia* is correct; the confusing picture in thin sections of *Rotalia* is produced by chamber form and by lip attachment. The symmetrical foraminal plates, producing the umbilico-spiral canals in *Operculina, Elphidium* and *Cellanthus* were correctly described by Hofker and by Reiss (opp.cit.).

Rotalia is evidently a primitive form, since it possesses a septal flap only and no foraminal or coverplates; it resembles strongly certain Discorbidae. The relationship of *Pararotalia* to *Calcarina* is evident from the ontogeny of the latter genus (Hofker, opp.cit.). The phylogenetic relationships among the Rotaliacea as proposed by various authors (Smout, 1955; Drooger, 1960; Reiss, 1963, etc.) still require a thourough investigation.

The classification within the suborder Rotaliina (all lamellar perforate foraminiferids) as proposed by Loeblich & Tappan (1964) can be largely retained. The Discorbacea, the Anomalinacea and the Cassidulinacea require, however, careful study with regard to their wall ultrastructure, viz. primary layering and the relationship between optical and ultrastructural properties of crystals building their tests. Representative genera of these groups are being investigated by the present authors.

The present investigation once more indicates – as pointed out earlier by Drooger (1954) and by Reiss (1963) – the difficulties in establishing a hierarchy of characters in the classification of the Foraminiferida.

Appendix

After the completion of the present paper a galley-proof of S. Parvati's publication "A study of some rotaliid foraminifera" was sent to Z. Reiss by Professor C. W. Drooger. Although terminologies employed differ considerably, the morphological descriptions of *Ammonia* and *Rotalia* as given here are largely in agreement with those given by Parvati. Such points of disagreement as e.g. Parvati's claim that the lamellae are not enveloping in *Ammonia* on the dorsal side is clarified by the present electron microscopical study.

Dansk sammendrag

Repræsentanter for foraminifer-slægterne *Ammonia, Pseudorotalia, Pararotalia, Calcarina, Operculina, Elphidium, Cellanthus, Asterorotalia* og *Rotalia* er blevet undersøgt i scanning elektron mikroskop. Alle undersøgte former opbygger deres primære vægge efter det »bilamellære« princip. Væggenes ydre og indre lamel er opbygget af stakke af tynde calcitplader. Den ydre og indre lamel adskilles af et mellem-lag, der er dannet af parrede calcit-krystaller, som ligger i en organisk matrix. Alle de undersøgte skaller er optisk radiate. Rotaliderne besidder en »septal flap«, som med det forudgående septum danner et intercameralt rum, der kan være delvis tildækket – enten primært eller sekundært. Foraminale plader, der strækker sig i distal retning fra »septal flap«, er til stede i alle undersøgte slægter med undtagelse af *Rotalia*. Hos *Ammonia, Pseudorotalia, Pararotalia* og *Asterorotalia*, samt i tidlige ontogenetiske stadier hos *Calcarina*, findes en umbilical dækplade, der strækker sig fra foraminal-pladen ind i det forudgående kammer, hvor den er fasthæftet til foraminal-pladen.

Sekundær laminering dækker alle blottede overflader af de forudgående kamre samt siderne og bunden af de interloculære rum, hvor den dog bliver særdeles tynd. På siderne af ornamentale strukturer kunne ligeledes observeres aftagende tykkelse af de sekundære lameller. Alle ornamentale strukturer er af den type som normalt omtales som »inflational« og er udelukkende opbygget af ydre lameller.

Hans Jørgen Hansen
Institut for historisk Geologi og Palæontologi,
Østervoldgade 5, DK–1350 København K, Denmark

Zeev Reiss
Department of Geology, The Hebrew University
Jerusalem, Israel

November 12th, 1970

References

Brotzen, F. 1948: The Swedish Paleocene and its foraminiferal fauna. *Sver. geol. Unders.* **42,** 1–140.

Cifelli, R. 1962: The morphology and structure of *Ammonia beccarii* (Linné). *Contr. Cushman Found. foram. Res.* **13,** 119–126.

Davies, L. M. 1932: The genera *Dictyoconoides* Nuttall, *Lockhartia* nov. and *Rotalia* Lamarck: Their type-species, generic differences, and fundamental distinction from the Dictyoconus group of forms. *Royal Soc. Edinburgh, Trans.* **57,** 397–428.

Drooger, C. W. 1954: Remarks on the species concept in paleontology. *The Micropaleontologist* **8,** 4 only.

Drooger, C. W. 1960: Some early rotaliid foraminifera I–III. *Proc. Koninkl. Nederl. Akad. Wetensch.* Ser. B. **63,** 287–334.

Hansen, H. J. 1968: A technique for removing gold from plated calcareous microfossils. *Micropaleontology* **14,** 499–500.

Hansen, H. J. 1969: Combined light and electron microscope studies of thin sections. *Micropaleontology* **15,** 246 only.

Hansen, H. J. 1970: Electron-microscopical studies on the ultrastructures of some perforate calcitic radiate and granulate foraminifera. *Biol. Medd. Dan. Vid. Selsk.* **17** (2), 1–16.

Hansen, H. J., Reiss, Z. & Schneidermann, N. 1969: Ultramicrostructure of bilamellar walls in foraminiferida. *Rev. Espanola Micropal.* **1,** 293–316.

Hofker, J. 1951: The foraminifera of the Siboga Expedition. *Siboga Expeditie. Mon.* **1V,** (c), 3, 514 pp.

Hofker, J. 1960: The aperture of *Pararotalia tuberculifera* (Reuss). *Natuurhist. Maandbl. Limburg* **49,** 79–83.

Hofker, J. 1963: Once again *Pararotalia tuberculifera* (Reuss). *Natuurhist. Maandbl. Limburg* **52,** 80–82.

Hofker, J. 1968: Studies of foraminifera. *Publ. Natuurh. Genoot. Limburg* **18,** 135 pp.

Krasheninnikov, V. A. 1960: Mikrostruktura stenki u Miotsenovykh diskorbid i rotaliid. *Voprosy Mikropal.* **3,** 41–49.

LeCalvez, Y. 1949: Révision des Foraminiféres Lutétiens du Bassin de Paris. II Rotaliidae et familles affines. *Mém. Explic. Carte Géol. France,* 1–54.

Loeblich, A. R. & Tappan, H. 1957: Morphology and taxonomy of the foraminiferal genus *Pararotalia* Le Calvez, 1949. *Smithsonian Misc. Coll.* **135** (2), 1–24.

Loeblich, A. R. & Tappan, H. 1962: The status and type species of *Calcarina, Tinoporus* and *Eponides* (Foraminiferida). *Contr. Cushman Found. foram. Res.* **13,** 33–38.

Loeblich, A. R. & Tappan, H. 1964: Sarcodina chiefly "Thecamaebians" and Foraminiferida. In: *Treatise on Invertebrate Paleontology* (ed. R. C. Moore). Part **C.** Prostista 2, 1–900. Lawrence: Univ. of Kansas Press.

Marszalek, D. S., Wright, R. C. & Hay, W. W. 1969: Function of the test in foraminifera. *Trans. Gulf Coast Ass. geol. Soc.* **19,** 341–352.

McGowran, B. 1966: Bilamellar walls and septal flaps in the Robertinacea. *Micropaleontology* **12,** 477–488.

Reiss, Z. 1957: Notes on foraminifera from Israel, 5: Studies on Victoriellidae. *Bull. geol. Surv. Israel* **11,** 1–9.

Reiss, Z. 1960: Structure of so-called *Eponides* and some other rotaliiform foraminifera. *Bull. geol. Surv. Israel* **29,** 1–28.

Reiss, Z. 1963: Reclassification of perforate Foraminifera. *Bull. geol. Surv. Israel* **35,** 1–111.

Reiss, Z. 1967: *Victoriella* (Foraminiferida) from Israel. *Israel J. Earth-Sci.* **16,** 111–119.

Reiss, Z. & Merling, P. 1958: Structure of some Rotaliidae. *Bull. geol. Surv. Israel* **21,** 1–19.

Reiss, Z. & Schneidermann, N. 1969: Ultrastructure of *Hoeglundina. Micropaleontology* **15,** 135–144.

Towe, K. M. & Cifelli, R. 1967: Wall ultrastructure in the calcareous foraminifera: crystallographic aspects and a model for calcification. *J. Paleont.* **41,** 742–762.

Smout, A. H. 1954: *Lower Tertiary foraminifera of the Qatar Peninsula.* British Mus. (Nat. Hist.), London, 1–96.

Smout, A. H. 1955: Reclassification of the Rotaliidea (Foraminifera) and two new Cretaceous forms resembling *Elphidium. J. Wash. Acad Sci.* **45,** 201–210.

Ujiié, H. 1965: Shell structure of Japanese smaller foraminifera Part 1. *Ammonia tochigiensis* (Uchio, 1951). *Trans. Proc. Palaeont. Soc. Japan,* N. S. **60,** 156–165.

Ujiié, H. 1966: Shell structure of Japanese smaller foraminifera part 2. *Pararotalia nipponica* (Asano, 1936). *Trans. Proc. Palaeont. Soc. Japan,* N. S. **61,** 191–200.

Wade, M. 1957: Morphology and taxonomy of the foraminiferal family Elphidiidae. *J. Wash. Acad. Sci.* **47,** 330–339.

Wood, A., Haynes, J. & Adams, T. D. 1963: The structure of *Ammonia beccarii* (Linné). *Contr. Cushman Found. foram. Res.* **14,** 156–157.

Wood, A. 1949: The structure of the wall of the test in the foraminifera; its value in classification. *Q. Jl geol. Soc. Lond.* **104,** 229–255.

Plate 1

Figs 1–3. *Ammonia beccarii* (Linné). Recent, Gulf of Elat, Israel.

1. Deeply etched section through wall of penultimate chamber showing organic material of median layer intimately connected with organic pore-linings. (R-88). × 1050.

2. Horizontal section through part of septum showing arrays of platelets in outer lamella and inner lining, as well as the paired crystals in the median layer. (R-32). × 5620.

3. Vertical section through septum showing inner lining, outer lamella (the latter with primary lamination), and the separating median layer. Note veneer in outer lamella. (R-29). × 2970.

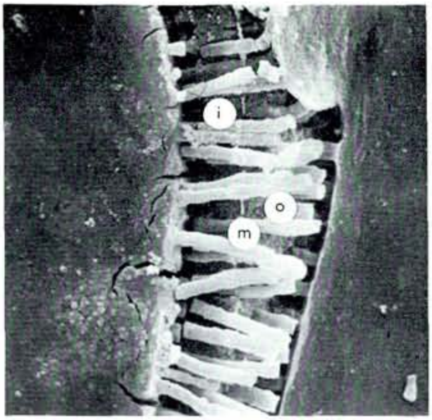
Figs 4–6. *Cibicides lobatulus* (Walker & Jacob). Recent, Kattegat, Denmark.

4. Horizontal section through part of septum showing outer lamella and inner lining built of irregularly stacked platelets and pairer crystals in median layer. Very slightly etched. (R-136). × 2250.

5. Horizontal section through outer wall of antepenultimate chamber showing inner lining, median layer and outer lamella covered by secondary lamination (outer lamellae of two last chambers). (R-136). × 1500.

6. Oblique view of deeply etched section through septum showing the high concentration of organic material in the median layer. (R-136). × 1500.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *v* – veneer; *p* – primary lamination; *s* – secondary lamellae.



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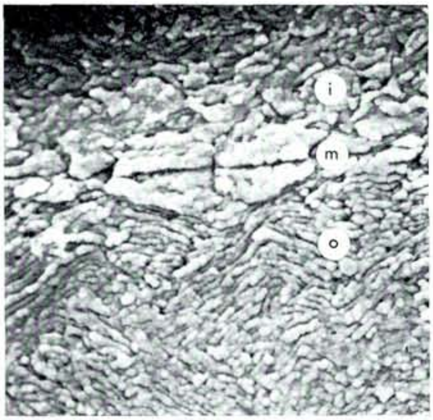

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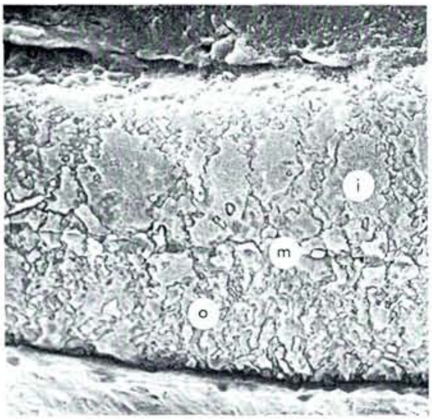

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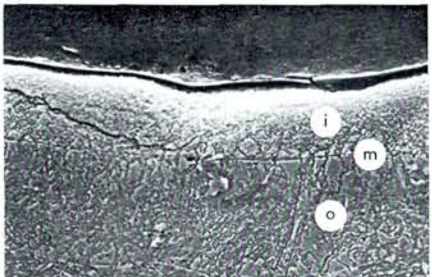

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Plate 2

Fig. 1. *Cibicides lobatulus* (Walker & Jacob). Recent, Kattegat, Denmark. Horizontal section through septum showing furrow left in place of median layer where organic material and crystals have been tourn out. (R-136). × 1500.

Fig. 2. *Heterolepa* cf. *subhaidingeri* (Parr). Recent, New Zealand. Horizontal section through part of septum showing outer lamella and inner lining composed of platy crystals, and large crystals enveloped in organic material of the median layer. (R-137). × 3860.

Fig. 3. *Lenticulina orbicularis* (d'Orbigny). Recent, Kei Islands, Pacific Ocean. Horizontal section through secondarily laminated outer chamber wall showing consecutive outer lamellae built of stacked calcite platelets producing herringbone pattern. (R-63). × 4570.

Figs 4–6. *Ammonia beccarii* (Linné). Recent, Rimini, Italy.

4. Horizontal section through junction between final chamber with the preceding one near test periphery and beginning of interlocular space. Note termination of the median layer of last chamber and continuation of inner lining as septal flap, as well as its adherence to previous septal wall. (R-32). × 1610.

5. section like in fig. 4 in older part of the test and nearer the spiral side. Note secondary lamination. (R-32). × 1125.

6. Oblique umbilical view of fractured specimen showing foramen, foraminal plate and septal flap. (R-85). × 146.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *s* – secondary lamellae; *fp* – foraminal plate; *sf* septal flap; *x* – crystal in median layer.

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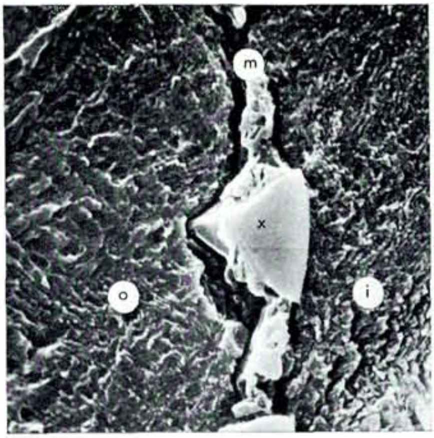

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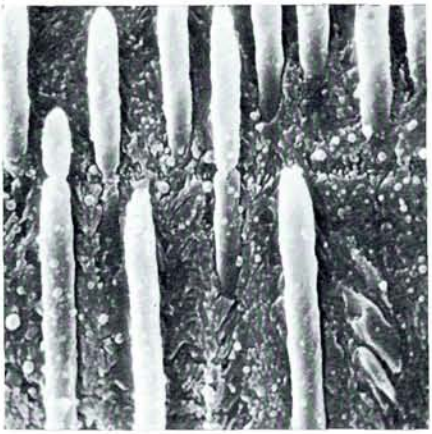

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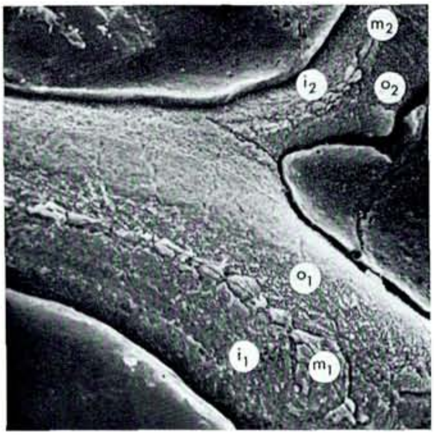

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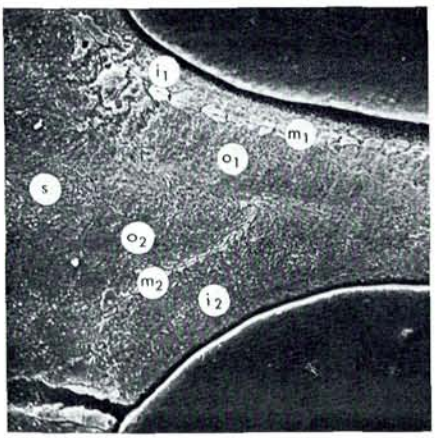

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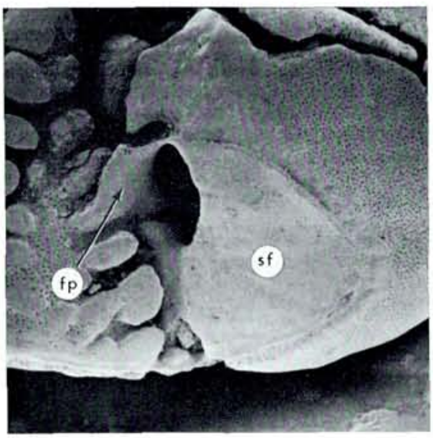

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Plate 3

Figs 1–6. *Ammonia beccarii* (Linné). Figs 1–2, specimen from Rimini, Italy; figs 3–6, specimens from Gulf of Elat, Israel.

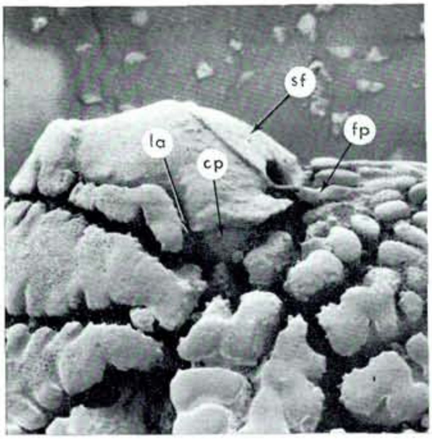
1. Oblique umbilical view showing relationship between septal flap, foraminal plate and coverplate. Note posterior labial aperture. (R-85). × 101.

2. Oblique umbilical view showing umbilical coverplate and posterior labial aperture. (R-85). × 207.

3–4. Horizontal section showing foraminal plates and their relationship to septal flap and coverplate (fig. 4 detail of fig. 3). (R-116). Fig. 3, × 51; Fig. 4, × 161.

5–6. Horizontal section in umbilical region, passing through lips and labial apertures, as well as coverplates. (R-32). Fig. 5, × 112; fig. 6, × 442.

Abbrevations: *la* – umbilical labial aperture; *cp* – coverplate; *sf* – septal flap; *fp* – foraminal plate; *l* – lip.



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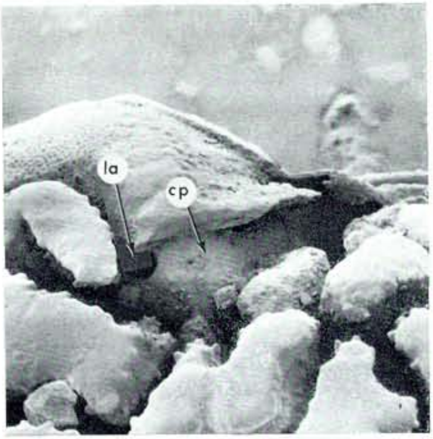

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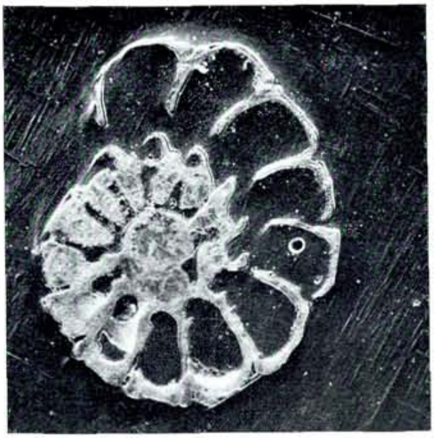

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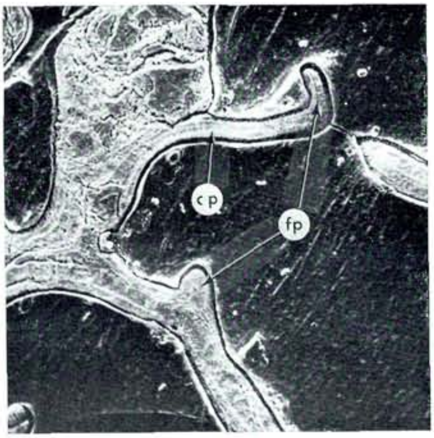

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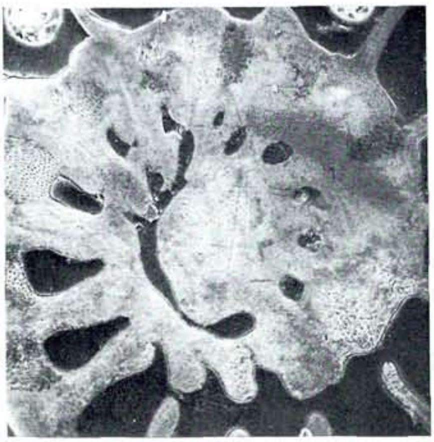

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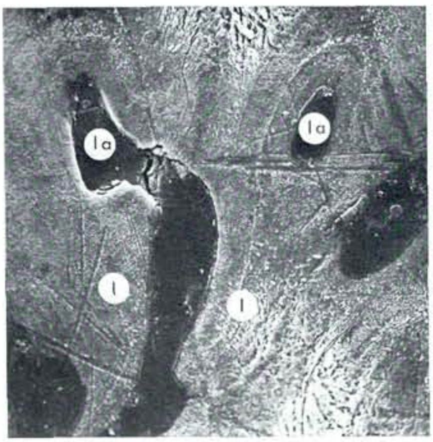

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Plate 4

Figs 1–6. *Ammonia beccarii* (Linné). Gulf of Elat.

1. Detail of Pl. 3, fig. 5. Note median layer in lips and coverplates. (R-32). × 788.

2. Vertical, partly tangential section showing interlocular spaces on umbilical side and secondary lamination thinning out on the walls of the interlocular space. (R-29). × 322.

3–4. Horizontal section through umbilical area showing secondary lamination on foraminal and coverplates, as well as median layer in the latter. (R-32). Fig. 3, × 157; fig. 4, × 1490.

5. Horizontal section through secondarily laminated outer chamber wall showing interlamellar organic sheets intimately connected with the organic pore linings. (R-88). × 2100.

6. Deeply etched horizontal section through secondarily laminated outer chamber wall. Note pore constrictions at lamellar boundaries. (R-32). × 982.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *s* – secondary lamellae; *cp* – coverplate.

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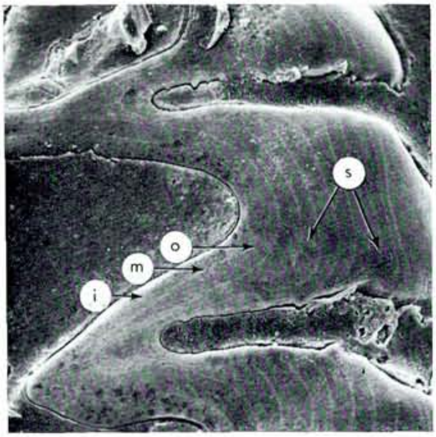

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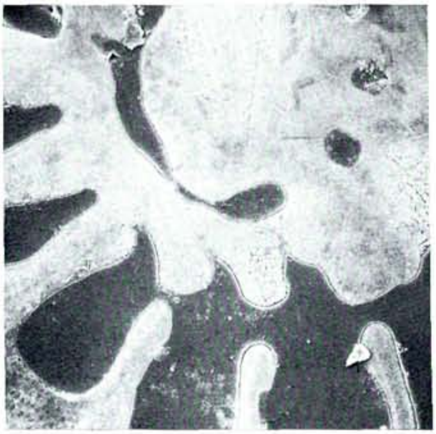

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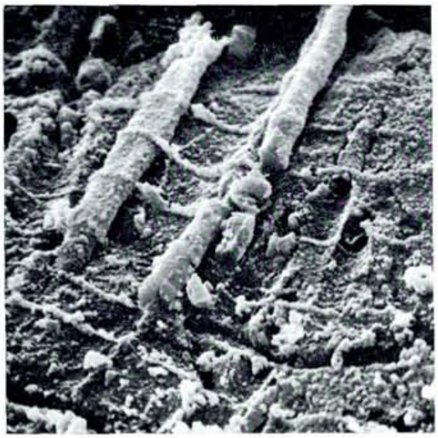

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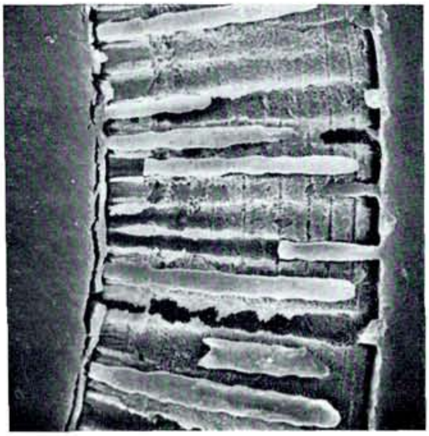

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Plate 5

Figs 1–4. *Ammonia beccarii* (Linné). Gulf of Elat, Israel.

1. Vertical section through septum near its junction with lateral spiral wall showing disposition of various layers. Note continuity of outer lamellae of consecutive chambers. (R-29). × 825.

2–3. Oblique umbilical views of specimen with final chamber preserved. Note posterior labial aperture (in fig. 2), fusion of lips, interlocular spaces, inflational ridges, and pustules on imperforate septal face (in fig. 3). (R-35). Fig. 2, × 56; fig. 3, × 120.

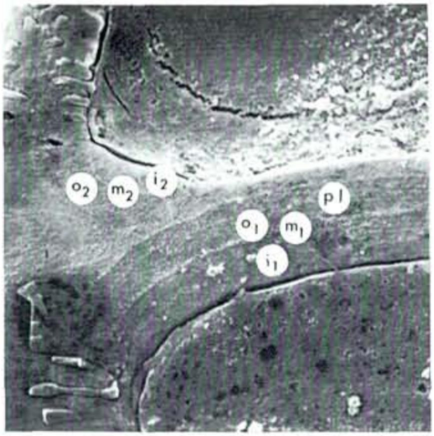
4. Oblique spiral view of last suture of specimen figured in figs 2–3. Note the absence of interlocular space. (R-35). × 750.

Figs 5–6. *Ammonia batava* (Hofker). Recent, Kattegat, Denmark.

5. Oblique umbilical view of specimen with broken final chamber showing attachment of lip and labial aperture. (R-39). × 105.

6. Oblique umbilical view of same specimen as in fig. 5, showing apertural infold, the septal flap and foraminal plate, as well as the shallow, interlocular space along the spiral suture. (R-39). × 105.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *pl* – primary lamination; *is* – interlocular space; *sf* – septal face; *la* – labial aperture; *l* – lip; *ai* – apertural infold; *lia* – lip attachment.



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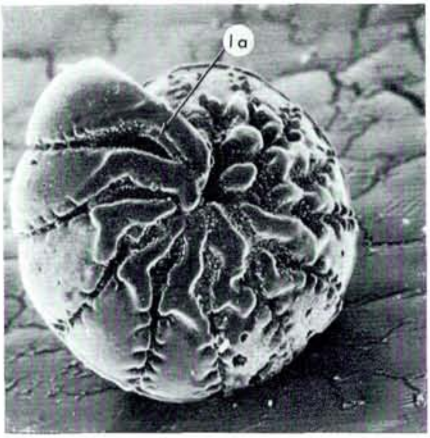

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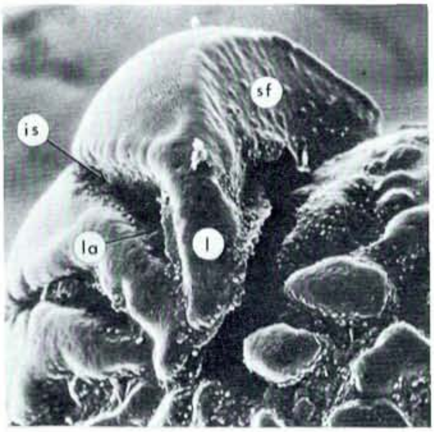

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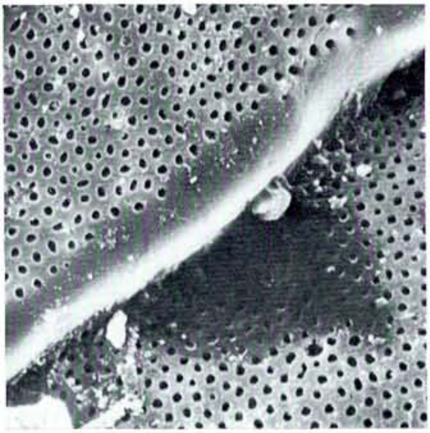

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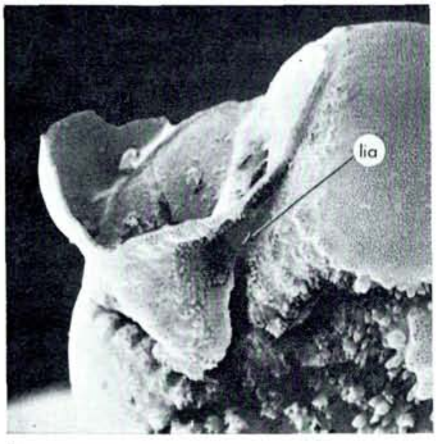

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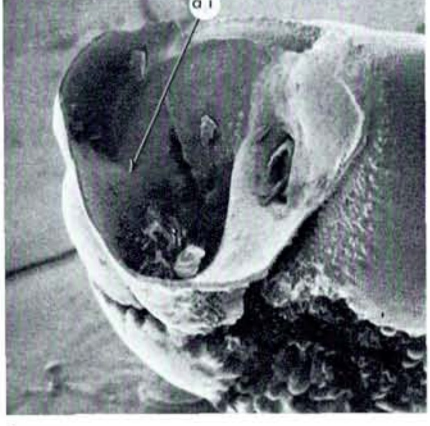

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Plate 6

Figs 1–5. *Pseudorotalia schroeteriana* (Carpenter, Parker & Jones). Recent, Java.

1. Detail of section through perforate lateral chamber wall showing arrays of platelets and veneer in outer lamellae. (R-20). × 4120.

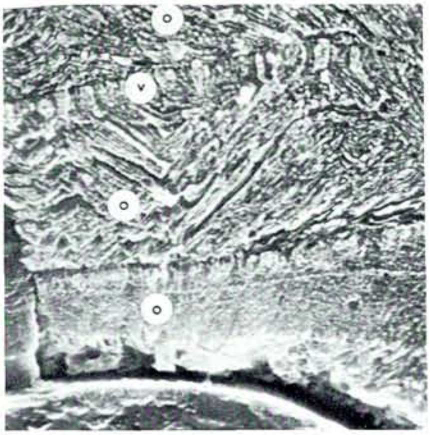
2. Detail of horizontal section through septum at bottom of interlocular-space, showing inner linings, outer lamellae and median layers of consecutive chambers (septal wall and septal flap), as well as secondary lamination, thinning out on the sides of the interlocular space and thickening towards its bottom. Note termination of median layer in septal flap at its junction with preceding septal face. (R-18). × 525.

3. Part of horizontal section through a septum at its junction with secondarily laminated outer test wall, showing continuity of secondary lamellae over interlocular space. (R-19). × 1240.

4. Section similar to that in fig. 3, showing thinning out of secondary lamellae on the walls of the interlocular space. (R-19). × 405.

5. Horizontal section showing relationship between septal flap, foraminal plate, and coverplate. (R-94). × 32.

Abbrevations: *o* – outer lamella; *v* – veneer; *i* – inner lining; *m* – median layer.



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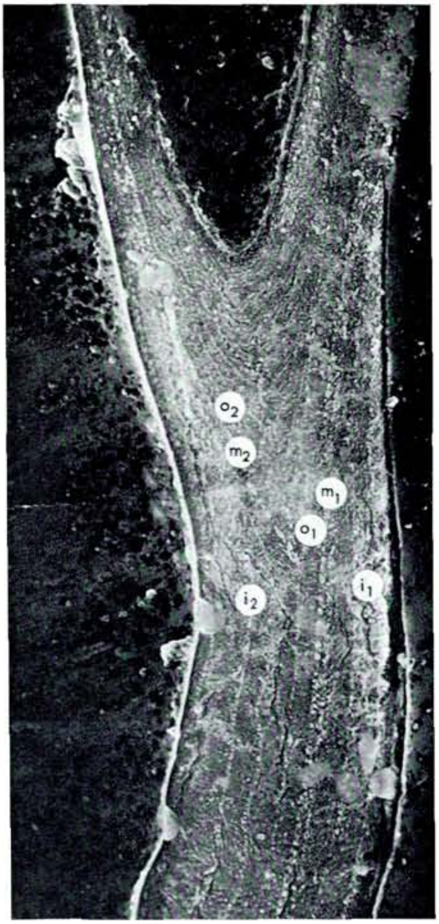

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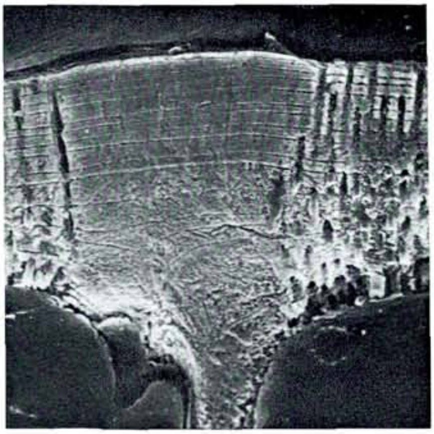

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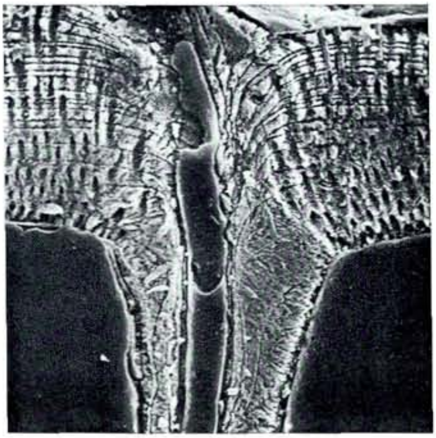

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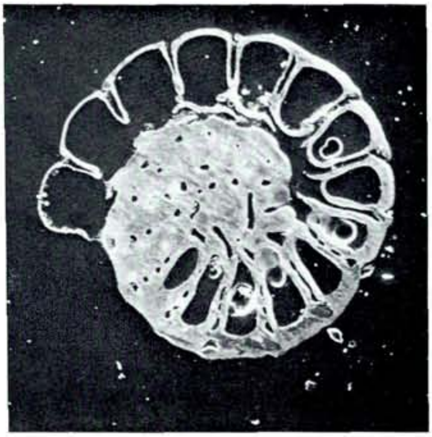

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Plate 7

Figs 1–6. *Pseudorotalia schroeteriana* (Carpenter, Parker & Jones). Recent, Java.

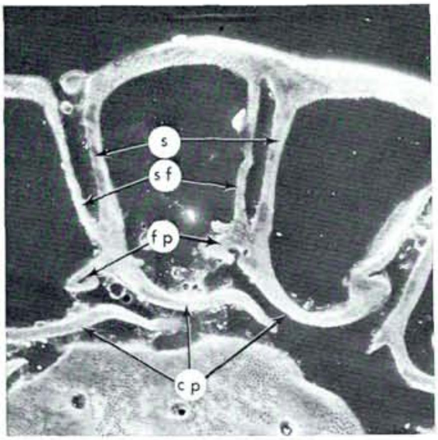
1. Detail of pl. 6, fig. 5, showing relationship between septal flap, foraminal plate, and coverplate. (R-94). × 105.

2–3, 5. Horizontal section showing attachment of foraminal and cover plates. Note termination of median layer in cover plate at point of attachment. (R-93). Fig. 2, × 28; fig. 3, × 252; fig. 5, × 709.

4. Strongly oblique horizontal section showing attachment of foraminal plate to axial wall (former coil) and succeeding coverplate. (R-89). × 788.

6. Oblique horizontal section showing relationship between septal flap, foraminal and coverplates at various levels of the test. (R-77). × 26.

Abbrevations: *s* – septum; *sf* – septal flap; *fp* – foraminal plate; *cp* – coverplate; *i* – inner lining; *m* – median layer.



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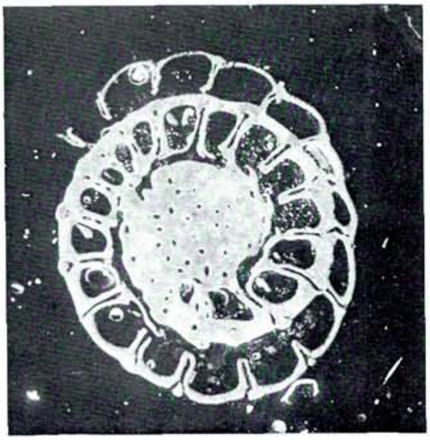

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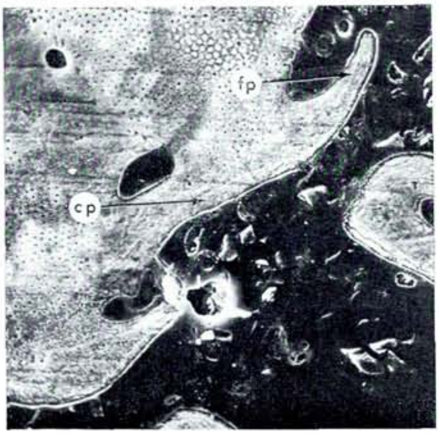

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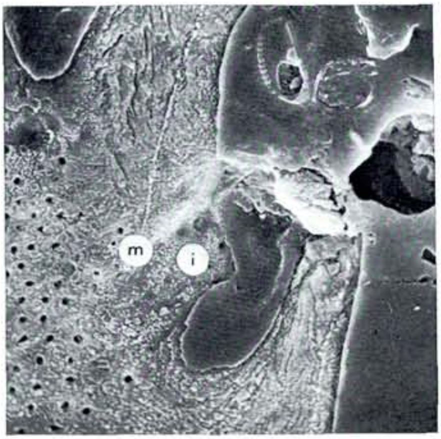

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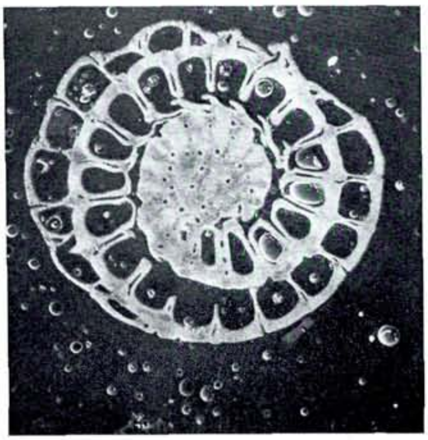

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Plate 8

Figs 1–5. *Pseudorotalia schroeteriana* (Carpenter, Parker & Jones). Recent, Java.

1. Vertical oblique section showing overlapping coverplates in successive chambers. Note foraminal plates. (R-72). × 31.

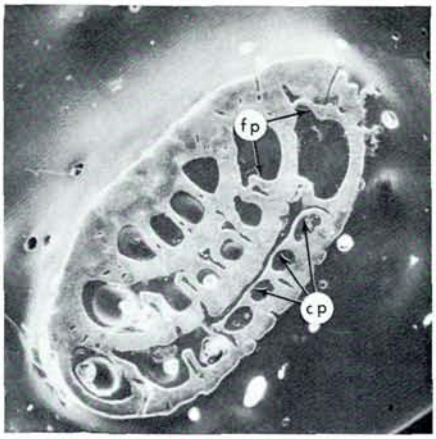
2. Outer view of imperforate inflational thickenings at margins of interlocular space. Note coalescence in places. × 175.

3–4. Details of horizontal section showing imperforate thickenings at margins of interlocular space covered by secondary lamination. Note formation of residual openings and thinning out of secondary lamination at their entrance. (R-19). Fig. 3, × 405; fig. 4, × 409.

5. Section through foraminal plate showing strong backward fold at distal end. Note median layer. (R-94). × 762.

Fig. 6. *Pararotalia inermis* (Terquem). Lutetian, Grignon, France. Detail of horizontal section through septum showing outer lamella and inner lining, as well as median layer. (R-114). × 5100.

Abbrevations: *fp* – foraminal plate; *cp* – coverplate; *s* – secondary lamellae; *o* – outer lamella; *i* – inner lining; *m* – median layer.



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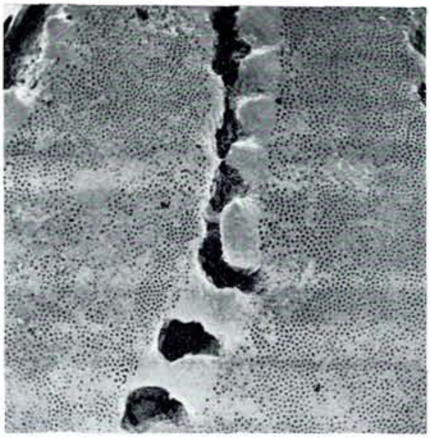

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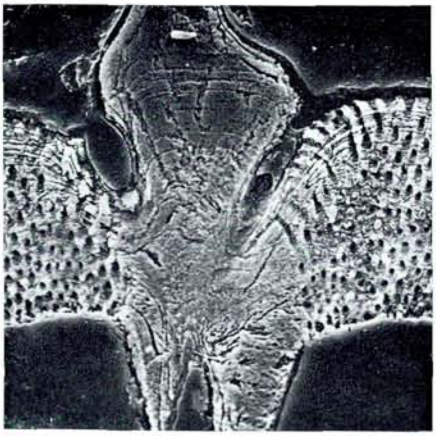

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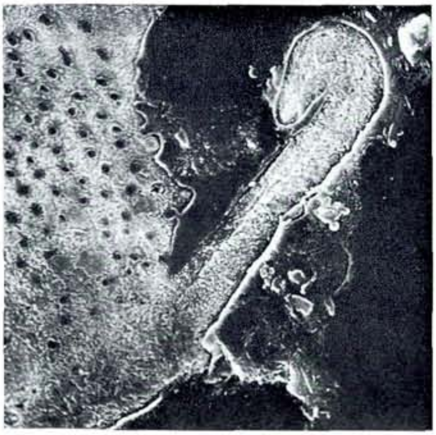

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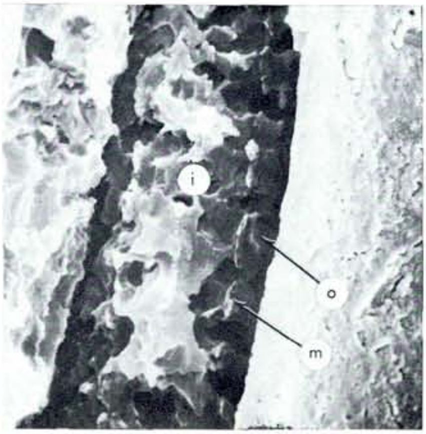

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Plate 9

Figs 1–5. *Pararotalia calcar* (d'Orbigny). Recent, Gulf of Elat, Israel.

1. Part of horizontal section through septum showing outer, inner and median layers. (R-106). × 7980.

2–5. Horizontal section and details thereof showing relationship between septal flap, foraminal plate, and coverplate, as well as presence of thickened rim at outer border of foramen. (R-42). Fig. 2, × 89; fig. 3, × 630; fig. 4, × 300; fig. 5, × 559.

Fig. 6. *Pararotalia inermis* (Terquem). Lutetian, Grignon, France. Oblique horizontal section showing foraminal and coverplates. (R-114). × 156.

Abbrevations: *m* – median layer; *cp* – coverplate; *fp* – foraminal plate; *s* – septum; *t* – thickening.

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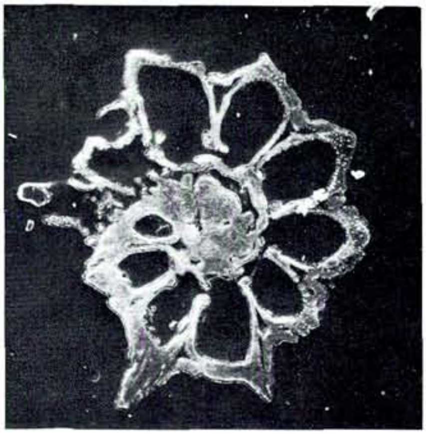

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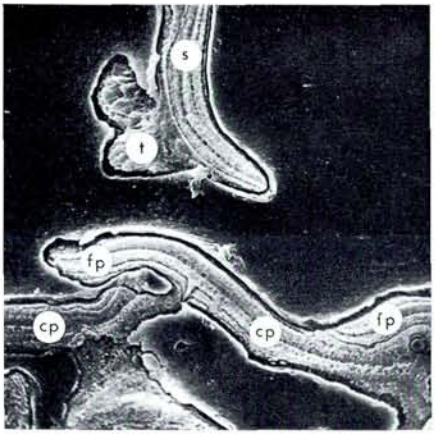

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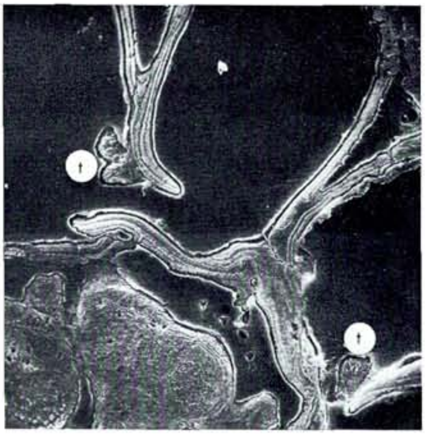

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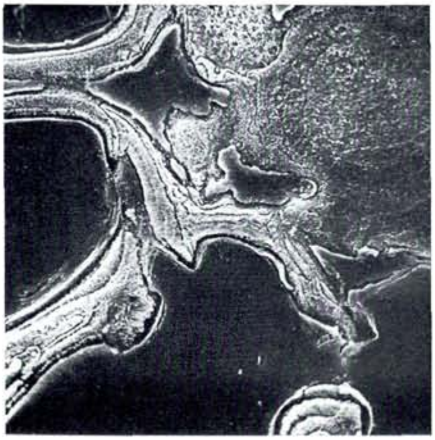

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Plate 10

Fig. 1. *Pararotalia* sp. Oligocene, Gaas, France. Horizontal section showing septal flaps, foraminal plates and coverplates. (R-103). × 552.

Fig. 2. *Pararotalia mexicana mecatapecensis* (Nuttall). Lower Miocene, Australia. Horizontal section showing septal flaps, foraminal and coverplates. (R-97). × 57.

Fig. 3. *Pararotalia inermis* (Terquem). Lutetian, Grignon, France. Oblique umbilical view of specimen with broken final chamber showing attachment of septal flap, the protruding foraminal plate, and the umbilical labial apertures. (R-4). × 98.

Figs 4–6. *Pararotalia calcar* (d'Orbigny). Recent, Gulf of Elat, Israel.

4. Profile view of specimen with final chamber intact. Note form of aperture. (R-3). × 36.

5. Umbilical view of same specimen as in fig. 4 showing elongated thickenings leading into the interlocular space, as well as peripheral spines. Note residual openings into interlocular space. (R-3). × 34.

6. Detail of horizontal section showing interlocular spaces, their communications to the outside of the test and secondarily formed intramural cavities. (R-42). × 300.

Abbrevations: *la* – labial aperture; *fp* – foraminal plate; *sf* – septal flap; *ro* – residual openings.

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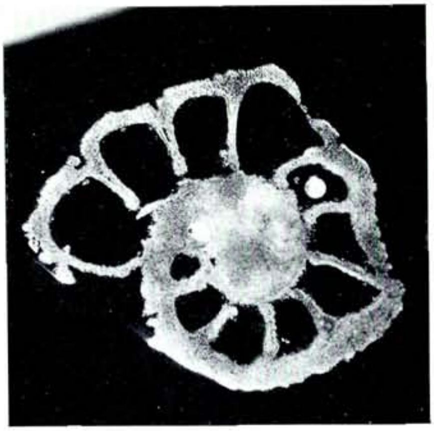

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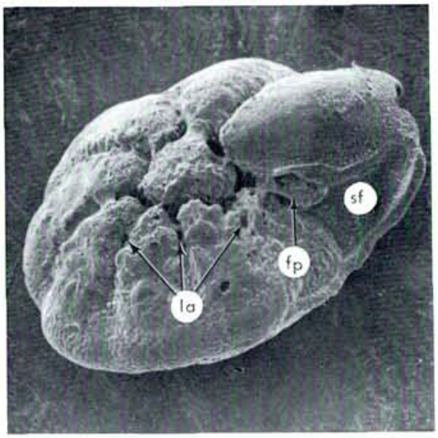

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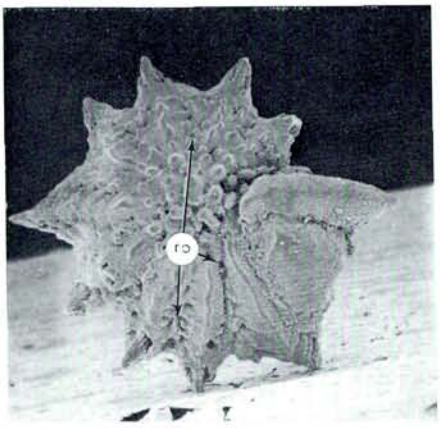

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Plate 11

Figs 1–6. *Calcarina spengleri* (Gmelin). Recent, Mollucan Islands.

1. Detail of horizontal section through septum and its junction to outer wall showing distribution of different layers. (R-55). × 1200.

2. Detail of horizontal section through septum showing relationship between septal flap and preceding septal wall in area of adherence. Note herringbone pattern and primary lamination in septal flap. (R-55). × 3990.

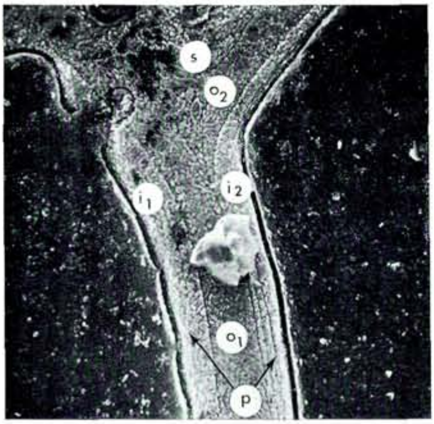
3. Detail of horizontal section through outer wall showing inner lining, median layer, and outer lamella, as well as secondary outer lamella. (R-55). × 3990.

4. Oblique umbilico-apertural view of broken final chamber showing multiple foramina and their thickened rims. (R-126). × 207.

5. View of same specimen as in fig. 4, from behind showing the multiple foramina piercing the septal flap. (R-126). × 225.

6. Detail of horizontal section through early ontogenetic stage of test showing relationship between septal flap, foraminal plate and coverplate. (R-132). × 371.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer.



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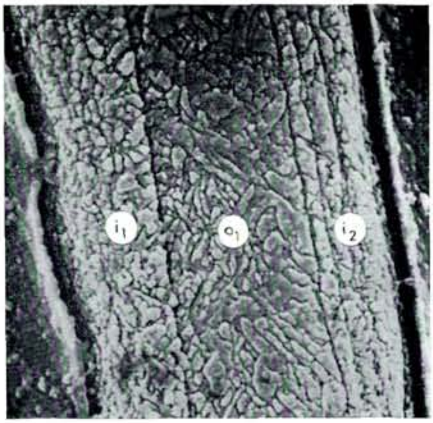

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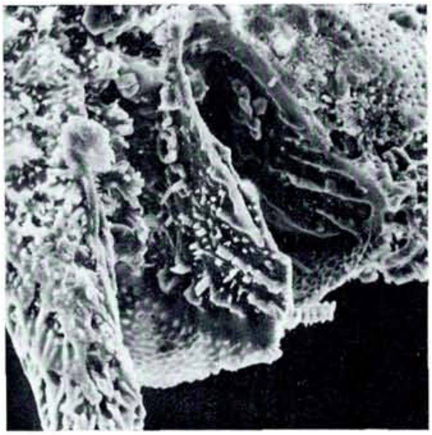

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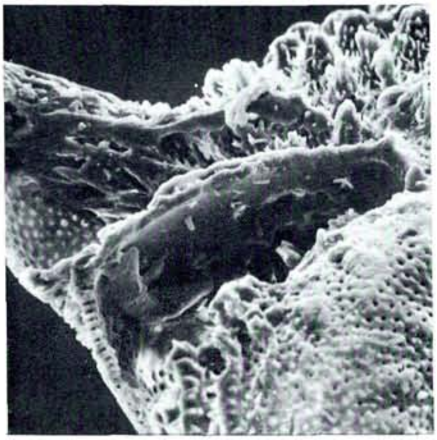

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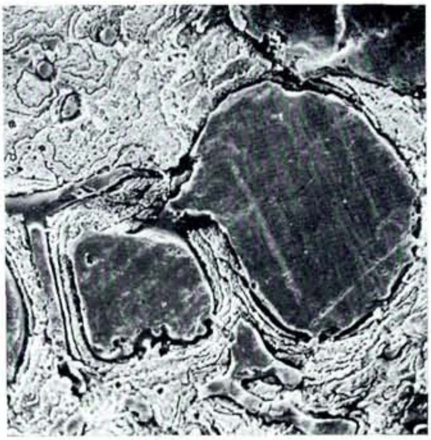

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Plate 12

Figs 1–5. *Calcarina spengleri* (Gmelin). Recent, Mollucan Islands.

1. Oblique apertural view of final chamber (partly damaged) showing multiple aperture with thickened rims and elongated ridges on imperforate, finely pustulated apertural face. (R-127). × 112.

2. Umbilical view of specimen with preserved final chamber showing ornamentational pattern along interlocular space and in peripheral region. (R-127). × 112.

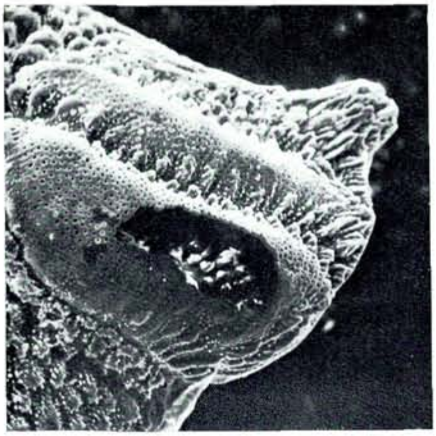
3. View of canaliculate inflational spine showing anastomosing pathways and delicate ridges along them on the thick ridges (compare with fig. 5). (R-127). × 157.

4. Detail of horizontal section showing intramural cavity trapped off by secondary lamination. (R–55). × 1180.

5. Detail of horizontal section through secondarily laminated spine. (R-55). × 1610.

Fig. 6. *Operculina* sp. Recent, Gulf of Elat, Israel (collected in living state). Detail of horizontal section through septum showing herringbone pattern of calcite platelets. (R-30). × 9500.

Abbrevations: *imc* – intra mural cavity; *s* – secondary lamellae.



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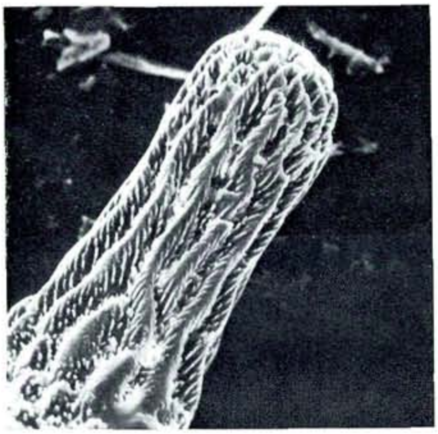

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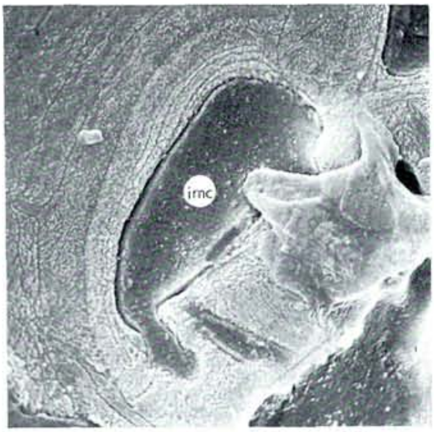

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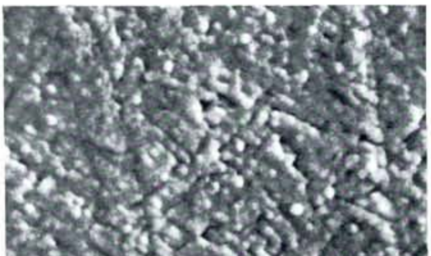

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Plate 13

Figs 1–6. *Operculina* sp. Recent, Gulf of Elat, Israel (collected in living state).

1. Detail of horizontal section through septum showing paired crystals of median layer. (R-24). × 3990.

2. Detail of horizontal section through septum showing empty space left after crystals and organic material have been removed. (R-24). × 3990.

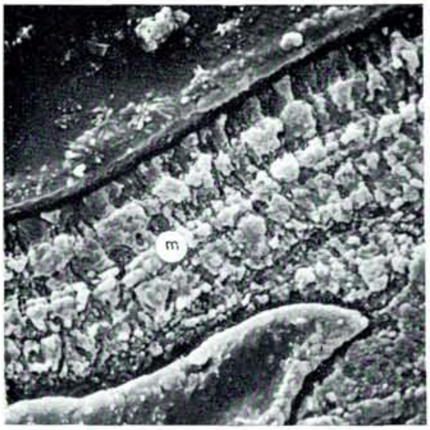
3. Detail of vertical section through part of septum at its junction with the lateral chamber wall showing disposition of various layers. Note continuity of outer lamellae in secondarily laminated parts of the test. (R-30). × 2530.

4. Apertural view of final chamber showing multiple interio-areal apertures and anastomosing thickenings on apertural face continuing into the marginal cord. (R-9). × 185.

5. Profile view of specimen with broken final chamber showing the septal flap and the symmetrical foraminal plates of this chamber. Note interio-marginal resorbed foramen. (R-37). × 107.

6. Oblique profile view of final chamber showing irregular thickenings along the edge of the septal face. (R-9). × 400.

Abbrevations: *i* – inner lining; o – outer lamella; *m* median layer; *s* – secondary lamellae; *sf* – septal flap; *fp* – foraminal plate.



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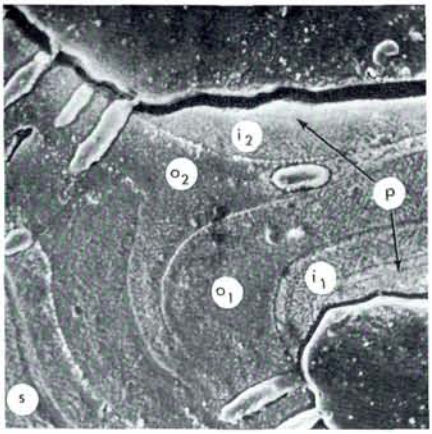

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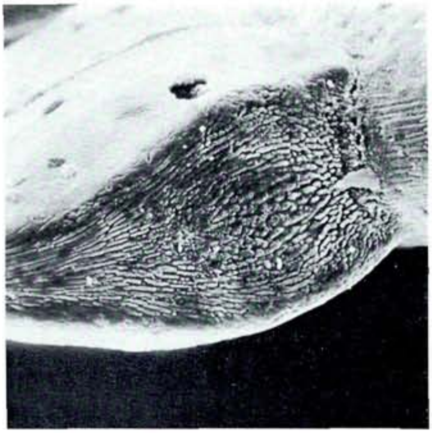

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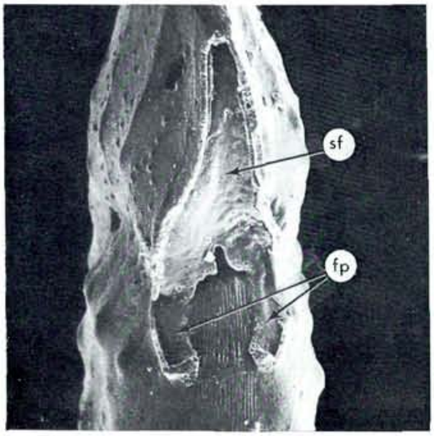

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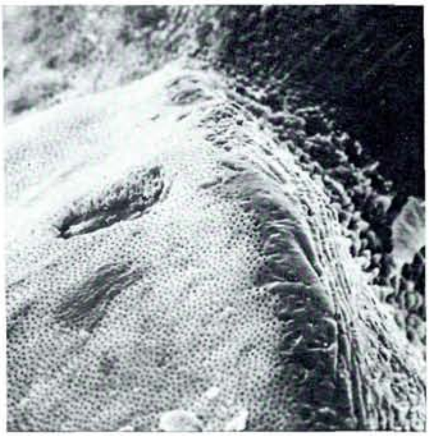

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Plate 14

Figs 1–6. *Operculina* sp. Recent, Gulf of Elat, Israel (collected in living state).

1. Detail of lateral view showing irregular coalescence of thickenings along interlocular space (last suture) and residual openings into the latter. (R-9). × 352.

2. Detail of horizontal section showing interlocular space subdivided by adherence of septal flap to ridges of septal face. (R-24). × 1390.

3. Detail of horizontal-tangential section through marginal cord showing polygonal outline of "islands" which are secondarily laminated. (R-24). × 1380.

4. Detail of horizontal section at junction between septum and marginal cord showing a vertical channel leading from interlocular space into cord. (R-53). × 945.

5. View of septal flap in final chamber showing corrugations caused by adherence of flap to ridges of previous septal face, as well as multiple areal foramina. (R-133). × 450.

6. Detail of horizontal section showing foraminal plates extending from septal flap and fused to septal face, as well as their anterior opening. (R-52). × 200.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* median layer; *vc* – vertical canal; *af* – areal foramen; *fp* – foraminal plate.

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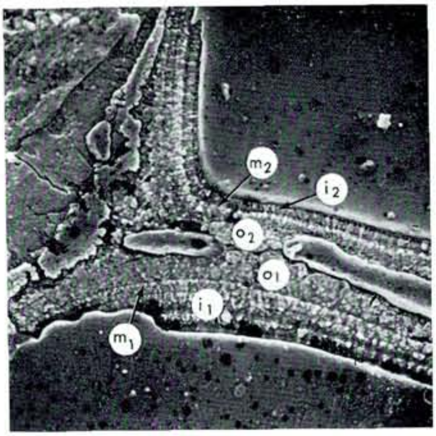

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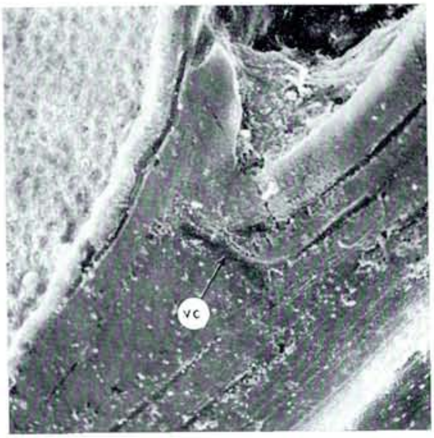

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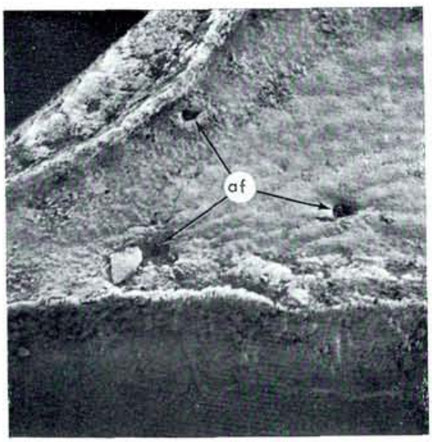

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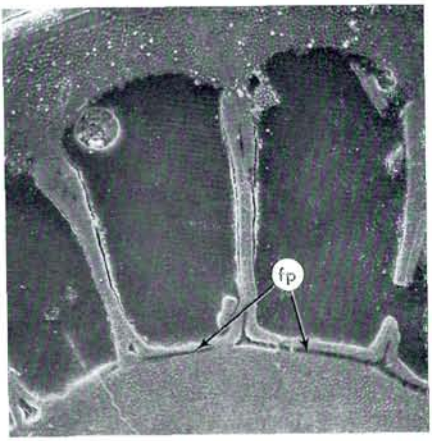

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Plate 15

Fig. 1. *Elphidium macellum* (Fichtel & Moll). Recent, off Napoli, Italy. Detail of horizontal section through outer wall near its junction with a septum showing organic material of median layer after removal of the paired crystals, as well as herringbone pattern of platelets in outer lamella and inner lining. Note veneer of outer lamella. (R-109). × 10500.

Fig. 2. *Cellanthus craticulatus* (Fichtel & Moll). Recent, Mollucan Islands. Detail of horizontal section through septal flap showing inner lining, median layer with paired crystals and outer lamella covered by thin secondary lamellae. (R-59). × 3940.

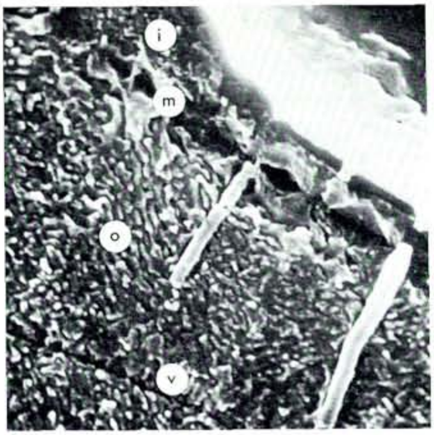
Figs 3–4. *Elphidium macellum* (Fichtel & Moll). Recent, off Napoli, Italy.

3. Detail of horizontal section through tip of septum attached to previous coil and showing disposition of various layers. (R-110). × 1935.

4. Oblique, tangential-horizontal section through secondarily laminated outer wall of retral processes with fossettes between them. Note thinning out of lamination in fossettes and the presence of inflational spines in the latter. (R-110). ×640.

Fig. 5. *Cellanthus craticulatus* (Fitchtel & Moll). Recent, Mollucan Islands. Detail of strongly oblique horizontal section through septum and its junction to outer wall showing interlocular space and strong secondary lamination on septal flap. Note structure of inflational pustules. (R-59). × 787.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *v* – veneer; *s* – secondary lamellae.



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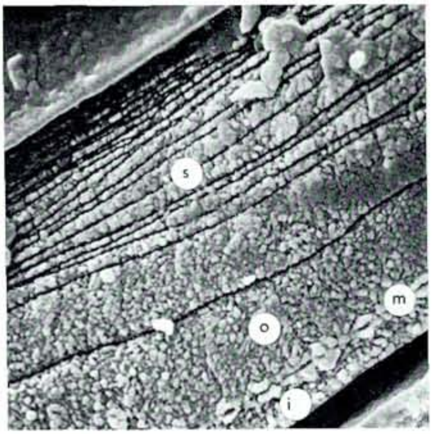

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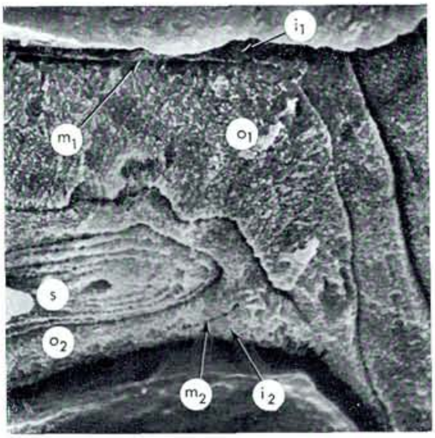

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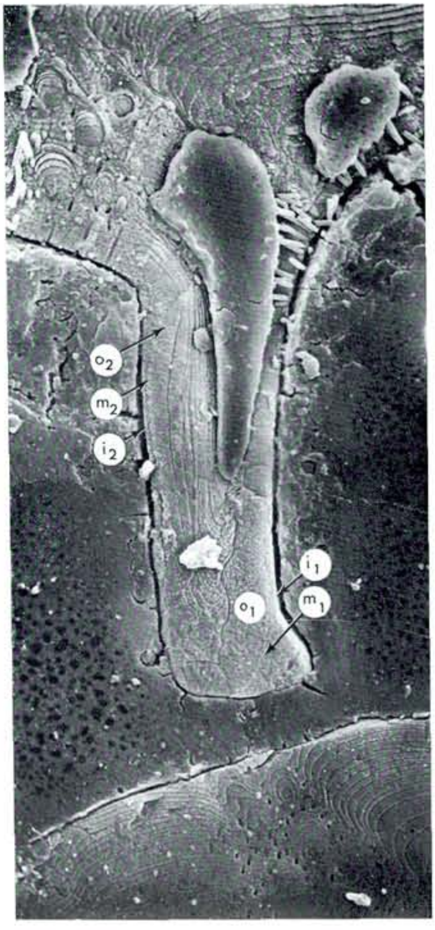

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Plate 16

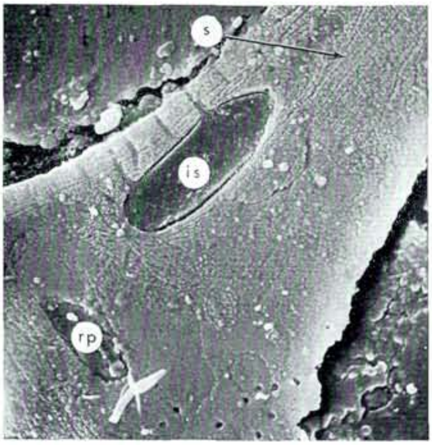
Figs 1–5. *Cellanthus craticulatus* (Fichtel & Moll). Recent, Mollucan Islands.

1. Tangential-horizontal section of septum at its junction with lateral wall showing secondary lamination in interlocular space and lack of secondary lamination inside the retral process. (R-59). × 1910.

2–3, 5. Vertical, very deeply etched section of specimen infilled with Lakeside showing vertical umbonal canals originating from "umbilico-spiral" canal. Note the thinning out of secondary lamellae in vertical umbonal canal and impressions of spinose projection of wall material near the outlet of the canal. (R-134). Fig. 2, × 45; fig. 3, × 231; fig. 5, × 742.

4. Part of horizontal section showing disposition of primary and secondary layers at bottom of interlocular space. Note secondarily laminated inflational pustules. (R-59). × 1575.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *s* – secondary lamellae; *is* – interlocular space; *rp* – retral process; *uc* – umbonal vertical canal; *sc* – spiral canal.



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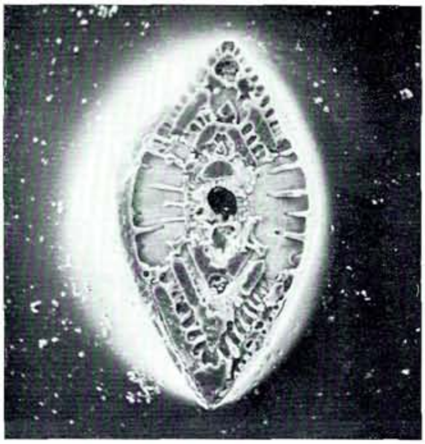

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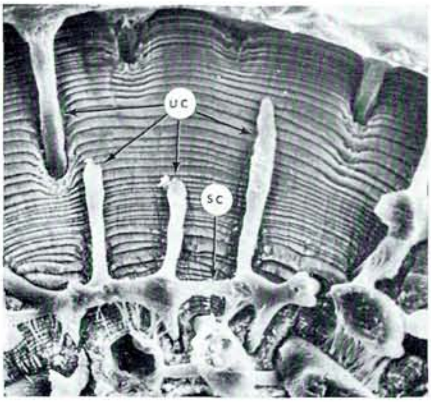

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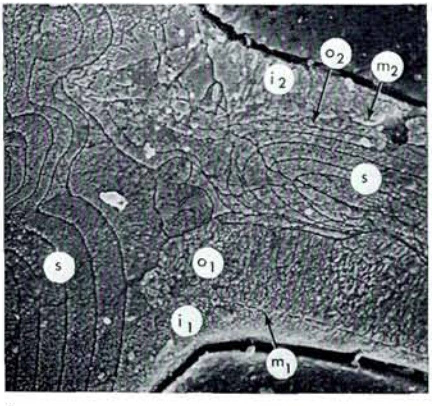

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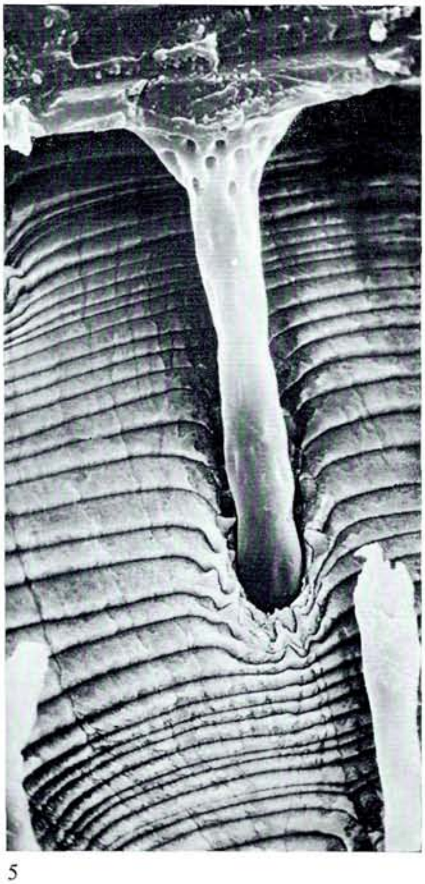

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Plate 17

Figs 1–6. *Asterorotalia pulchella* (d'Orbigny). Recent, Siam Bay.

1. Detail of horizontal section through septum showing septal flap adhering to outer lamella, the latter is separated from the inner lining by the median layer with paired crystals. Note herringbone pattern. (R-66). × 3900.

2. Oblique apertural view of final chamber showing apertural rim and infold of apertural face partly covered by umbilical chamber projection. (R-123). × 264.

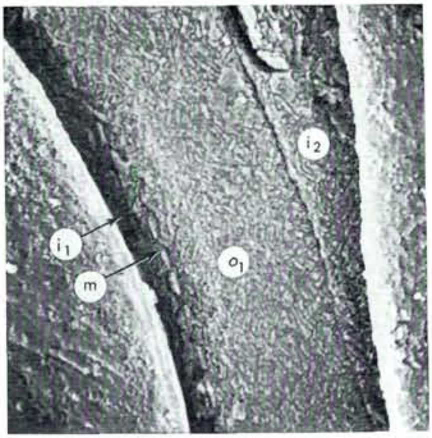
3. Umbilical view of specimen showing suprasutural covers of interlocular spaces. (R-64). × 100.

4. Detail of fig. 3 showing termination of suprasutural cover near periphery on umbilical side. (R-64). × 375.

5. Partial umbilical view of specimen showing openings along suprasutural covers. (R-123). × 314.

6. Apertural view of final chamber. Note shape of interio-marginal aperture, thickened rim and pustulate septal face, as well as infold and projection on umbilical side. (R-123). × 165.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *ar* – apertural rim; *ai* – apertural infold.



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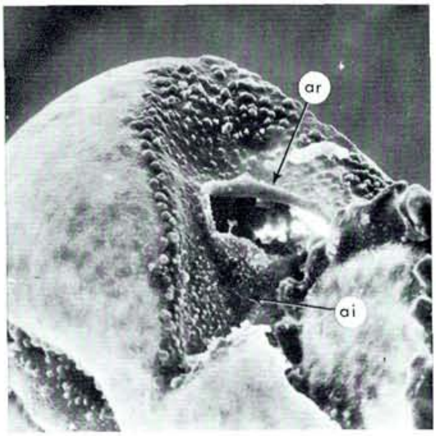

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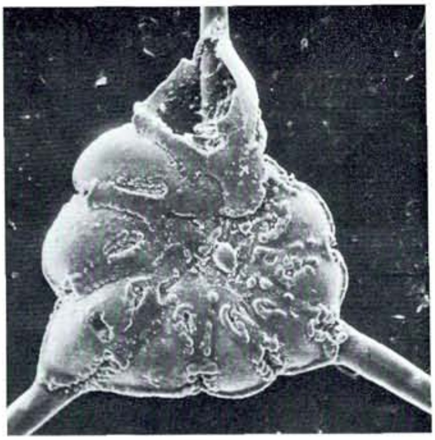

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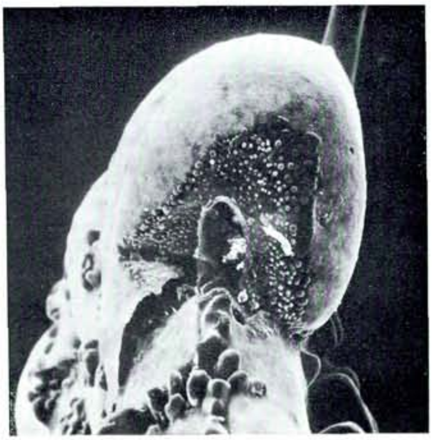

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Plate 18

Figs 1–6. *Asteroratalia pulchella* (d'Orbigny). Recent, Siam Bay.

1. Apertural view of specimen with interio-areal aperture and collar-like rim. (R-123). × 169.

2. View of penultimate chamber showing attachment of septal flap to previous septal face, as well as the foraminal plate. (R-123). × 214.

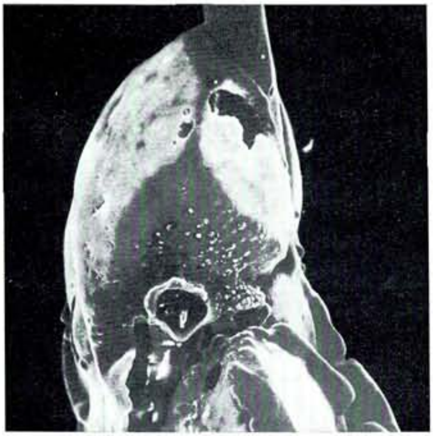
3. Profile view of specimen with broken final chamber showing septal flap partly adhering to previous septal face and partly forming the interlocular space, as well as the foraminal plate. (R-123). × 230.

4. Horizontal section showing foraminal plates and their relationship to coverplates and septal flap. (R-65). × 189.

5. Detail of umbilical view of broken final chamber showing adherence of chamber wall to spine originating from earlier interlocular space. (R-64). × 151.

6. Detail of vertical section showing secondary lamination on the sides and bottom of interlocular space under suprasutural cover. (R-135). × 150.

Abbrevations: *sf* – septal flap; *fp* – foraminal plate; *is* – interlocular space; *cp* – coverplate; *s* – secondary lamellae.



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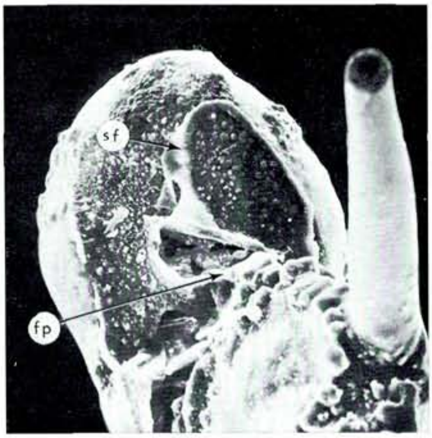

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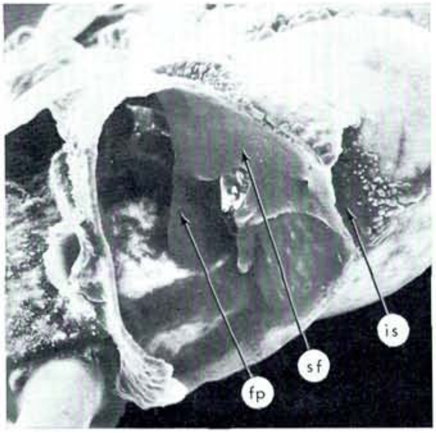

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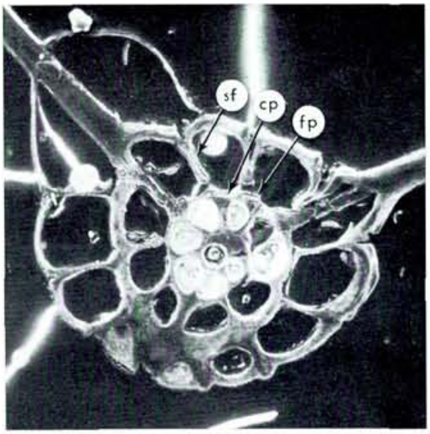

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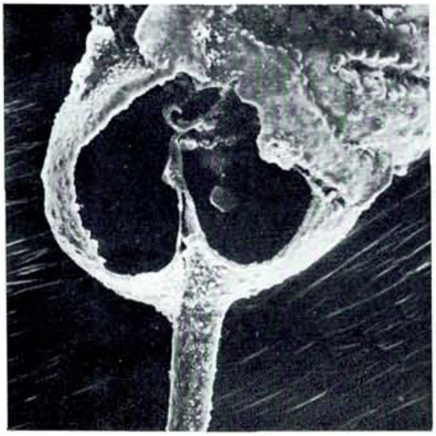

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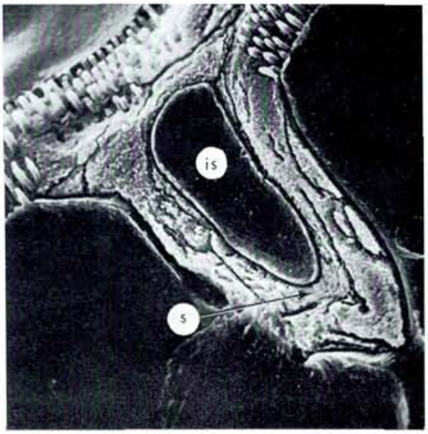

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Plate 19

Figs 1–6. *Rotalia trochidiformis* (Lamarck). Lutetian, Grignon, France.

1. Detail of horizontal section through septal wall showing inner lining, outer lamella and median layer. (R-61). × 2250.

2. Detail of section through septum showing relict herringbone pattern of calcite platelets. (R-61). × 3780.

3. Detail of oblique, horizontal half-section showing polygonal outline of pores on the inner wall surface. (R-61). × 1125.

4. Oblique umbilical view of specimen with final chamber preserved showing aperture, lip, posterior and anterior, as well as umbilical labial apertures. (R-125). × 127.

5. View of half-section showing inframarginal sulci and inward projecting extensions of apertural face. (R-61). × 47.

6. Oblique umbilical view of specimen showing attachment of lip in final chamber and the posterior labial aperture. Note inflational ornamentation along interlocular space and along umbilical labial aperture. (R-125). × 150.

Abbrevations: *i* – inner lining; *o* – outer lamella; *m* – median layer; *a* – aperture; *l* – lip; *ula* – umbilical labial aperture; *pla* – posterior labial aperture; *ala* – anterior labial aperture.

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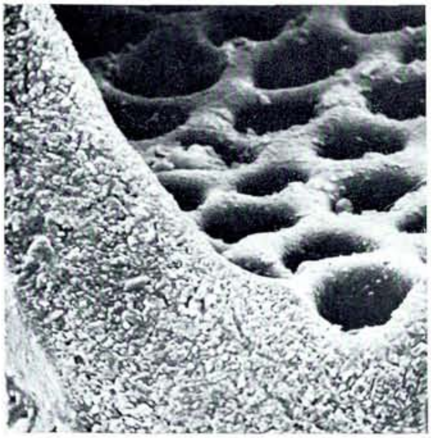

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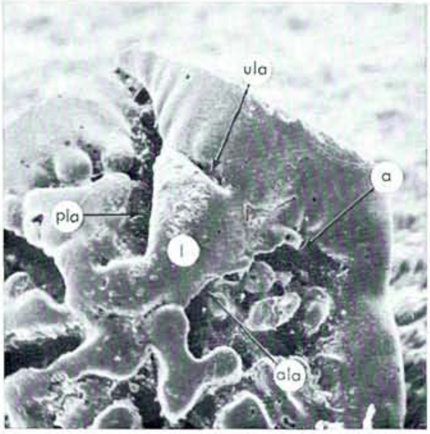

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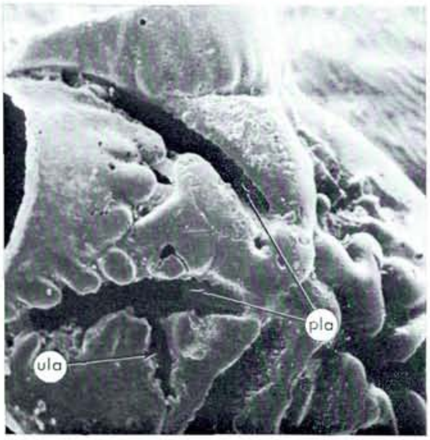

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Plate 20

Figs 1–5. *Rotalia trochidiformis* (Lamarck). Lutetian, Grignon, France.

1. Horizontal section showing interlocular spaces and furrows between lips and chambers. (R-61). × 40.

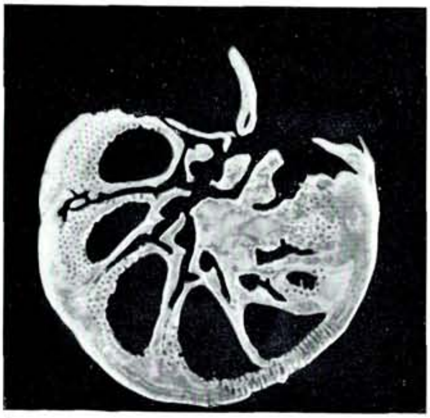
2. Umbilical view of broken specimen showing plastering of wall material on axial chamber wall (previous coil), interlocular space and the umbilical labial apertures. (R-96). × 114.

3. Detail of vertical half-section showing infold at line of attachment between lip and chamber wall ("astral furrow"). (R-68). × 97.

4. Detail of umbilical view showing lip and umbilical labial aperture. (R-125). × 375.

5. Detail of vertical half-section showing illusion of a "toothplate" produced by chamber shape. (R-68). × 75.

Abbrevations: *is* – interlocular space; *ula* – umbilical labial aperture; *l* – lip.



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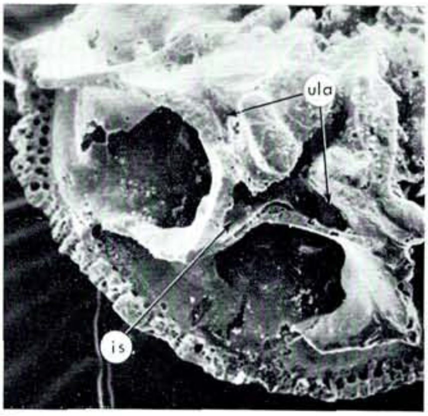

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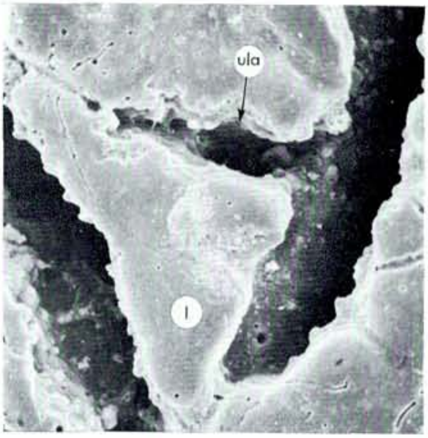

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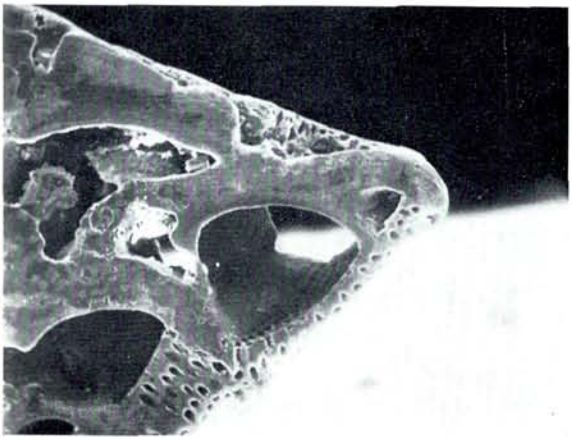

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Plate 21

Figs 1–6. *Rotalia trochidiformis* (Lamarck). Lutetian, Grignin, France.

1–5. Oblique umbilical and umbilical-peripheral views of broken specimen showing position of lips, posterior, anterior and umbilical labial apertures, as well as septal flap, septal face and umbilical chamber wall. (R-153). Fig. 1, × 58; fig. 2, × 95; fig. 3, × 190; fig. 4, × 190; fig. 5, × 190.

6. Oblique umbilical view of broken specimen showing secondary thickening around umbilical labial apertures. (R-154). × 98.

Abbrevations: *l* – lip; *ala* – anterior labial aperture; *ula* – umbilical labial aperture; *uc* – umbilical chamber wall; *sf* – septal flap; *sw* septal wall; *pla* – posterior labial aperture.

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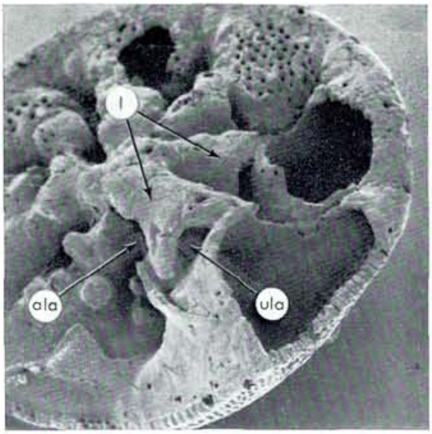

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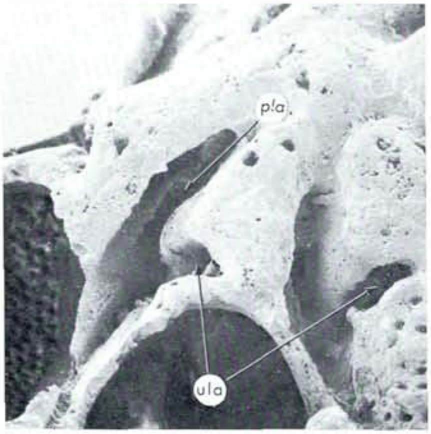

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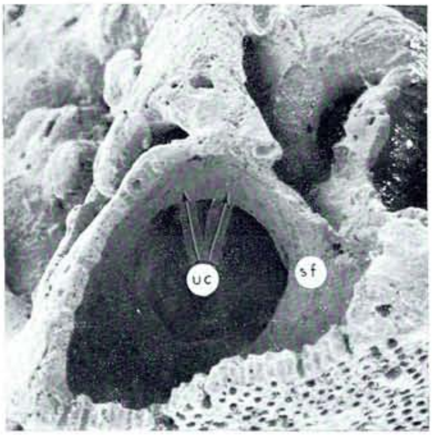

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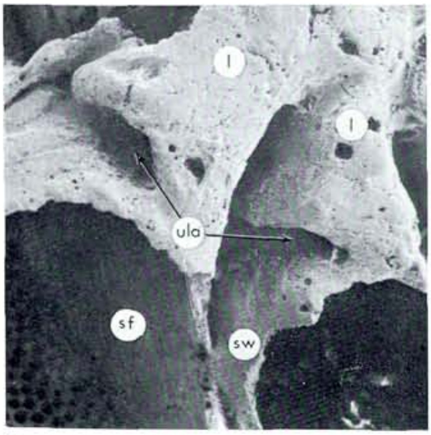

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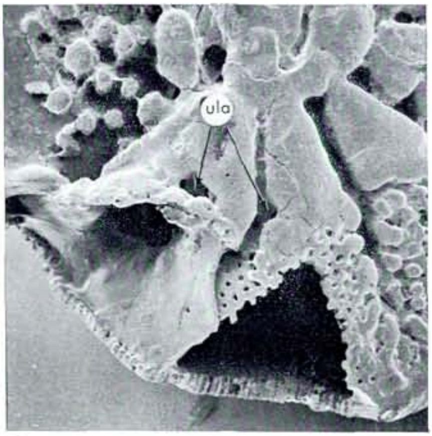

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