Wall structure and classification of fossil and recent elphidiid and nonionid Foraminifera

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Many regional or systematic descriptions and revisions contain a nucleus of results which are of immediate and general interest in international palaeontology and stratigraphy. It is expected that authors of such papers will to some extent duplicate their publication in the form of an article for a journal, in the first place *Lethaia.*

Wall structure and classification of fossil and recent elphidiid and nonionid Foraminifera

HANS JØRGEN HANSEN AND ANNE-LISE LYKKE-ANDERSEN

Hansen, H. J. & Lykke-Andersen, Anne-Lise 1976 11 15: Wall structure and classification of fossil and recent elphidiid and nonionid Foraminifera. *Fossils and Strata*, No. 10, pp. 1–37, Pls. 1–22. Oslo. ISSN 0300-9491. ISBN 82-00-09427-9.

A comparative study of 44 species representing 14 genera shows that all are bilamellar, that optical wall structure has no taxonomic value above species level, and that septal flaps are present in a variety of forms (e.g. *Pullenia*, *Melonis*) outside the Rotaliidae, besides being developed to a different degree in different forms. These features therefore cannot form a basis for classification. Furthermore, the presence of retral processes is a character of degree and cannot be used for classification. Umbilical spiral canals are present in *Elphidium* and *Elphidiella* but are absent in nonionids (except for *Astrononion*). *Cellanthus*, *Cribroelphidium* and *Cribrononion* are considered synonyms of *Elphidium*. *Florilus*, *Nonionellina* and *Protelphidium* are considered synonyms of *Nonion*.

[Хансен, Х. Й. и Люкке-Андерсен А.-Л.: Строение стенки и классификация ископаемых и современных эльфидиид и нонионид.]

Сравнительное изучение 44 видов, представляющих 14 родов, показывает, что все они двуслойны, что оптическое строение стенки не имеет таксономического значения за пределами вида и что септальные клапаны имеются у многих форм (например, у *Pullenia*, *Melonis*), за исключением роталиид, будучи развиты в различной степени у разных форм. Эти черты, следовательно, не могут служить основанием для классификации. Кроме того, септальные мостики не являются надёжным признаком и также не могут быть использованы для классификации. Умбиликальные спиральные каналы имеются у *Elphidium* и *Elphidiella*, но отсутствуют у нонионид (за исключением *Astrononion*). *Cellanthus*, *Cribroelphidium* и *Cribrononion* считаются синонимами *Elphidium*. *Florilus*, *Nonionellina* и *Protelphidium* отождествляются с *Nonion*.

Hans Jørgen Hansen, Institute of Historical Geology and Palaeontology, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark; Anne-Lise Lykke-Andersen, Labyrinten 17, 8220 Brabrand, Denmark, 21st April, 1976.

Contents

Introduction

The elphidiids and nonionids include both simple and complicated morphological forms, and are among the dominant foraminiferal elements in shallow water temperate and arctic seas. Therefore the problems involved in the taxonomy of these groups are of particular interest for micropalaeontology and stratigraphy.

The elphidiids provided the first example of inhomogeneity with respect to optical wall structure (Buzas 1966) that thereby cast doubt on the value of this character for classification at a supraspecific level.

During our work with Quaternary stratigraphy and recent distribution in the Limfjord we have often met the problem of genus determination for forms belonging to the groups here treated. For that reason an investigation was initiated in order to clarify some of the problems involved using all characters available such as morphology (external and internal), wall structure and lamellarity. An essential part of the study was therefore the examination of type species of the relevant genera when material was available.

Eleven of the 14 genera investigated are represented by their type species while the remaining 3 are represented by closely allied forms. In addition to the type species a series of other species belonging to the genera of the subfamily Elphidiinae (*sensu* Loeblich & Tappan 1964) has been studied. In all, 44 species have been studied, of which 545 specimens and preparations have been photographed with the scanning electron microscope, resulting in 2,010 pictures. Since many of these photographs show essentially the same features (such as layering of septa and walls), only a small selection has been chosen to illustrate this paper.

Acknowledgements.—Much of the material was placed at our disposal by collegues from other institutions. We express our sincere gratitude to the following persons: Inger Bang, Cand.mag., Copenhagen; Dr. D. Curry, London; Lis Gustafsen, Cand.scient., Århus; Dr. H. Hagn, Munich; Karen L. Knudsen, Cand.scient., Århus; Dr. P. G. Laga, Leuven; Drs. Helen Tappan and A. R. Loeblich, Los Angeles; Dr. J. Murray, Exeter; Dr. Francis Parker, La Jolla; Dr. J. H. van Voorthuysen, Haarlem; and Dr. Valentina Yanko, Odessa.

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The Geological Institute, University of Copenhagen, is thanked for permission to use the facilities of the Laboratory of Electron Microscopy along with the collections of the Laboratory of Micropalaeontology.

All specimens and preparations used in this study are kept in the Laboratory of Electron Microscopy of the Geological Institute, University of Copenhagen.

Dr. R. Feyling-Hanssen, Århus and Dr. J. Murray, Exeter both read the manuscript and kindly suggested improvements.

Dr. R. G. Bromley, Copenhagen kindly corrected the language of the manuscript.

Methods

Specimens of all species were prepared in the following way.

For depiction of outer morphology one or several examples were mounted on a specimen stub by aid of a small piece of double adhesive tape.

Foramina and often the aperture (if veiled by tuberculation) were studied in 'half sections'. These were prepared by grinding specimens embedded in Lakeside 70 cement to the horizontal midplane. Wet carborundum paper of grade 600 was used for grinding, made slightly less abrasive with the edge of a microscope slide to reduce grinding speed.

In some cases a vertical tangential section was cut through the final chamber so as to allow inspection of the aperture of the shell from the inside. The embedding medium was removed by placing the section and microscope slide in a dish in 96% ethanol. With a brush the sectioned specimens were recovered under the binocular microscope and after drying were placed on specimen stubs on a piece of double adhesive tape.

This kind of preparation provided information on foramina, aperture and retral processes. However, where retral processes are not very well developed they were studied more successfully on artificial moulds left after removal of the shell. This technique, dating in fact back to Carpenter et al. (1862) who decalcified specimens with natural moulds of 'iron silicates', was modified several times during the study in order to obtain informative preparations routinely. The serious problems involved in getting chamber lumina as well as canals filled in, avoiding air bubbles, was overcome in the following way. The specimens were embedded in horizontal position on a microscope slide and sectioned to the level of the proloculus. The section was then reheated with additional Lakeside 70 cement and while the cement was still soft the sectioned specimen was turned over with a hot needle so that the section plane came into contact with the microscope slide. After the cement had cooled, the excess cement on the shell surface was removed under the binocular microscope with a pointed scalpel. It is our experience that a rather thick covering layer is desirable, since the Lakeside cement is rather brittle and can then be removed in splinters so as to leave the embedded shell with exposed surface. The microscope slide is then placed in 10% HCl for some minutes. It is desirable to obtain a vigorous CO_2 gas development, since this may loosen minor pieces of cement that have escaped the manual preparation.

The specimens are then washed in water to remove the HCl and are left to dry. With a glass cutting pencil and a vice the glass microscope slide is fractured so that the area with the Lakeside cement mould is small enough to be mounted on a specimen stub. It was found advantageous to moisten the mould with water prior to fractionating the glass slide to avoid breakage of the often delicate mould. The water apparently transfers the shock from the fracturing process.

At an early stage of this investigation we used another method, namely embedding with an epoxy resin (Araldit by CIBA), grinding to slightly below the equatorial plane, and decalcification followed by manual removal of the chamber infillings to expose the canal system. However, this frequently led to destruction of the canals since the removal of the chamber infillings under the microscope requires an extremely steady hand and the method was therefore found to be less satisfactory than that outlined above.

The lamellarity of the walls was studied in specimens embedded in Lakeside cement on glass slides, ground on wet carborundum paper grade 600, polished on a rotating wet velvet-covered disc with either MgO powder or AlO_2 paste as polishing medium and finally washed with concentrated oil-free detergent. They were etched in an aqueous EDTA solution buffered to pH 7.0 by NaOH for periods of 15–60 seconds according to wall thickness. The specimens were then mounted on specimen stubs with double adhesive tape after cutting and fracturing the glass as described above.

All preparations were plated with 250–500 Å gold under vacuum from two tungsten filaments simultaneously while rotating. The angles of evaporation were 5 and 45°. The plated specimens were studied in a Cambridge Stereoscan Mk. IIa scanning electron microscope.

The optical orientation of the wall material was determined under the light microscope between crossed nicols on crushed specimens mounted in Canada balsam.

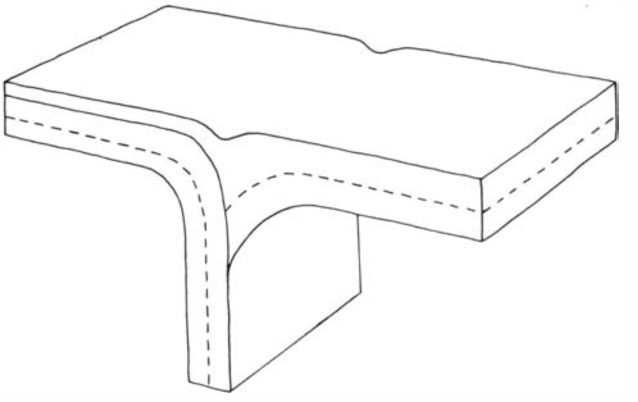


Fig. 1. Addition of a new chamber (right) according to the basic bilamellar model.

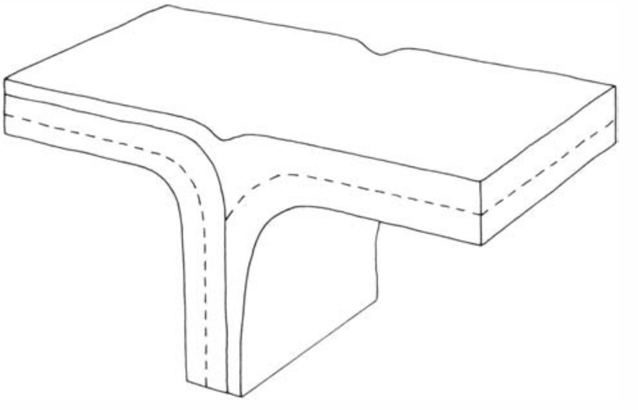


Fig. 2. Addition of a new chamber (right) with development of a septal flap.

Terminology

The terminology here applied with respect to wall construction follows that of Reiss (1963), Hansen, Reiss & Schneidermann (1969) and Hansen & Reiss (1971, 1972a, b). Thus a bilamellar septum and primary wall is composed of two calcareous secreted layers (outer lamella and inner lining) separated by a sheet of organic material of varying thickness and appearance (the median layer). When a new chamber is added to a shell in accordance with this principle, the inner lining stops or wedges out at the junction with a previous septum while the outer lamella continues over exposed previous chambers and adds one secondary lamella (Fig. 1).

In cases where the inner lining continues and covers the previous septum the term 'septal flap' is used for that part of the inner lining covering the previous septum (Fig. 2).

In this way a three-layered septum is formed consisting of inner lining and outer lamella plus inner lining of the following chamber.

Retral processes have been discussed by several authors (see e.g. Ujiié 1956; Wade 1967). In this study we follow Wade, who stressed that retral processes are extensions of the chamber lumen and should be looked for on the inside of the chambers. Often the term retral process has been applied in a broader sense to include also the surrounding wall spanning the suture. We here suggest the term ponticulus (latin: small bridge) to characterise the prolongations of the wall that span the sutures. Thus a ponticulus may be hollow (if it delimits a retral process) or it may be massive but it will always be present in the suture between the ultimate and penultimate chamber. Accordingly a genus like *Pseudorotalia* will be excluded from the group of forms having ponticuli. In *Pseudorotalia* the sutures are deeply depressed, so deeply in fact that Hansen & Reiss (1971) used the term interlocular space for sunken sutures of the type often found within the rotaliaceans. In *Pseudorotalia* the alternating row of openings found in ontogenetically earlier sutures are formed by the addition of secondary laminae which after some three or four chamber-forming instars coalesce to produce bridges across the interlocular space (Figs. 3–4).

This alternating row of openings in the sutures in the genus *Pseudorotalia* that is left after the secondarily created bridge system has spanned a suture is not homologous with the openings between ponticuli in forms like *Elphidium crispum*.

The entrances between ponticuli in the sutures of *Elphidium* are termed fossettes (thereby following common usage in more recent publications). The fossettes are the routes of communication from the interlocular space ('sunken suture') to the shell surface. Their presence is intimately connected with the presence of ponticuli.

The term pore as used in the present work refers exclusively to the minute perforations traversing the walls of the shells, being equipped with an organic tubular lining subdivided by sieve plates each of which corresponds to a boundary between two secondary laminae or to the median layer. Their diameter normally ranges from 0.2 to 3.0 μm.

The term does not include structures like 'apertural pores' which by authors in the past have characterized the single shell openings constituting a multiple aperture.

The term pore has likewise been used in connection with the openings between ponticuli in *Elphidium* (namely as 'sutural pores') which in this work are termed fossettes while in the genus *Elphidiella* the term pore has been used to characterise the tubular communications from the shell surface leading into the subsutural canals (expressions like "double row of sutural pores").

The broad use of the term pore should be abandoned as it easily leads to confusion and it is recommended that the term should be restricted to pore-tubules of the shell wall (sometimes also found in the septa) but not to any other openings or communication paths of the shell.

With respect to optical wall structures we make a distinction between optically radiate versus optically granulate (compare Wood 1949; Towe & Cifelli 1967; Hansen 1968, 1970a).

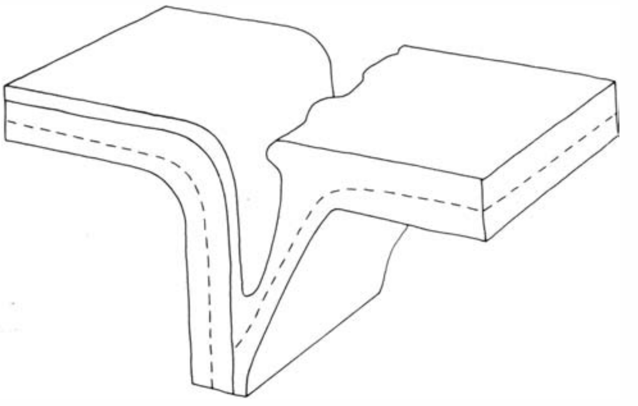


Fig. 3. Incipient formation of bridges across the interlocular space in *Pseudorotalia*.

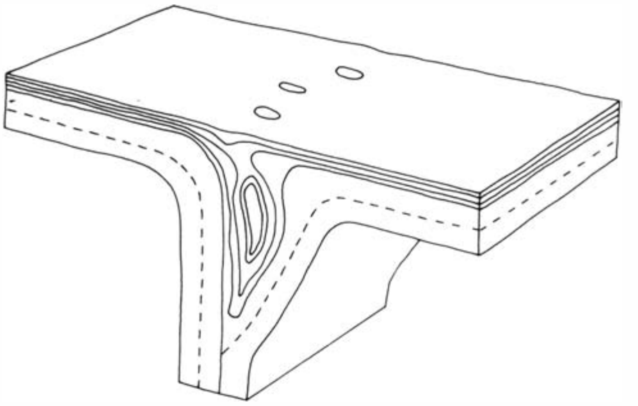


Fig. 4. Completed cover over the interlocular space in *Pseudorotalia* after formation of three additional chambers.

Introduction to the systematic revision

In the following we do not conform with the generally applied classification system of Loeblich & Tappan (1964).

Species are arranged in an order such that the first listed members are those most 'typical' for the systematic groupings here recognized.

The lists of synonyms are not complete (for such lists the reader is referred to other publications) but we have concentrated on limiting the majority of references to those where the species in question have been placed in different genera.

Discussions of generic relationships are collected in the later chapter entitled "Discussion and conclusions" (p. 24) rather than under the respective species, in order to avoid numerous undesirable repetitions. We have tried to make a distinction between descriptions (which are observational with a minimum of interpretations) and the interpretive part which is separated in the later chapter.

We have arranged our descriptions according to a fixed scheme so as to make it easier for the reader to orient himself in the individual description. Thus each description follows the same pattern with general morphological characters followed by wall structure, internal morphology and special lamellar characters.

Genus *Elphidium* Montfort, 1808

Elphidium macellum (Fichtel & Moll, 1798)

Pl. 1:1–9

□ 1798 *Nautilus macellus* var. β Fichtel & Moll, p. 66; Pl. 10:h–k. □ 1808 *Elphidium macellum* (Fichtel & Moll); Montfort, p. 15.

The material studied is Recent from off Mahdia, Tunisia; off Famagusta, Cyprus; beach of Mallorca and from the Gulf of Naples, all in the Mediterranean Sea.

Description.—Test planispiral, involute, somewhat compressed with about 16 chambers in the final whorl. Chambers narrow and strongly curved in a proximal direction. General outline smooth. Periphery angled with a rounded keel. Sutures curved and somewhat depressed. Umbilici depressed with coarse tuberculation. Aperture multiple interiomarginal. Apertural face around the apertural region densely pustulate. About half of the lateral chamber surface occupied by ponticuli.

The wall is perforate, laminated and optically radiate. Primary wall and septa bilamellar. A septal flap is present. Pore diameter about 0.2 μm.

Plastic moulds in the SEM demonstrated the presence of large retral processes and an umbilical spiral canal system with vertical umbilical canals as well. The spiral canal system formed through coalescense of sealed-off umbilical chamber parts forms an interconnected anastomosing framework between the umbilical knobs and tubercles. The system communicates with each interlocular space. Etched horizontal sections demonstrated the presence of the sealing-off plates between the chamber lumina and the umbilical parts forming the umbilical spiral canal system.

Discussion.—This species is the type species of the genus *Elphidium* Montfort, 1808. It can be distinguished from *E. crispum* by its lack of umbonal boss and by its more compressed shape.

The holotype figured by Fichtel & Moll (1798, Pl. 10: i and k) is, however, not strongly compressed compared to Fichtel & Moll's illustration of *E. crispum* (their Pl. 4: e and f) but the number of chambers in the final whorl on their figured specimens is considerably lower in *E. macellum* than in *E. crispum.*

Hofker (1971) described supplementary areal multiple apertures in his material of *E. macellum* from the sea around the island of Mallorca. Such areal apertures were not found in our specimens. Neither in the SEM nor in vertical sections studied under the light microscope were such structures found. From vertical sections published by Hofker (1971) it appears that his material is considerably more compressed than our material. Since, however, our specimens are in good agreement with the holotype in all characters according to the illustration by Fichtel & Moll, we do not feel convinced that the material described by Hofker is in fact *E. macellum.* In our material off the Tunisian coast we found specimens resembling the ones figured by Hofker in being strongly compressed. These forms in vertical section strongly resemble Hofker's specimens also with respect to presence of supplementary areal apertures. However, as pointed out by Hofker, they would appear to be the recent representatives of the evolutionary lineage involving *E. fichtellianum* and *E. ortenburgense.* They are nevertheless different from the true *E. macellum.*

Elphidium crispum (Linnaeus, 1758)

Pl. 1:10–12; Pl. 2:1–2

☐ 1758 *Nautilus crispus* Linnaeus, p. 709. ☐ 1822 *Polystomella crispa* (Linnaeus); Lamarck, p. 625. ☐ 1927 *Elphidium crispum* (Linnaeus); Cushman & Grant, p. 73; Pl. 7:3a, b.

Our material originates from Recent sediments from the beach of Rimini as well as from the Gulf of Naples.

Description.—Test planispiral, involute, biconvex with more than 20 chambers in the final whorl. Chambers narrow and curved in proximal direction. General outline of the test smooth. Periphery sharply angled with blunt keel. About half of the lateral chamber surface is occupied by ponticuli. The ponticuli are attached to the smooth chamber margin of the preceeding chamber. There are no communications through the ponticuli into the preceeding chamber. Except for the ponticuli the proximal chamber wall bends inwards to become attached to the preceeding apertural face in the interiomarginal region of the latter, thus leaving an open space (the interlocular space). The openings between the ponticuli leading into the interlocular space (generally termed fossettes) were called toothplate apertures by Hofker (1971).

The fossettes are tuberculate. The area in front of the aperture carries a dense tuberculation. The umbilical plugs (or umbonal bosses) are pierced by vertical canals with a diameter almost that of the fossettes and, like these, are provided with tubercles.

Where the ponticuli are attached to the previous septum the outer lamella wedges out and only the inner lining remains as previously described by Hansen & Reiss (1971).

The secondary lamination connected with the addition of new chambers adds considerable thickness to the outer walls of the chambers and ponticuli. This process extends the fossettes often to 2–3 times their original length. In this respect they are similar to the umbilical vertical canals of the umbilical region.

Aperture multiple interiomarginal with slight protruding lips. The central part of the apertural face is tuberculate. Tuberculation is more strongly developed on the lips and around the aperture. The marginal part of the apertural face is smooth.

Wall constructed of perforate, laminated, optically radiate calcite. Primary wall and septa bilamellar with a septal flap. Pore diameter about 0.2 μm.

Plastic moulds in the SEM demonstrated that the umbilical chamber parts have a posterior aperture opening into the interlocular space. With the addition of a new chamber the aperture in the 'umbilical corner' of the apertural face will be converted into part of the spiral canal system. In the penultimate chamber a plate is deposited sealing off the umbilical chamber part from the main lumen of that chamber thereby leading to the formation of the umbilical spiral canal system. In some of the chambers an additional umbilical aperture remains open, and with the addition of secondary laminae this will be converted into an umbilical, vertical canal piercing the umbilical plug. Oblique vertical canals leading from the interlocular space of the preceeding coil into the spiral canal of the following whorl are prominent. The remaining fossettes of the preceeding coil open into the chambers of the following whorl.

Elphidium craticulatum (Fichtel & Moll, 1798)

Pl. 2:3–9

☐ 1798 *Nautilus craticulatus* Fichtel & Moll, p. 51; Pl. 5:h–k. ☐ 1808 *Cellanthus craticulatus* (Fichtel & Moll); Montfort, p. 51. ☐ 1826 *Polystomella craticulata* (Fichtel & Moll); d'Orbigny, p. 284; No. 3. ☐ 1933 *Elphidium craticulatum* (Fichtel & Moll); Cushman, p. 48; Pl. 11:5.

Our material originates from Recent sediments from the Kei Islands, Banda Sea.

Description.—Test thick, large, planispiral, involute, lenticular with numerous chambers in the final whorl in the adult. General outline smooth. Periphery angled with a blunt keel. Sutures gently curved with numerous distinct ponticuli. With the addition of secondary lamination the ponticuli become broadened and extended in both proximal and distal directions to form ridge-like bars on the lateral chamber wall. In some specimens the ponticuli bifurcate at the point of attachment to the margin of the previous chamber. The entrance between the bifurcating ponticuli leads, like the fossettes, into the interlocular space. With the addition of secondary laminae these structures lead to the formation of double rows of openings (sutural pores of authors). There are no differences between the two rows of openings. However, in many specimens only one row is present. These are termed fossettes, while for reason of a more precise terminology we term the openings between the bifurcating ponticuli and the chamber margin of the previous chamber 'parafossettes'.

The test is characterised by very large umbilical plugs which are pierced by vertical umbilical canals. The aperture as well as the foramina are multiple and interiomarginal. Additional umbilical apertures are found at the umbilical tips of the chamber, one at each umbilicus.

The primary chamber wall is two layered, as demonstrated earlier by Hansen & Reiss (1971), and the septa are provided with a septal flap. Secondary lamination is present in the interlocular space. Wall built of optically radiate calcite. Pore diameter about 0.2 μm.

Plastic moulds showed in the SEM the presence of retral processes and an umbilical spiral canal system. With the addition of a new chamber the aperture in the 'umbilical corner' of the apertural face will be the means of communication between the umbilical spiral canal and the chamber lumen of the final chamber. At the same time a plate is deposited across the lumen of the umbilical part of the previous chamber, sealing off this part from the chamber lumen proper.

The umbilical chamber part is slightly contorted and bent in an anterior direction as well as having a minor conical prolongation in a posterior direction. In the posterior part of the umbilically drawn-out chamber part there is an aperture leading into the interlocular space formed between the ultimate chamber and the penultimate one. In fact, the umbilical tip of the final chamber contains three apertures i.e. one posterior leading into the interlocular space, one umbilically directed and one anterior (the one mentioned above as placed in the 'umbilical corner' of the apertural face). The majority of the umbilical apertures become closed by deposition of secondary laminae. However, a few of them remain open. With the addition of secondary laminae they are converted into vertical, umbilical canals the openings of which are found in the large umbilical plug.

These are not to be confused with the oblique vertical canals connecting the interlocular spaces of the preceeding coil with the umbilical spiral canal of the following coil. These oblique canals are nothing but the most umbilical fossettes which open into the umbilical chamber parts of the following whorl (which from the penultimate chamber onwards, is converted into the spiral canal). The number of oblique vertical canals corresponds to the number of interlocular spaces in the whorl where they originate, but not to the number of chambers in the whorl where they terminate.

Discussion.—Mould preparations of *E. craticulatum* were studied already as early as 1862 by Carpenter et al. Their very impressive illustration is basically correct although some details apparently were beyond the resolution power of the microscopes at the time. Carpenter's figure was reproduced by Loeblich & Tappan (1964: C 634, Fig. 3) who reproduced Voloshinova's 1958 reproduction of the original figure.

Elphidium advenum (Cushman, 1922)

Pl. 2:10–12; Pl. 3:1

☐ 1884 *Polystomella subnodosa* Brady (not *Robulina subnodosa* Münster, 1838), p. 734; Pl. 110:1a, b. ☐ 1922 *Polystomella advena* Cushman, p. 56; Pl. 9:11–12. ☐ 1930 *Elphidium advenum* (Cushman); Cushman, p. 25; Pl. 10:1–2.

Our material of this species is from Recent sediments off Banyuls, France, Mediterranean Sea.

Description.—Test involute, planispiral and slightly compressed. It possesses a peripheral keel in the earlier part of the final whorl. The periphery in the later chambers of the final whorl is subangular. The chambers number about 12 in the final whorl and are rather strongly embracing, leaving a limited umbilical area. The sutures are gently curved and crossed by distinct ponticuli. In the later sutures are both fossettes and parafossettes. The latter are, however, closed by secondary lamination already in the penultimate or antepenultimate chamber. The parafossettes are formed by a bifurcation of the ponticuli at their place of attachment to the preceeding septal margin. The umbilical part of the chambers are drawn out into an anteriorly directed lobe. The umbilical chamber parts overlap rather strongly. The aperture as well as the formina are interiomarginal and multiple.

Test wall perforate, laminated and optically granulate. Primary walls and septa are bilamellar. A septal flap is present. Pore diameter about 0.2 μm.

Plastic moulds studied in the SEM demonstrated the presence of retral processes. With the addition of a new chamber the most umbilical apertures on the apertural face become part of the umbilical spiral canal system. This system is formed by the deposition in the penultimate chamber of a plate sealing off the umbilical chamber part from the main chamber. The umbilical part of the final chamber also has a posterior aperture leading into the youngest interlocular space (suture). The plate is deposited above this opening, which thus remains a route of communication between the spiral canal system and the shell surface (in this case represented by the interlocular space). The umbilicalmost fossettes of the sutures of the previous coil are converted through the addition of secondary laminae into oblique vertical canals opening into the 'bottom' of the spiral canal of the following whorl. True vertical canals are apparently not present. The openings in the umbilical area suggesting presence of such structures are in fact the umbilicalmost fossettes of the older part of the final whorl.

Elphidium margaritaceum Cushman, 1930

Pl. 3:2–6

□ 1930 *Elphidium advenum* (Cushman) var. *margaritaceum* Cushman, p. 25; Pl. 10:3. □ 1957 *Elphidium margaritaceum* Cushman; van Voorthuysen, p. 32; Pl. 23:13.

The material of this species originates from Recent sediments in Kattegat and from Quaternary deposits at Brovst, Denmark.

Description.—Test planispiral, involute, generally small, compressed with strongly embracing chambers; about 8–12 in the final whorl. General outline smooth. Periphery angled to somewhat rounded. In the earlier part of the final whorl with an acute peripheral keel. The sutures are curved with relatively few ponticuli. The umbilical area slightly if at all depressed. The whole surface, including the apertural face, ponticuli and fossettes, is covered by distinct tuberculation. The interlocular space is rather deep, although not as deep as in *E. macellum* and *E. crispum.* Aperture multiple, interiomarginal with small protruding lips. Additional multiple, areal apertures may be present, but were not present in all specimens studied.

Wall structure optically radiate. Shell constructed according to the bilamellar pattern. It is not evident if a septal flap is present covering also the central part of the septa. It appears that the tuberculation of the central part is smoothened but we have been unable to follow a septal flap in sections in the SEM, maybe due to the irregular borderline between the flap and the tuberculate outer lamella of the relevant septum. Pore diameter about 0.15 μm.

Plastic moulds studied in the SEM showed presence of large and distinct retral processes as well as of an umbilical spiral canal system. It is seen that the final chamber in its umbilical part is not sealed off from the remaining chamber lumen as is the case with all the previous umbilical chamber parts. The umbilical parts of the chambers are plate-like with a somewhat irregular shape. The irregular outline is due to the superposition of the wall onto the tuberculate surface of the earlier chamber. The umbilical posterior aperture connects the chamber lumen of the final chamber with the interlocular space of the youngest suture. This opening in the older sealed-off umbilical chamber parts retains the communication from the umbilical spiral canal system into the respective interlocular spaces.

Elphidium sagrum (d'Orbigny, 1839)

Pl. 3:7–10

□ 1839 *Polystomella sagra* d'Orbigny, p. 55; Pl. 6:12, 20. □ 1930 *Elphidium sagrum* (d'Orbigny); Cushman, p. 24; Pl. 9:5–6.

Our specimens originate from Recent sediments from Jamaica kindly put at our disposal by Dr. J. Murray.

Description.—Test planispiral, involute with rather strongly embracing chambers. About 12 chambers in the final whorl. Test compressed. General outline smooth but slightly lobate in the final part of the final whorl. Periphery subangular. A keel-like periphery is developed in the earlier part of the final whorl caused by addition of secondary laminae. Distinct ponticuli are present in the gently curved sutures. The side walls of the fossettes are tuberculate. The ponticuli are broadened by secondary lamination in the earlier part of the final whorl. Apertural face tuberculate as is also the area in front of the interiomarginal multiple aperture on the early part of the final whorl. There are no additional areal apertures or foramina.

The wall is laminated, perforate and optically granulate. Wall and septa are bilamellar and septal flaps are developed. Pore diameter about 0.2 μm.

Plastic moulds in the SEM showed presence of distinct retral processes. In addition a well developed umbilical spiral canal system was found along with vertical umbilical canals. It is constructed in the same way as in other forms described herein i.e. fusion of overlapping sealed-off umbilical parts of chambers communicating with the interlocular spaces.

Elphidium striatopunctatum (Fichtel & Moll, 1798)

Pl. 3:11–12; Pl. 4:1–7

□ 1798 *Nautilus striato-punctatus* Fichtel & Moll, p. 61; Pl. 9:a–c. □ 1929 *Elphidium striato-punctatum* (Fichtel &

Moll); Cushman & Leavitt, p. 19; Pl. 4:5–6. □ 1971 *Elphidiononion striato-punctatum* (Fichtel & Moll); Hofker, p. 68; Pl. 98:13–18; Pl. 106:4.

Our material of this species originates from the inner basin of the mangroves at Nabek about 50 km north of Sharm-e-Sheik, Gulf of Elat. The locality is situated in the Gulf of Elat but close to the Red Sea proper.

Description.—Test planispiral, involute with about 15–20 chambers in the final whorl. It is thick relative to its diameter. General outline smooth. Periphery very broadly rounded. The chambers are slightly curved. The apertural face is inflated but not strongly. Tuberculation is present close to the aperture and in front of it, but otherwise the apertural face is smooth. Ponticuli are numerous in the slightly curved sutures. As in many other species described herein, tuberculation is present in the fossettes. In the earlier part of the final whorl the secondary lamination smoothens the ponticuli to such a degree that they give the impression of low and broad costae running in the direction of coiling. At the suture between the two last-formed chambers ponticuli are found which are slightly widened at their point of attachment to the previous chamber so as to leave an opening communicating into the interlocular space (parafossettes) besides the regular fossettes. At the penultimate suture these widened parts coalesce through the addition of secondary laminae. This leads to the formation in the antepenultimate and earlier sutures of a ridge-like structure separating an anterior row of fossettes and a posterior row of parafossettes both communicating with the interlocular space. In addition, deposition of secondary lamination on the lateral chamber walls in an anterior direction takes place, leading to formation of costa-like ridges occasionally coalescing with the ponticuli. The aperture is multiple, interiomarginal with each opening surrounded by a small protruding collar-like lip. In the initial part (as seen in section) the multiple foramina are few but their number grow with additional available space.

Wall built of optically granulate calcite. Chamber walls and septa are bilamellar with a septal flap. Pore diameter about 0.2 μm.

A well developed umbilical spiral canal system was seen on plastic moulds in the SEM. It appears to be formed (as in other species) by fusion of the sealed-off umbilical chamber parts. Oblique vertical canals are distinct and additional umbilical apertures (although not on the umbilical part of every chamber) is through addition of secondary lamination converted into vertical umbilical canals. Each of the umbilical chamber parts have an aperture opening into the interlocular space of the respective suture. Retral processes are prominent.

Discussion.—Hofker (1971) commented on this species and placed it in his genus *Elphidiononion* since he was unable to observe retral processes in sections. Retral processes are, however, prominent and distinct in this species as is seen from the accompanying illustrations.

Elphidium voorthuyseni Haake, 1962

Pl. 4:8–12

□ 1962 *Elphidium voorthuyseni* Haake, p. 50; Pl. 5:6–7.

Our material of this species originates from Eemian deposits at Meetkerke, Belgium.

Description.—Test planispiral, involute and strongly compressed. 8–10 chambers in the final whorl. General outline smooth, slightly if at all lobate. Periphery compressed but well rounded. Sutures curved. The interlocular space does not reach the peripheral region but extend two thirds of the length of the chambers. Ponticuli rather few and somewhat irregular. The umbilical regions are slightly depressed and covered with fine tuberculation which also occurs on the side walls of the interlocular space as well as in front of the aperture. The aperture and foramina are interiomarginal and multiple.

Wall calcitic, optically granulate. Septa and primary wall bilamellar. Septal flaps are present. Pore diameter about 0.2 μm.

Plastic moulds studied in the SEM demonstrated the presence of retral processes as well as an umbilical spiral canal system. The latter was, however, very difficult to observe since the tests are very small and fragile, for which reason satisfactory preparations were not obtained. However, evidence is present showing the sealed-off umbilical chamber parts.

Elphidium williamsoni Haynes, 1973

Pl. 5:1–6

□ 1858 *Polystomella umbilicatula* (Walker); Williamson (non *Nautilus umbilicatulus* Walter & Jacob, 1798), p. 42; Pl. 3:81–82. □ 1930 *Elphidium excavatum* (Terquem); Cushman, p. 21: Pl. 8:1–7. □ 1965 *Cribrononion alvareziana* (d'Orbigny); Lutze, p. 101; Pl. 15:46. □ 1968 *Cribrononion articulatum* (d'Orbigny); Lutze, p. 27; Pl. 1:1–2. □ 1969 *Elphidium umbilicatulum* (Williamson); Lévy et al., p. 96; Pl. 1:6; Pl. 2:1–2. □ 1971 *Elphidium articulatum* (d'Orbigny); Murray, p. 153; Pl. 63:1–7. □ 1973 *Elphidium williamsoni* Haynes, p. 207; Pl. 24:7; Pl. 25:6, 9; Pl. 27:1–3.

Our material of this species originates from Recent sediments in Limfjorden as well as in Roskilde Fjord, Denmark.

Description.—The test is involute, planispiral with strongly embracing chambers. 10–14 chambers in the final whorl. The general outline is smooth but somewhat lobate in the final part. Periphery rounded. The sutures are curved. The test is smooth except for tuberculation in the fossettes and on the ponticuli in the final suture. The interlocular space is rather shallow. The ponticuli are very distinct. By addition of secondary lamination the older ponticuli become broadened and also smoothened while the sides of the ponticuli along with the remaining part of the fossettes retain their tuberculation. The aperture and foramina are multiple interiomarginal. Each opening is equipped with a collar-like lip. The apertural face is inflated, perforate and smooth except for the area around and in front of the aperture where tuberculation is developed.

Wall constructed of perforate laminated optically radiate calcite. Test wall and septa bilamellar. Septal flaps are developed. Pore diameter about 0.2 μm.

Plastic moulds in the SEM showed presence of an umbilical spiral canal system. The single elements of this spiral canal system consist of the sealed-off umbilical chamber prolongations which in *E. williamsoni* are very narrow. Each sealed-off part has a communication leading into the interlocular space of the corresponding suture. The umbilical tips of the chambers are generally fused with the neighbouring elements with whom they communicate through the most umbilical-ward foramen. In addition to these, umbilical apertures may be developed that, with the addition of secondary lamination, form short vertical umbilical canals opening into the furrow around the umbilical plug (or plugs). These openings are inferred from study of the moulds, since direct observations on the test are greatly hampered by the presence in the relevant areas of a strongly developed tuberculation.

The retral processes are distinct and well developed in this species.

Elphidium gerthi van Voorthuysen, 1957

Pl. 5:7–12

☐ 1951 *Elphidium* sp. 1 van Voorthuysen, p. 25; Pl. 2:19. ☐ 1957 *Elphidium gerthi* van Voorthuysen, p. 32; Pl. 23:12.

Our material of this species originates from Recent deposits in Kattegat and from Eemian deposits at Meetkerke, Belgium.

Description.—Test involute, planispiral with about 10–12 chambers in the final whorl. Chambers slightly curved. Test strongly compressed. Periphery rounded to subangular. Sutures curved and somewhat depressed. There is a few ponticuli in each suture. Parafossettes may be present in the suture of the final chamber but are covered over by secondary lamination already in the penultimate or antepenultimate suture. The interlocular space is rather shallow. Umbilical parts of the chambers commonly fused with neighbouring chambers giving the impression of a ring-shaped area around the umbilical knobs or tubercles. Secondary lamination strongly reinforces the earlier part of the final coil and thereby partly veils the ponticuli of that part of the shell. Shell surface generally smooth except for the tuberculation present in the fossettes and in the umbilici. Apertural face perforate and smooth except for a few scattered tubercles. Aperture and foramina multiple, interiomarginal with protruding apertural lips.

Septa and primary chamber wall bilamellar. The downward-bent chamber wall that together with the preceeding septum delimits the interlocular space does not cover the septum but stops shortly after the interlocular space. Thus no true septal flap is developed. Wall constructed of laminated, perforate, optically granulate calcite. Pore diameter about 0.2 μm.

Plastic moulds in the SEM demonstrated presence of retral processes and umbilical spiral canal system. Due to the small size of the shells it was connected with considerable problems to obtain sufficiently good preparations. In spite of this difficulty it appears from the preparations that the umbilical spiral canal system is constructed of interconnected umbilical chamber parts sealed off from their respective chambers. They also communicate with the interlocular space of the respective suture.

Elphidium excavatum (Terquem, 1876)

Pl. 6:1–6

☐ 1876 *Polystomella excavata* Terquem, p. 429; Pl. 2:2a–d. ☐ 1932 *Elphidium (Polystomella) excavatum* (Terquem); Heron-Allen & Earland, p. 439; Pl. 16:22–23. (☐ For additional synonyms, see Feyling-Hanssen 1972.)

Our material originates from Quaternary deposits at Hirtshals, Denmark as well as from Recent sediments from Chandlers Fjord, Canada and from Recent sediments from off West Greenland.

Description.—Test involute, planispiral and compressed. General outline slightly lobate. Periphery rounded to subacute. 8–11 chambers in the final whorl commonly 9 or 10. Sutures gently curved, depressed with few irregularly spaced ponticuli. Slight tuberculation may occur in the sutures and in the umbilici. The umbilical regions bear one or few umbilical bosses. The apertural face is smooth and imperforate. The aperture is multiple, interiomarginal and commonly associated with a little tuberculation. The foramina are like the aperture; in the initial part, however, they have fewer openings than in later stages; their number gradually increases with available space.

The wall is perforate, laminated and optically radiate. Test construction bilamellar with septal flaps. Pore diameter about 1.2 μm.

Plastic moulds in the SEM showed few but distinct retral processes. On the surface the fused umbilical chamber parts cover an umbilical spiral canal system which is deep-seated. It is constructed of the sealed off umbilical parts of the penultimate and earlier chambers interconnected through the umbilical most anteriorly placed foramina. Unlike the earlier chambers, the ultimate chamber does not have a plate deposited across the umbilical part. All interlocular spaces communicate with the umbilical spiral canal.

By contrast to the majority of species with umbilical spiral canal system studied herein, the system proper is difficult to observe in the kind of preparation used here. In order to visualize it more clearly a series of chamber moulds were removed whereby the 'lower' system was exposed 'above' the overhanging chamber tips.

A further complication is introduced by the almost horizontally bent sealing-off plate. Vertical umbilical canals (former umbilical apertures) open into the bottom of the furrow around the umbilical knob. The furrow is equipped with tubercles the impressions of which are seen in the mould.

Discussion.—Feyling-Hanssen (1972) concluded in his discussion of *E. excavatum* and its variant forms that materials previously recorded as *E. clavatum, E. selseyensis* and *E. lidoense* are apparently no more than ecological variants showing intergradation.

We agree with Feyling-Hanssen that the *forma* concept (not recognized by ICZN) may be very useful for characterising the dominating ecological variant within a population of *E. excavatum* and that the names *clavatum, selseyensis* and *lidoense* should not be regarded as valid even at a subspecies level.

Elphidium groenlandicum Cushman, 1933

Pl. 6:7–12

☐ 1933 *Elphidium groenlandicum* Cushman, p. 4; Pl. 1:10.
☐ 1939 *Elphidiella groenlandica* (Cushman); Cushman, p. 66; Pl. 10:3.

Our material of this species originates from Quaternary deposits at Hirtshals, Denmark.

Description.—Test involute, planispiral with 11–16 chambers in the final whorl. Chambers embracing but not strongly so, leaving a large umbilical plug. General outline smooth to very slightly lobate. Periphery subangular. The ponticuli constitute a small part of the lateral wall area. They lie rather deep in the sutures and sometimes give the impression that such structures are absent in the ultimate and penultimate sutures. However, through the addition of secondary lamellae the ponticuli and thereby the fossettes between them become clearly distinguishable on the shell surface. The interlocular space is deep-seated and shallow. The addition of secondary lamellae in the sutural regions often causes a slight irregularity in the appearance of the fossettes sometimes giving the impression of either alternating fossettes ('sutural pores') or a double row of fossettes. This may well be the reason why authors have placed this species in the genus *Elphidiella.* The aperture is multiple and interiomarginal as are also the foramina.

Wall composed of perforate, laminated optically radiate calcite. Septa and primary wall bilamellar. Septal flaps are developed. Pore diameter about 0.2 μm.

Plastic moulds studied in the SEM showed distinct retral processes as well as presence of an umbilical spiral canal system. In contrast to most other elphidiids described herein, however, the umbilical part of the chambers have some tube-like extensions into the umbilical plug area where some of them may develop into plate-like bodies some of which may anastomose. They communicate with the interlocular spaces between the chambers as in other forms described and they are isolated from the chamber lumina proper by deposition of a plate across the umbilical part of the chambers in the penultimate and earlier chambers. Umbilical apertures in some of the sealed-off chamber parts remain open and with the addition of the heavy secondary lamination are converted into vertical umbilical canals, the sides of which are equipped with tubercles.

Elphidium translucens Natland, 1938

Pl. 7:1–11

☐ 1938 *Elphidium translucens* Natland, p. 144; Pl. 5:3–4.
☐ 1970 *Cribrononion translucens* (Natland); Daniels, p. 88, Pl. 7:13.

Our material originates from beach sand at Rimini, Italy.

Description.—Test somewhat compressed, planispiral, involute with strongly embracing chambers. About 10 chambers in the final whorl. General outline smooth, may become slightly lobate in the final part of the final whorl. Periphery rounded. Sutures almost radial with indistinct small ponticuli. With the addition of secondary lamination the ponticuli become broadened and the fossettes are partly closed. Apertural face perforate and smooth. The aperture and the foramen are interiomarginal and multiple. In addition each chamber in its umbilical plate-like chamber prolongation contains one or more umbilical apertures.

The primary chamber wall is bilamellar. Thin septal flaps are present. The wall is optically radiate. Pore diameter about 4 μm.

Plastic moulds in the SEM demonstrated the presence of a well developed umbilical spiral canal system. The umbilical chamber prolongations are drawn out with a posterior part having one aperture opening into the interlocular space of the final suture. With the addition of a new chamber the anterior aperture nearest the umbilicus is converted into a foramen connecting the umbilical spiral canal system with the lumen of the umbilical prolongation of the final chamber. At the same time as a new chamber is added an apparently two-layered plate is deposited sealing off the umbilical chamber prolongation of the penultimate chamber from the main lumen of that chamber. Thus an umbilical spiral canal system is formed consisting of the sealed-off umbilical chamber parts interconnected through the former umbilical anterior apertures. At the same time each sealed-off part communicates with its corresponding interlocular space as well as with the shell surface through the umbilical apertures. Some of these (but not all) are converted into vertical umbilical canals through the addition of secondary laminae. As the overlap of the umbilical chamber parts is relatively large the umbilical spiral canal system when studied as moulds appears as a series of somewhat twisted interconnected plates. Retral processes are present but are rather small.

Elphidium vadescens (Cushman & Brönnimann, 1948)

Pl. 7:12; Pl. 8:1–9

☐ 1948 *Cribroelphidium vadescens* Cushman & Brönnimann, p. 18, Pl. 4:5.

The material of this species originates from Recent sediments from the Gulf of Paria, Trinidad (Station 31; coll. Brönnimann) and kindly placed at our disposal by Dr. Francis Parker.

Description.—Test planispiral, involute with about 10 chambers in the final whorl. The test is somewhat compressed with a rounded periphery. Sutures almost radial and depressed in the final part of the test. Ponticuli few and broad. Chamber wall in the earlier part considerably thickened by secondary lamination. Umbilicus with a boss. Aperture multiple interiomarginal with raised collars. The specimens studied showed no additional areal apertures. Apertural face smooth and imperforate. The apertural surroundings covered by fine tuberculation.

Wall calcitic, laminated and optically radiate. Primary wall and septa bilamellar. Septal flaps are present. Pore diameter about 3 μm.

Plastic moulds in the SEM showed the presence of an umbilical spiral canal system apparently constructed by sealed-off umbilical parts of chambers interconnected through the umbilicalmost interiomarginal aperture with an additional posterior aperture opening into the interlocular space. Retral processes are few but distinct.

Discussion.—This species is the type species of the genus *Cribroelphidium* Cushman & Brönnimann 1948. It shows a strong resemblance to *E. guntheri* and *E. oceanense* (*sensu* Murray 1971). They differ in only one character, namely total size. It appears that all species occur in shallow waters and the slight differences in detailed morphology of the ornamental features as well as total test size may well be due to environmental factors. Thus we regard *E. vadescens* as an independent species only tentatively.

Elphidium guntheri Cole, 1931

Pl. 8:10–12; Pl. 9:1–3

☐ 1931 *Elphidium guntheri* Cole, p. 34; Pl. 4:9–10.

The material of this species originates from Eemian deposits at Meetkerke, Belgium and from Recent sediments from Limfjorden, Denmark.

Description.—Test planispiral, involute with 8–11 chambers in the final whorl. General outline smooth. Periphery very broadly rounded. About one third of the lateral wall of the final chamber is occupied by ponticuli. The ponticuli are broad and smooth, while the sides in the latest suture are already stongly tuberculate, which also applies to the septal face as observed through the fossettes. With addition of secondary lamination the final whorl gradually takes on a rather massive appearance owing to broadening of the ponticuli. The umbilical regions are equipped with rather large, flat topped knobs that are tuberculate on the sides. Aperture interiomarginal, multiple with or without additional multiple apertures arranged in a single row above the interiomarginal row. The apertural face is slightly inflated and smooth except for the area close to the multiple apertures where a dense tuberculation is developed. Tuberculation is also present on an area just in front of it. The apertural face is imperforate.

Wall built of optically radiate calcite. Chamber wall and septa are bilamellar. Septal flaps are present. Pore diameter about 3 μm.

Plastic moulds in the SEM showed distinct retral processes as well as presence of an umbilical spiral canal system. Due to the prominent umbilical knobs it was difficult to obtain complete preparations for study of the spiral canal system. The spiral canal system appears to be constructed of the fused overlapping umbilical parts of chambers isolated from their respective main chamber lumina by vertical plates. They communicate with the interlocular space.

Discussion.—As mentioned above, *E. vadescens* is most likely identical with *E. guntheri,* in which case it becomes a junior synonym. Van Voorthuysen (1957) compared his *E. guntheri* var. *waddensis* with topotypes of *E. guntheri* from California and found them to be identical. In spite of this, Haynes (1973) raised Voorthuysen's *E. guntheri* var. *waddensis* to species rank, thereby making a positive junior synonym.

E. oceanense (d'Orbigny 1826) is a nomen nudum since d'Orbigny did not illustrate his species and no description was made.

Dr. Yolande Le Calvez kindly informed us that no holotype of *E. oceanense* exists.

Elphidium kugleri (Cushman & Brönnimann, 1948)

Pl. 9:4–8

☐ 1948 *Cribroelphidium kugleri* Cushman & Brönnimann, p. 18; Pl. 4:4.

Our material of this species originates from Recent sediments of the Gulf of Paria, Trinidad (Station 31; coll. Brönnimann) kindly placed at our disposal by Dr. Francis Parker.

Description.—Test planispiral involute with strongly embracing chambers. There are 7–8 chambers in the final whorl. General outline smooth. Periphery broadly rounded. The final part of the final whorl may be slightly lobate. Chambers moderately inflated. Sutures slightly depressed and almost radial. Ponticuli short and distinct. Umbilicus hardly depressed and marked by the fused umbilical chamber parts the junctions of which are smoothened by addition of secondary lamination.

Apertural face in its central part imperforate. Aperture interiomarginal multiple with additional multiple areal openings. The foramina are like the aperture.

The wall is constructed of laminated, perforate, optically radiate calcite. The wall and septa are bilamellar. Septal flaps are developed. Pore diameter about 2 µm.

The openings of the multiple interiomarginal aperture that are nearest the umbilicus are larger than the remaining openings. With addition of new chambers these apertures make up the connection between the umbilical chamber ends forming the umbilical spiral canal system. This is constructed of the sealed-off umbilical chamber parts. These are delimited by a plate deposited in such a position that direct communication between the sealed-off part and the main lumen of the chamber is impossible. This process takes place in the penultimate and earlier chambers but not in the ultimate one. Retral processes are present. They are small but distinct.

Elphidium poeyanum (d'Orbigny, 1839)

Pl. 9:9–12; Pl. 10:1–5

☐ 1839 *Polystomella poeyana* d'Orbigny, p. 55; Pl. 6:25–26. ☐ 1930 *Elphidium poeyanum* (d'Orbigny); Cushman, p. 25; Pl. 10:4–5. ☐ 1964 *Cribroelphidium poeyanum* (d'Orbigny); Loeblich & Tappan, p. C 635:508,3. ☐ 1951 *Elphidiononion poeyanum* (d'Orbigny); Hofker, p. 356.

The material of this species originates from Recent sediments from Florida, U.S.A. (Station 62–4; coll. D. Scholl) as well as from off the coast of Brazil at Tramandai (coll. D. Closs and M. C. Barbarena).

Description.—Test planispiral, involute, slightly compressed with about 10 chambers in the final whorl. The later part of the final whorl shows a slightly lobate outline. Periphery rounded. The ponticuli are short. The fossettes of the earlier chambers become progressively closed with the addition of secondary laminae broadening the ponticuli. Such secondary material also smoothens the umbilical area in the earlier part of the final whorl. The apertural face is smooth and imperforate. The most umbilical openings of the interiomarginal multiple aperture are larger than the remaining openings. With the addition of a new chamber the interiomarginal multiple aperture along with the areal additional apertures are converted into foramina.

Wall built of perforate, laminated, optically radiate calcite. Septa and chamber wall bilamellar. Septal flaps present. Pore diameter about 2 µm.

Plastic moulds in the SEM showed presence of distinct but rather short retral processes. An umbilical spiral canal system is developed by successively sealed-off umbilical chamber parts, which are interconnected through the most umbilical-ward apertures. Each umbilical chamber part communicates with the interlocular space between the respective chamber and the preceeding one through a posterior sutural aperture. Only few vertical canals are present. The oblique umbilical canals are in fact the fossettes nearest the umbilicus of each interlocular space of the previous whorl, which connect the respective interlocular space with the umbilical spiral canal of the following whorl.

Discussion.—This species was selected by Hofker as type species of his genus *Elphidiononion.*

Elphidium bartletti Cushman, 1933

Pl. 10:6–12

☐ 1933 *Elphidium bartletti* Cushman, p. 4; Pl. 1:9. ☐ 1946 *Elphidium goësi* Stschedrina, p. 144; Pl. 4:20. ☐ 1951 *Cribroelphidium arcticum* Tappan, p. 6; Pl. 1:27–28. ☐ 1952 *Elphidium vulgare* Voloshinova, p. 53; Pl. 8:3–8.

Our material originates from Quaternary deposits at Hirtshals, Denmark, and from Recent sediments from South-west Greenland.

Description.—Test involute planispiral with smooth to slightly lobate general outline. About 10 inflated chambers in the final whorl. Sutures and umbilical area depressed. Periphery broadly rounded. Apertural face somewhat inflated and densely tuberculate. The tuberculation extends in an umbilico-posterior direction onto the lateral chamber wall of the final chamber. With the addition of a new chamber the tuberculate part of the lateral chamber wall appears like one ray of the star-like umbilical tuberculate figure. Later secondary lamination adds extra tuberculation on the anterior side of the suture, thus broadening the rays of the star-like figure. Likewise the secondary lamination smoothens the ponticuli in the earlier part of the final whorl. This is especially evident in the peripheral part which in the earlier part appears to lack ponticuli completely; they are, however, buried below secondary lamellae. The ponticuli are small. The interlocular space is shallow. The aperture as well as each foramen is a low arch-shaped interiomarginal, equatorial opening confined to the central part with additional multiple areal apertures in one or two rows.

In addition to the interiomarginal equatorial central aperture, *E. bartletti* possesses two apertures in the interiomarginal umbilical 'corners' of the apertural face. Besides these interiomarginal openings a posterior aperture on both sides leads into the suture and connects the chamber lumen of the final chamber with the interlocular space of the last suture.

Test constructed of laminated, perforate, optically radiate calcite. The apertural face is heavily tuberculate while the septa are smooth or almost so, which indicates the presence of umbilical flaps. Wall and septa bilamellar. Pore diameter about 0.4 µm.

Plastic moulds in the SEM demonstrated that with the addition of a new chamber a plate is added sealing off the umbilical part of the penultimate chamber from the lumen of the main chamber. Communication with the lumen of the final chamber takes place through the former umbilical 'corner aperture', which at this stage is converted into an anterior umbilical foramen. Additional umbilical apertures apparently also exist. These openings into the umbilicus are with the addition of secondary lamination converted into vertical umbilical canals the openings of which are seen in the umbilical region on the shell surface. Thus a fully developed umbilical spiral canal system exists. Small but distinct retral processes are present.

Elphidium hallandense Brotzen, 1943

Pl. 11:1–7

☐ 1943 *Elphidium* (*Elphidiella*) *hallandense* Brotzen, p. 268:109–2. ☐ 1944 *Elphidium subarcticum* Cushman, p. 27; Pl. 3:34–35. ☐ 1969 *Cribroelphidium subarcticum* (Cushman); Gudina, p. 38; Pl. 12:11–12.

The material originates from Quaternary deposits at Hirtshals, Denmark.

Description.—Test involute, compressed with umbilical regions slightly depressed. Periphery rounded, general outline somewhat lobate. 7–10 chambers in the final whorl, commonly 8. Sutures only slightly curved, slightly depressed and bridged by ponticuli. Rather broad bands of tubercles are situated along the sutures as well as ornamenting the umbilici. The aperture is a low interiomarginal equatorial arch often obscured by tuberculation covering the apertural face. Supplementary scattered areal apertures are present. With the addition of a new chamber the apertures are converted into foramina unaltered except for the loss of the veiling tuberculation in front of the aperture, which is reduced considerably.

The wall is built of laminated perforate optically radiate calcite. Test construction according to the bilamellar pattern. The inner lining of a chamber does not cover the central part of the preceeding septum but stops shortly after having formed together with the outer lamella the interlocular space. Pore diameter about 0.6 μm.

Plastic moulds in the SEM demonstrated presence of a well developed umbilical spiral canal system, being constructed by the isolated umbilical chamber parts except for the final chamber, where the umbilical part is in direct contact with the older umbilical chamber parts as well as with the interlocular space of the youngest suture. In the penultimate and earlier chambers a plate is deposited that seals off the relevant parts of the chambers. Small but distinct retral processes are present.

Elphidium oregonense Cushman & Grant, 1927

Pl. 11:8–13

☐ 1927 *Elphidium oregonense* Cushman & Grant, p. 79; Pl. 8:3. ☐ 1941 *Elphidiella oregonense* (Cushman & Grant); Cushman, p. 34; Pl. 9:8–9.

The material originates from Quaternary deposits of the North Sea basin kindly placed at our disposal by Dr. J. H. van Voorthuysen, Haarlem, and Dr. P. G. Laga, Louvain.

Description.—Test very large in the adult, planispirally coiled with a tendency to become evolute in the final whorl, 17–20 chambers in the final whorl. Test compressed with large umbilical elevations. Periphery rounded. Sutures slightly curved. Ponticuli distinct. The interlocular space is rather shallow. Owing to incomplete material the aperture has not been observed. Foramen rather narrow interiomarginal slit-like with additional multiple areal foramina. In some specimens they are arranged in two rows running in peripheral direction.

Wall composed of perforate, laminated, optically radiate calcite. Wall and septa bilamellar. Septal flaps are present. Pore diameter about 1.2 μm.

Plastic moulds in the SEM showed presence of rather small retral processes. A prominent umbilical spiral canal system is developed, apparently constructed by the fused and sealed-off umbilical chamber parts. However, the final chamber has not been observed in this kind of preparation due to lack of complete specimens. A few vertical umbilical canals were found. Oblique vertical canals (i.e. fossettes opening into the floor of the spiral canal) are present also. The moulds have a rough and uneven surface, indicating a very rough internal wall surface. This was observed on opened specimens also, where the septa on both distal and proximal side as well as the lateral wall were covered with an apparently agglutinated layer. Polished and etched sections showed that the particles are present on the surface only.

Discussion.—Anderson (1963) described an agglutinated layer on specimens of *E. oregonense* from the Bering Sea.

Elphidium tuberculatum (d'Orbigny, 1846)

Pl. 12:1–4

☐ 1846 *Nonionina tuberculata* d'Orbigny, p. 108; Pl. 5:13–14. ☐ 1857 *Nonionina subgranosa* Egger, p. 299; Pl. 14:16–18. ☐ 1958 *Porosononion subgranosum* (Egger); Putrya, p. 135.

Our material is from Egger's type locality Marienhof, Bavaria, Germany. It was kindly placed at our disposal by Dr. H. Hagn. In addition material originating from Miocene deposits from the southern part of the U.S.S.R. was kindly donated by Dr. Valentina Yanko.

Description.—Test involute, planispiral with about 11 chambers in the final whorl. Sutures gently curved slightly depressed near the periphery becoming more strongly depressed in the umbilical direction. Chambers slightly inflated. General outline smooth to slightly lobate in the final part of the whorl. Periphery broadly rounded to somewhat compressed. Apertural face slightly inflated and imperforate in the central and basal part.

The development of secondary lamination is very pronounced leading to the formation of one or more larger umbilical knobs as well as coarse umbilical tuberculation. In addition the chamber borders along the depressed sutures towards the umbilicus are broadened leading to structures superficially resembling ponticuli. Aperture interiomarginal, multiple with additional multiple areal apertures. The foramina are like the aperture.

The wall is constructed of perforate, laminated optically radiate calcite. Lamellar character unknown due to poor preservation of the material studied. Pore diameter about 2.5 μm.

Plastic moulds in the SEM showed no presence of retral processes. However, an umbilical spiral canal system appears to be present. As in other species described herein, this system also communicates with the interlocular space. The interlocular space (sunken suture) does not exist in the peripheral part of the shell.

Discussion.—This species was selected (1958) by Putrya as type species for a new genus, *Porosononion.* The latter was regarded by Loeblich & Tappan (1964) as a synonym of the genus *Protelphidium* (Haynes, 1956). Putrya referred to the species as *N. subgranosa* (Egger, 1857) in spite of the fact that Marks (1951) listed this species as a synonym of *N. tuberculatum* (d'Orbigny, 1846).

Elphidium incertum (Williamson, 1858)

Pl. 12:5–9

☐ 1858 *Polystomella umbilicatula* var. *incerta* Williamson, p. 44; Pl. 3:82a. ☐ 1930 *Elphidium incertum* (Williamson); Cushman, p. 18; Pl. 7:4–9. ☐ 1965 *Cribrononion incertum* (Williamson); Lutze, p. 103; Pl. 21;43–44.

Our material originates from Recent sediments from Limfjorden and Kattegat, Denmark.

Description.—Test planispiral, involute with rather strongly embracing chambers; 8–11 in the final whorl, commonly 9–10. General outline smooth to slightly lobate in the final part of the final whorl. Sutures curved, depressed between the lateral chamber walls but less so in the periphery. Periphery rounded to subacute. Apertural face curved, perforate and smooth. In front of and around the interiomarginal multiple aperture on the apertural face and on the earlier part of the latest whorl is a dense, fine tuberculation which is developed also in the depressed umbilicus and in the depressed parts of the sutures. The foramina are like the aperture. Scattered ponticuli occur, being generally most conspicuous on the earlier part of the final whorl. The interlocular space is rather shallow and does not cross the periphery. The fossettes are strongly tuberculate on the sides and are rather long.

Wall constructed of perforate, laminated, optically granulate calcite. Wall and septa bilamellar. Septal flaps are present. Pore diameter about 1 μm.

Plastic moulds in the SEM demonstrated presence of few, short and scattered retral processes. An umbilical spiral canal system is present, formed by the sealed-off umbilical parts of the penultimate and earlier chambers. The spiral canal system also communicates with the interlocular space through an opening which originally was a sutural posterior aperture of the respective chamber. No vertical umbilical canals were observed.

Elphidium asklundi Brotzen, 1943

Pl. 12:10–12; Pl. 13:1

☐ 1943 *Elphidium (Elphidiella) asklundi* Brotzen, p. 267:109–1.

The specimens studied are from Quaternary deposits at Hirtshals, Denmark.

Description.—This large species appears to be identical to *Elphidium incertum* (Williamson, 1858) described above. The only character in which the two species differ is size. The different size may well be due to ecological conditions. The wall structure, retral processes and umbilical spiral canal system do not differ. However, due to the consistantly larger size of the specimens of *E. asklundi* compared to *E. incertum,* the two species are only tentatively regarded as separate.

The interlocular space of *E. asklundi* is constructed in a manner identical to that described from other species belonging to the genus *Elphidium* and is different from the construction principle of *Elphidiella*.

Elphidium magellanicum Heron-Allen & Earland, 1932

Pl. 13:2–6

☐ 1932 *Elphidium (Polystomella) magellanicum* Heron-Allen & Earland, p. 440; Pl. 16:26–28. ☐ 1939 *Elphidium magellanicum* Heron-Allen & Earland; Cushman, p. 62; Pl. 17:11–12.

The specimens studied originate from Eemian deposits at Meetkerke, Belgium and from Recent sediments from Kattegat, Denmark.

Description.—Test planispiral, involute, somewhat compressed with depressed umbilici. Periphery rounded. General outline lobate. 5–7 inflated chambers in the final whorl. Sutures slightly curved, depressed. The depressed sutures and umbilical regions covered by dense tuberculation, as are also the apertural face and earliest chambers in the final whorl. Ponticuli obscured by tuberculation. The aperture is an interiomarginal, equatorial low arch, not reaching the umbilici. It is veiled by tuberculation. The tuberculation veiling the aperture is evidently resorbed or pushed off when the aperture is converted into a foramen. Except for the tuberculation the foramina are like the aperture.

Wall calcitic, perforate, laminated and optically radiate. Test construction bilamellar with septal flaps. Pore diameter about 0.5 μm.

Plastic moulds demonstrated that retral processes are present but scattered and very small. An umbilical spiral canal system is present. It is formed by the sealing off of the umbilical chamber extensions in the penultimate and earlier chambers by deposition of a partitional plate. The lumen of the umbilical part of the chambers of this species is plate-like with a posterior sutural aperture opening into the interlocular space of the respective chamber. The anterior opening (aperture) in the umbilical chamber part of the final chamber is converted, with the addition of a new chamber, into a foramen connecting successive umbilical parts of chambers. This leads to the formation of an umbilical spiral canal system communicating with the interlocular spaces between earlier chambers but not with the lumen *per se* of these chambers. Only the lumen of the final chamber communicates directly with the spiral canal.

However, communication with the lumen of the earlier chambers can take place through the fossettes in the 'floor' of these chambers.

Elphidium ustulatum Todd, 1957

Pl. 13:7–12

☐ 1957 *Elphidium ustulatum* Todd, p. 230; Pl. 28:16. ☐ 1966 *Elphidium lenticulare* Gudina, p. 55; Pl. 3:7–9; Pl. 9:1. ☐ 1971 *Elphidium ustulatum* Todd; Feyling-Hanssen et al., p. 283; Pl. 13:12–13; Pl. 23:5–7 (and further synonyms therein).

Our material of this species is from Quaternary deposits, Lundergaard, Denmark, kindly placed at our disposal by Karen L. Knudsen Cand. scient.

Description.—Test involute, planispiral and somewhat compressed. Periphery angled to subacute. There are 8–10 chambers in the final whorl. Chambers strongly embracing leading to an almost flush umbilical region. General outline smooth, very slightly if at all lobate in the final part of the final whorl. Sutures extending from a short distance from the periphery into the umbilicus. However, the umbilical third of each suture is covered. Around and in front of the aperture as well as in the interlocular spaces a dense and fine tuberculation is developed. The aperture is interiomarginal, multiple and so are the foramina.

Wall constructed of perforate, laminated optically radiate calcite. Septa and primary wall bilamellar. Septal flaps are present. Pore diameter about 0.8 μm.

Plastic moulds in the SEM showed that with the addition of a new chamber, the umbilical part of the previous chamber becomes sealed-off by deposition of a plate preventing direct communication from the umbilical part into the lumen of the chamber proper. In the final chamber, however, there is no such plate. The umbilical part of the chambers are narrow and tube-like and coalesce in the umbilicus. In addition to this communication each umbilical part communicates with the corresponding part of the previous chamber through the most umbilical aperture. In addition there is a communication leading from the umbilical sealed-off chamber-parts into the deep seated interlocular space. Thus an umbilical spiral canal system is present. However, no vertical umbilical canals or oblique vertical canals are present. The absence of the latter is intimately connected with presence of fossettes and since *E. ustulatum* can be considered as having only one fossette in each suture on each side of the shell this absence of oblique vertical canals is readily understood. Retral processes *per se* are not present, but the primary roof found in each suture in the most umbilical part of each suture could be interpreted as one retral process connected with one ponticulus.

Elphidium albiumbilicatum (Weiss, 1954)

Pl. 14:1–6

☐ 1954 *Nonion pauciloculum* Cushman subsp. *albiumbilicatum* Weiss, p. 157; Pl. 32:1–2. ☐ 1957 *Nonion depressulus* (Walker & Jacob) forma *asterotuberculatus* van Voorthuysen, p. 28; Pl. 23:3. ☐ 1969 *Protelphidium asterotuberculatus* (van Voorthuysen); Gudina, p. 35; Pl. 12:6. ☐ 1971 *Elphidium albiumbilicatum* (Weiss); Feyling-Hanssen et al., p. 268; Pl. 10:15–19; Pl. 19:4–8.

The specimens studied originate from Quaternary deposits, Hirtshals, Denmark.

Description.—Test planispiral, involute and compressed, with somewhat depressed umbilical regions. Periphery rounded, general outline very slightly lobate in the later part of the final whorl. 6–11 chambers in the final whorl, commonly 7 or 8. Sutures curved, near the umbilical areas depressed. Few ponticuli are present. The depressed parts of the sutures, the umbilical regions, the apertural face together with the earliest part of the final whorl are covered by dense tuberculation. At the apertural face and in front of the aperture the tuberculation is arranged in parallel stripes. The aperture is an interiomarginal, equatorial low arch not reaching the umbilici. The foramina are like the aperture.

The wall is perforate, laminated and optically radiate. Test construction bilamellar with septal flaps. Pore diameter about 0.5 μm.

Plastic moulds studied in the SEM showed that the few ponticuli on the surface do not correspond to retral processes which are not developed in this species. In the umbilical area a spiral canal system is developed. Owing to serious preparational difficulties caused by the dense tuberculation cover, only part of a system could be exposed. This showed that the apparently plate-like umbilical parts of the chambers are fused to form a spiral canal interconnected and communicating with the locally secondarily covered interlocular space (depressed suture).

Genus *Elphidiella* Cushman, 1936

Elphidiella arctica (Parker & Jones, 1864)

Pl. 14:7–12; Pl. 15:1–7

☐ 1864 *Polystomella arctica* Parker & Jones; p. 471; Pl. 48:18. ☐ 1930 *Elphidium arcticum* (Parker & Jones); Cushman, p. 27; Pl. 11:1–6. ☐ 1936 *Elphidiella arctica* (Parker & Jones); Cushman, p. 89.

Our material originates from Recent sediments from Iceland and West Greenland as well as from Quaternary deposits in Hirtshals, Denmark.

Description.—Test planispiral involute somewhat compressed with 10–12 chambers in the final whorl. General outline smooth to slightly lobate. The sutures and umbilical regions slightly depressed. The chambers are moderately inflated and gently curved. The periphery is broadly rounded. The test is characterised by being finely but densely tuberculate on all exposed areas including sutures and apertural face. Occasionally non-tuberculate narrow bands are present in the sutures, but this is the exception rather than the rule. In the sutures are found openings in single or double rows sometimes giving the impression of an alternating series. Associated with these openings there are shallow grooves on the shell surface which from a posterior row run in posterior direction and opposite from an anterior row. They are parallel or almost so to the periphery. The aperture is an interiomarginal equatorial partly subdivided low arch and so are the foramina. Supplementary multiple areal apertures and foramina are present.

Wall built of optically radiate calcite. Primary wall and septa bilamellar with septal flaps. Pore diameter about 0.7 μm.

Plastic moulds studied in the SEM showed no retral processes. The entrances to the subsutural canals are arranged in single or double rows of varying regularity. One preparation demonstrated that the umbilical part of the final chamber is developed as a plate-like cavity, rather broad and with several anteriorly directed umbilical apertures as well as a direct communication into the ultimate subsutural canal. In previous instars this part of each chamber is sealed off from the main chamber lumen by a plate while the communication with the umbilical part of the following chamber takes place through the anteriorly directed umbilical foramina (former apertures) owing to a partial overlap between the umbilical part of one chamber with that of the following one.

Sectioned, polished and etched specimens in the SEM showed that the outer lamella crosses the interlocular space primarily. This is different from the situation in representatives of *Elphidium,* where the interlocular space is nothing but a sunken suture (compare Hansen & Reiss 1971). If this were the case with *Elphidiella* the outer lamella would have to descend into the sunken suture to cover the walls of the interlocular space. Furthermore, such a situation with an uninterrupted outer lamella crossing the interlocular space is possible in *Elphidium* only when the section passes right through the middle of a retral process and its corresponding ponticulus. However, *E. arctica* does not have retral processes. Thus the structural situation observed is not compatible with the *Elphidium* model. Horizontal sections furthermore demonstrated that in the early part of the shell no subsutural canals are developed. These do not appear until instar number 9–12. The young *E. arctica* thus strongly resembles a *Nonion*-like form and would point to such a form as being ancestral to the species in question.

Elphidiella sibirica (Goës, 1894)

Pl. 15:8–12; Pl. 16:1–4

☐ 1894 *Polystomella sibirica* Goës, p. 100; Pl. 17:814. ☐ 1930 *Elphidium sibiricum* (Goës); Cushman, p. 29; Pl. 11:7. ☐ 1939 *Elphidiella sibirica* (Goës); Cushman, p. 66; Pl. 19:4.

The material of this species consists of three specimens from Quaternary deposits in Alaska. They were kindly placed at our disposal by Drs. Helen Tappan and A. R. Loeblich, Jr.

Description.—Test very large, planispiral, involute and compressed. About 20 chambers in the final whorl. General outline smooth. Periphery compressed but well rounded. Chambers curved. Apertural face smooth and imperforate. The umbilici are flush with the surface and pierced by canals. On the inner surface of the shell of the chambers shallow impressions are seen at the line of attachment of a chamber to the preceeding one, giving the impression of retral processes. These depressions are distinct but rather shallow. When viewed in the suture between the final and the penultimate chamber the 'ponticuli' are seen to be of a peculiar construction since they resemble ponticuli with linking bridges between thus leading to two 'fossettes' of which the posterior one is considerably broader than the anterior one. Older sutures show in most areas an alternating row of almost circular 'fossettes'. However, other areas show the 'fossettes' to occur in opposed pairs. The posterior row is found at the line of attachment between a chamber and the preceeding one while the anterior row is found exclusively surrounded by wall belonging to the new chamber. Examples with only one row of openings occur as well.

In section the final chamber shows a bilamellar structure with a rather thick median layer. At the junction between the final chamber and the penultimate one the outer lamella is seen to run uninterrupted across the suture and covers the penultimate chamber and earlier ones as a secondary lamella. The inner lining is seen to run inwards into the chamber where it is doubled. The inner lining continues inwards where it covers the septum producing a septal flap. The posterior (with respect to direction of growth) inner lining covers the outer lamella across the suture on the inside and wedges out at the outer lamella of the preceeding septum, thereby delimiting a space which is here called the subsutural canal. This canal is delimited by the doubled inner lining of a chamber and the outer lamella of the preceeding one. In the earlier subsutural canals no secondary lamination has been observed, which indicates that the subsutural canals are distinctly different from the interlocular space in forms like *Ammonia* and *Elphidium* where secondary lamination is found. The 'fossettes' are simple holes piercing the outer and inner lamella over the subsutural canals. The edges of the posterior 'fossettes' are thickened by secondary lamination, which thus, after two or three instars, leads to a partial closure of the originally rather broad openings. Since the deposition of secondary lamination in the posterior openings is often stronger in the one side than in the other they will commonly lie obliquely with respect to the corresponding anterior opening.

The term fossettes has been used with quotation marks since they in no way can be considered homologous to the fossettes of *Elphidium*. In *Elphidium* the fossettes are the route of communication for the plasma of the interlocular space and the shell exterior. Therefore the interlocular space, since it is covered by the outer lamella and carries secondary lamination, must in fact be considered shell surface ('sunken suture', compare Hansen & Reiss 1971). In *E. sibirica* the holes in the final suture connecting the sutural canal with the shell surface are supplementary sutural apertures connecting with the chamber interior, i.e. the subsutural canal delimited by the inner lining and septum of the penultimate chamber.

Aperture multiple interiomarginal with additional areal multiple openings. The foramina are like the aperture.

Wall constructed of laminated, perforate, optically granulate calcite. Primary wall and septa bilamellar. Septal flaps are developed. Pore diameter about 3.0 μm.

Plastic moulds studied in the SEM showed distinct retral processes as well as an umbilical spiral canal system. This system is formed by the sealed-off overlapping umbilical parts of chambers. These parts of chambers are rather flattened, which gives the lumen of the spiral canal an appearance of trochospiralling overlapping plates. With the addition of secondary laminae the umbilical apertures are converted into vertical umbilical canals piercing the massive-looking umbilical area. The subsutural canals in the penultimate and earlier chambers are prevented from communication with the chamber lumen proper of the corresponding chamber by deposition of a plate.

Elphidiella hannai (Cushman & Grant, 1927)

Pl. 16:5–10

☐ 1927 *Elphidium hannai* Cushman & Grant, p. 77; Pl. 8:1. ☐ 1939 *Elphidiella hannai* (Cushman & Grant); Cushman, p. 66; Pl. 19:1.

Our material is from Quaternary deposits in Antwerp, Belgium.

Description.—Test planispirally coiled, lenticular involute, chambers strongly embracing. Periphery rounded. About 10 chambers in the final whorl. General outline smooth, subcircular. Sutures slightly curved, flush with the shell surface. The apertural face is densely tuberculate and so is the area in front of the aperture veiling it.

One or two rows of openings are found in the sutures. If two rows are present they are generally arranged in an alternating series. However, an opposed arrangement of the openings has been found as well.

Fractured or sectioned specimens showed the aperture to be multiple, interiomarginal consisting of relatively few openings like the foramina.

Wall made of laminated, optically granulate calcite. Wall and septa bilamellar. Septal flaps are present. Pore diameter about 0.3 μm.

Plastic moulds in the SEM showed the presence of questionable retral processes that are not reflected in the surface morphology of the shell; i.e. there are no ponticuli. The moulds also showed presence of an umbilical spiral canal system formed in the penultimate and earlier chambers by the sealed-off, narrow umbilical parts of chambers connected with the subsutural canal of the respective chamber. Vertical umbilical canals are present but were difficult to obtain in good preparations. Polished and etched sections showed the subsutural canals to be formed by the doubled inner lining. Only one example of secondary lamination inside the subsutural canal was observed. The general lack of secondary lamination in the subsutural canals is most probably connected with the fact that the sutural openings are very narrow.

Elphidiella prima (ten Dam, 1944)

Pl. 16:11–12; Pl. 17:1–3

☐ 1944 *Elphidium primum* ten Dam, p. 109; Pl. 3:15. ☐ 1948 *Elphidiella prima* (ten Dam); Brotzen, p. 70; Pl. 8:2.

Our material consists of 2 specimens from the Palaeocene clay at Ystad, kindly donated by Lis Gustafsen, Cand. scient. as well as 6 specimens from Danian deposits from the Copenhagen region kindly donated by Inger Bang, Cand. mag.

In addition, 6 'paratypes' determined by ten Dam from the type locality in Holland was kindly placed at our disposal by Dr J. H. van Voorthuysen. These specimens have not been used since they were wrongly identified (they appear to belong to *Nonion graniferum* (Terquem, 1882)).

Description.—Shell involute, planispiral with 11 or more chambers in the final whorl. Sutures slightly curved flush with the shell surface or very slightly depressed. General outline smooth. Periphery rounded to subangular. Shell very moderately compressed. The openings connecting the subsutural canals with the exterior form irregular single or double rows in the sutures. Aperture multiple interiomarginal.

The wall is calcitic perforate, laminated and optically granulate. The poor state of preservation precluded observations of the lamellarity (except for secondary lamellae). Pore diameter about 0.5 μm.

Plastic moulds studied in the SEM showed that no retral processes are present. However, a distinct umbilical spiral canal system is developed. It is constructed by the sealed-off umbilical parts of chambers connected through umbilical foramina and each part is connected to the subsutural canal of the respective chamber. This, however, is true only of the penultimate and earlier chambers since the final one is not sealed-off. Vertical umbilical canals are present and so are oblique vertical canals.

Discussion.—Brotzen's figure (1948) illustrating a vertical section correctly shows the subsutural canal as well as the communication canals to the shell surface. However, the "foramina interiora" indicated on that figure do not represent true primary structures of the shell. An analogous structure was seen in many subfossil and Quaternary specimens particularly connected with the presence of pyrite in the shells. This is due to the general difference in thickness of the wall of the subsutural canal formed primarily between the preceeding septum (normal wall thickness) and the doubled inner lining, which is thinner. In other words, the anterior wall is more easily destroyed by recrystallisation and other diagenetic processes than is the posterior wall of the subsutural canal.

Brotzen (1948) also showed forking communication canals from the subsutural canals to the shell exterior in the sutures. This is not found on the actual specimens but may well be due to neighbouring canals superimposed optically in thin sections as studied under the light microscope.

Elphidiella heteropora (Egger, 1857)

Pl. 17:4–10

☐ 1857 *Nonionina heteropora* Egger, p. 300; Pl. 14:19–21. ☐ 1964 *Cribrononion heteropora* (Egger); Loeblich & Tappan, p. C 637:509, 1. ☐ 1972 *Cribrononion heteroporum;* Kristoffersen, p. 31; Pl. 2:6; Pl. 3:1–6; Pl. 4:4–6. (☐ For additional synonyms, see Kristoffersen 1972.)

The material studied originates from Miocene deposits at Marienhof near Ortenburg, Lower Bavaria, Germany which is the type locality for *E. heteropora.* The material was kindly placed at our disposal by Dr. H. Hagn.

Description.—Test planispiral, involute, somewhat compressed. Periphery broadly rounded. General outline smooth. Umbilical regions only slightly depressed. 6–7 chambers in the final whorl. Sutures gently curved, hardly depressed. Scattered sutural openings leading into the subsutural canals are present. The apertural face together with the earliest part of the final whorl is covered by dense tuberculation which extends into the umbilical regions. The aperture is interiomarginal, subdivided but not multiple. It is obscured by tuberculation on the exterior. The tuberculation forms what may appear as an additional apertural chamberlet.

The wall is laminated, perforate and optically granulate. Test construction bilamellar with septal flaps. The pore diameter is about 1.5 μm.

Plastic moulds studied in the SEM showed that no retral processes exist. Subsutural canals are found to be interconnected in the umbilical region through what is supposed to be an umbilical spiral canal system. The additional anastomosing canals in the umbilical regions are most likely formed secondarily between the tubercles.

Polished and etched sections in the SEM showed in spite of the poor state of preservation of the ultrastructures that the outer lamella of a chamber crosses the subsutural canal.

Discussion.—This species is the type species of the genus *Cribrononion* Thalmann, 1947.

The construction principle of the subsutural canals, in which the outer lamella crosses the sutures indicates that *E. heteropora* must belong to the genus *Elphidiella.*

Elphidiella subnodosa (Münster, 1838)

Pl. 17:11–12; Pl. 18:1–3

☐ 1838 *Robulina subnodosa* Münster, p. 391; Pl. 3:61. ☐ 1855 *Polystomella subnodosa* (Münster); Reuss, p. 240; Pl. 4:51. ☐ 1939 *Elphidium subnodosum* (Münster); Cushman, p. 40; Pl. 11:2.

The material of this species originates from Oligocene deposits at Sophienlund, Denmark.

Description.—Shell rather large, lenticular, planispiral, involute with about 15 chambers in the final whorl. Sutures moderately curved and depressed but not strongly so. Pronounced tuberculation occurs in front of the aperture and in the umbilical region extending into the sutures. General outline smooth to very slightly lobate. Periphery subangular in the earlier part with a blunt keel. In the sutures where the tuberculation is dense a row of openings is present. With the addition of secondary lamination the tuberculation between the openings gradually takes on the appearance of ponticuli. They are, however, not homologous with the ponticuli of e.g. *Elphidium crispum.* Aperture multiple, interiomarginal, often veiled by tuberculation.

Wall calcitic, perforate, lamellar and optically radiate. Primary wall and septa bilamellar with septal flaps. Pore diameter about 0.3 μm.

Plastic moulds studied in the SEM showed that no retral processes are developed. On the other hand a well-developed umbilical spiral canal system is found. The shape of the lumen of the umbilical parts of chambers is plate-like and drawn out in a posterior direction. These parts are sealed-off in the penultimate and earlier chambers, thereby forming the umbilical spiral canal system the single parts of which are interconnected by chamber overlap and the anterior apertures nearest the umbilicus. The spiral canal is also connected to the subsutural canals which, in this species, appear to be formed in the same way as in the species of the genus *Elphidiella* described herein. In sectioned and etched specimens the lack of retral processes in relation to the apparently continuous outer lamella crossing the subsutural canal, strongly indicate that *E. subnodosum* should be referred to the genus *Elphidiella* and not to *Elphidium*.

However, the relatively poor state of preservation (heavy pyritisation) makes definite conclusions impossible. Accordingly the species is here only tentatively referred to *Elphidiella*.

Discussion.—The lack of retral processes along with the superficial resemblance of the secondarily formed sutural bridging by ornamental structures led Hofker (1971) to place this species in his genus *Elphidiononion*.

Genus *Notorotalia,* Finlay, 1939

Notorotalia zelandica Finlay, 1939

Pl. 18:4–12; Pl. 19:1–2

☐ 1939 *Notorotalia zelandica* Finlay, p. 518. ☐ 1964 *Polystomellina zelandica* (Finlay); Loeblich & Tappan, p. C 642:513, 7.

Our material of this species originates from Recent sediments from off New Zealand. The material was kindly placed at our disposal by Dr. J. Murray.

Description.—Shell trochospirally coiled. Almost lenticular with involute umbilical side and evolute spiral side exposing all earlier chambers. About 11 chambers in the final whorl. Periphery sharply angled in the latest part, somewhat rounded in the earlier part. General outline smooth to slightly lobate. Sutures slightly curved and raised. In each suture is a double row of small openings each with a slightly raised rim. Shell surface ornamented by ridges running almost parallel to the periphery. Apertural face plane and ornamented by almost radiating ridges. Between the ridges on the chamber walls and on the apertural face is a dense and fine tuberculation. Aperture and foramina are multiple in a row near base of apertural face, each opening with a raised collar-like rim.

Wall perforate, laminated and built of optically radiate calcite. Primary wall bilamellar with septal flaps. Pore diameter about 0.3 μm.

Plastic moulds studied in the SEM showed that in the central umbilical region a distinct spiral canal system is developed. It is formed by sealing off the most umbilical part of the chamber lumina as in other forms described earlier in this paper. Likewise, a posterior umbilical aperture exists, communicating from the spiral canal into the subsutural canals of the umbilical side.

These canals being constructed like those in the sutures on the spiral side as well as in the spiral suture of that side. The moulds showed distinct retral processes that, however, do not show up in the external morphology of the test (i.e. as hollow ponticuli). Polished and etched vertical sections showed the subsutural canals to be constructed in a profoundly different manner from that of *Elphidium*. The sections demonstrate that with the addition of a new chamber, the inner lining of the bilamellar chamber wall continues to cover the preceeding septum, forming a septal flap. The outer lamella continues in a posterior direction and bridges the suture, after which it forms secondary lamination on the exposed earlier part of the shell.

Besides these layers a third layer is formed around the subsutural canal where the outer and inner lamellae separate. The layer covering the walls of the subsutural canal found between the inner and outer lamella could be considered outer lamella. Such an interpretation would apparently be supported by the fact that the inner surface of the early subsutural canal is often covered by some secondary lamellae. There are, however, some indications that it is not the outer, but the inner lamella which is doubling around the subsutural canal. The first argument lies in the fact that a primary doubled outer lamella is unknown in any foraminiferal group studied so far. On the contrary a primary doubled inner lamella or lining is known from the family Asterigerinidae where it forms the wall dividing the main chamber from the chamberlet (Hansen & Reiss 1972). Moreover, it is the inner lining that forms the subdivision of the main chamber in *Heterostegina* (see e.g. Reiss 1963). If the subsutural canal is interpreted as being formed by the doubled inner lining we face the problem of having to explain how an inner lining can be covered by secondary lamination. However, such a phenomenon is known from *Ammonia*, where the inner lining of the umbilical lip with the deposition of the umbilical cover plate becomes separated from the chamber lumen proper and is overlain by secondary lamination. Thus when a part of the chamber with the inner lining in contact with intralocular cytoplasma is in some way prevented from its direct contact it becomes overlain by secondary lamination, and therefore may be regarded as functioning as outer lamella although it originally formed as an inner lining.

The present authors therefore favour the interpretation that the subsutural canal is formed by the doubled inner lining and not by the doubled outer lamella.

Whatever interpretation is favoured the construction principle is basically different from that of the interlocular space of *Elphidium* and associated forms. In the latter forms the interlocular space is in fact a sunken suture (Hansen & Reiss 1971). With the formation of a new chamber a double (or in some forms a single) row of openings ('sutural pores' of authors) is formed. These openings in *Notorotalia* are not homologous with the fossettes of *Elphidium*.

In the latest suture, where the subsutural canal must be chamber lumen according to the above interpretation, the sutural openings (single or double row) are apertures. In the earlier sutures where the subsutural canals become sealed-off from the main chamber lumen and thereby are excluded from direct communication, the 'sutural pores' may be considered relict apertures now functioning like the fossettes of *Elphidium*. Besides the difference in construction principle it should be emphasized that the fossettes of the final suture in *Elphidium* are not apertures but that the apertures of the final chamber communicating with the interlocular space are posterior umbilical leading into the most umbilical part of the interlocular space.

Discussion.—Hofker (1969) pointed out that *Notorotalia* probably evolved from *Elphidiella*-like forms rather than from *Elphidium*. This suggestion was based on the presence in *Notorotalia* of the double row of sutural openings. The close relationship between *Elphidiella* and *Notorotalia* is strongly indicated by the identity of construction principle of the subsutural canals.

Genus *Nonion* Montfort, 1808

Nonion depressulum (Walker & Jacob, 1798)

Pl. 19:3–6

☐ 1798 *Nautilus depressulus* Walker & Jacob, p. 641:33.
☐ 1965 *Nonion depressulus* (Walker & Jacob); Murray, p. 148; Pl. 26:7–8.

The material studied originates from Eemian deposits at Meetkerke, Belgium and from Recent sediments from the inner Danish waters.

Description.—Test planispiral, nearly involute and strongly compressed. Periphery subacute to rounded. General outline slightly lobate. 7–11 chambers in the final whorl, most commonly 9. Chambers slightly to moderately inflated. Sutures curved and depressed especially in the later part of the final whorl. The depressed part of the sutures most pronounced towards the umbilici and the umbilici carry distinct tuberculation. Apertural face perforate, ornamented with tubercles along the aperture. The aperture as well as the foramina is an interiomarginal equatorial low arch. The aperture is often obscured by tuberculation.

The wall is calcitic, perforate, laminated and optically granulate. Test construction is bilamellar without a complete septal flap. The flap extends half way down the septa midway between the periphery and the foramen. Pore diameter about 0.4 μm.

Plastic moulds studied in the SEM showed no retral processes as well as no umbilical spiral canal system. There do not appear to be any additional umbilical apertures.

Discussion.—Considerable confusion as to the proper meaning of the name *Nonion depressulum* has existed. Murray (1965) based on topotype material emended the diagnosis. Therefore the species *N. depressulum* is now well defined. It is a distinct and rather common species in shallower waters of North-west Europe.

The species has been referred to by different authors as *Nonion umbilicatulum* (see e.g. van Voorthuysen 1957; Haake 1962; Feyling-Hanssen et al. 1971).

Nonion germanicum (Ehrenberg, 1840)

Pl. 19:7–12

☐ 1840 *Nonionina germanica* Ehrenberg, p. 23; Pl. 2:1.
☐ 1965 *Protelphidium anglicum* Murray, p. 149; Pl. 25.

The specimens studied originate from Eemian deposits at Meetkerke, Belgium and from Recent sediments from the inner Danish waters.

Description.—Test planispiral, involute somewhat compressed, periphery rounded. General outline moderately lobate. 6–12 chambers in the final whorl, most commonly 8 or 9. Sutures curved, depressed near the umbilical regions, especially in the latest part of the final whorl. Tuberculation occurs in the depressed umbilical regions and in the depressed part of the sutures. The apertural face is slightly inflated, perforate and ornamented with tubercles along the aperture. The aperture is an interiomarginal equatorial low arch, often obscured by tuberculation. The foramina are like the aperture.

The wall is calcitic, perforate, laminated and optically radiate. Test construction bilamellar with a septal flap. Pore diameter about 0.5 μm.

Plastic moulds in the SEM showed no retral processes. Likewise no umbilical spiral canal system could be traced. The outer morphology of the umbilical region suggests that umbilical apertures are present but no such structures were found.

Nonion graniferum (Terquem, 1882)

Pl. 20:1–4

☐ 1882 *Nonionina granifera* Terquem, p. 42:8a–b.
☐ 1970b *Nonion graniferum* (Terquem); Hansen, p. 97; Pl. 11:1–2; Pl. 26:1–2.

Our material of this species originates from Danian deposits on Nugssuaq, West Greenland and from Palaeocene deposits in Holland. The Dutch material was kindly placed at our disposal by Dr. J. H. van Voorthuysen.

Description.—Test planispiral, involute, and somewhat compressed with about 7 chambers in the final whorl. Periphery broadly rounded. General outline smooth to slightly lobate, particularly in final part of the final whorl. Umbilici covered by a dense tuberculation which also covers the apertural area as well as the most umbilical part of the sutures. The sutures are gently curved and slightly depressed, but more depressed between the last formed chambers. Aperture a low, interiomarginal, equatorial arch. The foramina are like the aperture. In horizontally orientated sections the tuberculation present at the aperture is seen to be missing at the foramina.

Wall calcitic, optically granulate. Primary wall and septa bilamellar. A septal flap is present. Pore diameter about 0.5 μm.

Plastic moulds studied in the SEM showed that there are no retral processes and that no distinct umbilical spiral canal system is developed. On the other hand it appears that the umbilical part of the chambers has additional umbilical apertures opening into the tuberculate area. The overlap of a chamber onto the tuberculation of the previous coil, leads to a rather poorly defined umbilical lumen of the chambers.

Discussion.—This species was discussed earlier by Hansen (1970b) who stated erroneously, on the basis of light microscopy, that the septa are monolamellar. The present study by SEM showed the septa to be bilamellar and a septal flap to be present.

Nonion hofkeri (Haynes, 1956)

Pl. 20:5–9

☐ 1956 *Protelphidium hofkeri* Haynes, p. 86; Pl. 16:9a–c.

The specimens studied are topotypes from the Thanetian Reculver silts, England.

Description.—Test planispiral involute. Periphery broadly rounded. Chambers not strongly embracing, leaving a rather large umbilical area, which is covered by a dense and coarse tuberculation. There are 6–7 chambers in the final whorl. The sutures are distinct, being somewhat depressed on the lateral test surface and becoming more strongly depressed towards the umbilici. Sutures slightly curved to almost radial. The apertural face is slightly inflated and imperforate. The tuberculation is continuous from the umbilicus onto the lower part of the apertural face and the earlier part of the previous coil right in front of the aperture. This tuberculation veils the aperture which can be studied only from the inside of the shell (i.e. in fractured or opened specimens). The aperture is a low interiomarginal equatorial slit confined to the central part. The foramina are like the aperture except for the fact that tuberculation evidently is removed (resorption?) with the addition of a new chamber, thereby rendering the foramina clearly visible on opened or fractured specimens.

The wall is constructed of optically radiate calcite. The septa appear to be bilamellar but the rather unsatisfactory state of preservation of the fine structure of the wall precludes definitive conclusions. Pore diameter about 0.8 μm.

Plastic moulds in the SEM showed no signs of an umbilical spiral canal system. An exterior replica of the umbilical area in the SEM demonstrated the exterior passways between tubercles involving also the space in the depressed sutures. There are no umbilical apertures and no retral processes were found.

Discussion.—Haynes described a variation in the development of foramina in this species. He pointed out that more than one interiomarginal foramen may be present. He found no correlation between the development of foramina with ontogeny. The latter development may, however, be explained as secondary effect caused by imperfect removal of the tuberculation veiling the aperture, remnants of which may be found at the foramina.

Haynes (1956) designated this species type species of the genus *Protelphidium*.

Nonion orbiculare (Brady, 1881)

Pl. 20:10–13; Pl. 21:1

☐ 1881 *Nonionina orbicularis* Brady, p. 415; Pl. 21:5. ☐ 1930 *Nonion orbiculare* (Brady); Cushman, p. 12; Pl. 5:1–3. ☐ 1953 *Elphidium orbiculare* (Brady); Loeblich & Tappan, p. 102; Pl. 19:1–4. ☐ 1964 *Protelphidium orbiculare* (Brady); Feyling-Hanssen, p. 349; Pl. 21:3.

The specimens studied originate from Quaternary deposits from Hirtshals, Denmark.

Description.—Test planispiral, involute, slightly compressed. Periphery broadly rounded. General outline smooth to very slightly lobate. 7–9 chambers in the final whorl, commonly 8. Sutures gently curved, slightly to moderately depressed except for the peripheral part where they are almost flush with the surface. Umbilical regions slightly if at all depressed. The sutures and the umbilical regions covered by tuberculation and so is the apertural face and the earlier part of the final whorl. Apertural face perforate. The aperture is multiple interiomarginal. The foramina resemble the aperture.

Test wall perforate, laminated and optically radiate. Test construction bilamellar with a septal flap. Pore diameter about 0.3 μm.

Plastic moulds viewed in the SEM showed presence of very small but distinct retral processes that are, however, not reflected as ponticuli in the external morphology. No umbilical spiral canal system could be found in the numerous preparations made.

Nonion boueanum (d'Orbigny, 1846)

Pl. 21:2–4

☐ 1846 *Nonionina boueana* d'Orbigny, p. 108; Pl. 5:11–12. ☐ 1930 *Nonion asterizans* (Fichtel & Moll) Cushman, p. 6; Pl. 2:5–7. ☐ 1939 *Nonion boueanum* (d'Orbigny); Cushman, p. 12; Pl. 3:7–8. ☐ 1964 *Florilus asterizans* (Fichtel & Moll); Loeblich & Tappan, p. C 746:612,4.

The specimens studied are from Pliocene deposits at Moulin de Nidolères, France.

Description.—Test planispiral, involute to very slightly evolute. Periphery subacute in the earlier part later becoming angular but somewhat rounded. General outline smooth. Umbilical regions slightly depressed. About 12 chambers in the final whorl. The chambers are of uniform shape, high and rather narrow. Sutures curved and slightly depressed. Incised near umbilici. The umbilical regions and the incised parts of the sutures are ornamented with tubercles. The apertural face is subtriangular, perforate, covered by tubercles along the aperture. The aperture is a narrow interiomarginal equatorial opening.

The wall is perforate, laminated and optically granulate. Test construction bilamellar possibly without a septal flap. The construction pattern is rather difficult to observe as the wall appears to be built of block-like units with platy fine structure to some extent blurring the lamellar structures. Pore diameter about 0.9 μm.

Plastic moulds in the SEM showed neither retral processes nor umbilical spiral canal system.

Discussion.—This species is generally referred to as being the type species of the genus *Florilus* Montfort, 1808, under the name of *N. asterizans.*

Nonion labradoricum (Dawson, 1860)

Pl. 21:5–8

□ 1860 *Nonionina labradorica* Dawson, p. 191:4. □ 1927 *Nonion labradorica* (Dawson); Cushman, p. 148; Pl. 2:7–8. □ 1958 *Nonionellina labradorica* (Dawson); Voloshinova, p. 142. □ 1967 *Florilus labradoricus* (Dawson); Todd & Low, p. 35; Pl. 5:9.

The specimens studied are from Quaternary deposits, Hirtshals, Denmark and Recent sediments from the east coast of Greenland.

Description.—Test planispiral, involute, in the initial part trochoid. Periphery subacute. General outline smooth to slightly lobate. 7–10 chambers in the final whorl, most commonly 8. The chambers increase rapidly in size during ontogeny. The high final chamber covers the rather deeply depressed umbilici on both sides. Sutures gently curved, slightly depressed except near the umbilici, where they become somewhat incised. The apertural face is smooth, perforate, very broad and subtriangular. The aperture and foramina are basal slits. The wall is perforate, laminated and optically granulate. Test construction bilamellar with no septal flap. Pore diameter about 0.4 μm.

Discussion.—The bilamellar structure of wall and septa was previously published by Hansen & Reiss (1972, Pl. 2:1–2) and the reader is referred to that publication for illustration of the wall structure.

N. labradorica is the type species of the genus *Nonionellina* erected by Voloshinova 1958 and is distinguished by the fact that the initial shell portion is trochoid while the later part is planispiral.

Genus *Nonionella* Cushman, 1926

Nonionella atlantica Cushman, 1947

Pl. 21:9–12

□ 1947 *Nonionella atlantica* Cushman, p. 90; Pl. 20:4–5.

Our material originates from Recent sediments off Cabo São Tomé, Brazil.

Description.—Test trochospirally coiled and somewhat compressed. General outline smooth. Periphery rounded to subacute. Spiral side evolute, umbilical side involute with final chamber somewhat overhanging the umbilicus. About 12 chambers in the final whorl. The sutures are curved, depressed on both sides of the test but not in the periphery. Incised near the depressed umbilicus at the umbilical side. The umbilicus and incised part of the sutures ornamented with tubercles. The apertural face is perforate, covered with tubercles along the aperture. The aperture is an interiomarginal, equatorial low arch extending into the umbilicus under the overhanging umbilical chamber parts.

Wall perforate, laminated and optically granulate. Test construction bilamellar with a septal flap. Pore diameter about 0.2 μm.

Discussion.—Since no material of the type species of the genus *Nonionella*, namely *N. miocenica* Cushman, 1926, was available for study, *N. atlantica* was chosen instead to demonstrate the characters of the genus.

Genus *Pullenia* Parker & Jones, 1862

Pullenia bulloides (d'Orbigny, 1846)

Pl. 22:1–4

□ 1846 *Nonionina bulloides* d'Orbigny, p. 107; Pl. 5:9–10. □ 1943 *Pullenia bulloides* (d'Orbigny); Cushman & Todd, p. 13; Pl. 2:15–18.

Our material originates from Miocene deposits at Soos, Baden.

Description.—Test planispiral, involute, nearly spherical. Periphery broadly rounded, general outline smooth. 4–6 chambers in the final whorl, strongly embracing. Sutures radial, flush with the surface. The aperture is an interiomarginal low slit extending almost to the umbilici. It has a narrow overhanging lip. The foramina are identical to the aperture.

The wall is perforate, laminated and optically granulate. Test construction bilamellar with a septal flap. The median layer separating the outer lamella and the inner lining has the irregular beaded appearance known from other optically granulate bilamellar species. Pore diameter about 0.5 μm.

Discussion.—Pullenia bulloides is the type species of the genus Pullenia Parker & Jones, 1862.

Genus *Astrononion* Cushman & Edwards, 1937

Astrononion gallowayi Loeblich & Tappan, 1953

Pl. 22:5–9

☐ 1953 *Astrononion gallowayi* Loeblich & Tappan, p. 90; Pl. 17:4–7.

The material studied originates from Quaternary deposits at Hirtshals, Denmark.

Description.—The test is planispiral, involute, compressed with rounded periphery; general outline lobate but not strongly so. The umbilical regions are somewhat depressed. Test with about 8–10 chambers in the final whorl and strongly embracing chambers. The imperforate prolongations of the chamber wall reach the centre of the umbilicus. The main aperture is equatorial, interiomarginal extending almost to the centre of the umbilicus. The umbilical imperforate part of the chamber is drawn out and swung in a posterior direction, where it is attached to its own chamber wall and leaving a posterior labial sutural aperture. With the addition of a new chamber, the umbilical imperforate lips have a large overlap covering part of the umbilical lip and anterior aperture of the preceeding chamber. At the same time a plate is deposited sealing off the space below the imperforate umbilical lip of the previous chamber from the main lumen of that chamber. The resultant structure is a series of interconnected sealed-off umbilical parts of the chambers. They communicate with the lumen of the final chamber through the umbilical foramina and with the test surface through the posterior labial sutural apertures. Thus an umbilical spiral canal system is formed.

In spite of the incised sutures in the umbilical region representing a partly developed interlocular space, no septal flap exists in this optically granulate form. Primary wall and septa bilamellar. Pore diameter about 1.5 μm.

Discussion.—Since material of the type species of the genus *Astrononion* Cushman & Edwards, 1937, namely *A. stelligera* (d'Orbigny, 1839), was not available to the authors, specimens of *A. gallowayi* were used instead. From the illustrated specimens of other species of this genus it would appear that the basic structures here described are present in all species normally referred to *Astrononion.*

Genus *Melonis* Montfort, 1808

Melonis pompilioides (Fichtel & Moll, 1798)

Pl. 22:10–13

☐ 1798 *Nautilus pompilioides* Fichtel & Moll, p. 31; Pl. 2:a–c. ☐ 1808 *Melonis etruscus* Montfort, p. 66. ☐ 1959 *Nonion pompilioides* (Fichtel & Moll); Nørvang, p. 145:1–6. ☐ 1964 *Melonis pompilioides* (Fichtel & Moll); Loeblich & Tappan, p. C 761:627,1.

Our material originates from samples off Iceland as well as from the Mediterranean Sea off Banyuls.

Description.—Test planispiral, involute deeply umbilicate. Periphery broadly rounded and general outline smooth. 10–14 chambers in the final whorl. The sutures are very gently curved, flush and have the appearance of imperforate bands. The aperture is an interiomarginal, equatorial slit extending from one umbilicus to the other. The aperture is bordered by a narrow lip. The umbilical apertural parts of earlier chambers remain open. The chamber wall is perforate with coarse pores while the septa as well as the apertural face are imperforate.

The wall is laminated, perforate and optically granulate. Test construction bilamellar with septal flap. The wall structure is reminiscent of other optically granulate species where the median layer has a beaded appearance with irregularly distributed larger crystals. Pore diameter about 3.5 μm.

Discussion.—Melonis pompilioides, the type species of the genus *Melonis* Montfort, 1808, has been placed by earlier authors in the genus *Nonion,* but later Loeblich & Tappan (1964) recognized the genus *Melonis* and placed it in the family Anomalinidae.

Discussion and conclusions

In the classification by Loeblich & Tappan (1964) and its later revision (1974), optical orientation of the wall elements in calcitic perforate forms is placed at a very high hierarchical position in the taxonomic system. It is evident, however, that the forms described earlier in this work render this character quite valueless. According to Loeblich & Tappan's 1964 classification, forms like e.g. *Elphidium striatopunctatum, E. gerthi* and *E. incertum* should be placed within the Cassidulinacea, the genera of which superfamily they otherwise have nothing in common with.

Already in 1966 Buzas showed that *E. incertum* is optically granulate by contrast to other elphidiids and thereby threw serious doubts upon the validity of the radiate/granulate character at a suprageneric level. Towe & Cifelli (1967) stressed that only a slight tilt in the orientation of the supposed epitaxial nucleation matrices could lead potentially to a change in orientation of the calcitic wall elements.

Later, Hansen (1972) demonstrated two otherwise indistinguishable representatives of the genus *Turrilina*

Table 1. List of species of the genera *Elphidium* and *Elphidiella* with optical wall structure indicated.

	Radiate	Granulate
Elphidium macellum	+	
E. crispum	+	
E. craticulatum	+	
E. advenum		+
E. margaritaceum	+	
E. sagrum		+
E. striatopunctatum		+
E. voorthuyseni		+
E. williamsoni	+	
E. gerthi		+
E. excavatum	+	
E. groenlandicum	+	
E. translucens	+	
E. vadescens	+	
E. guntheri	+	
E. kugleri	+	
E. poeyanum	+	
E. bartletti	+	
E. hallandense	+	
E. oregonense	+	
E. tuberculatum	+	
E. incertum		+
E. asklundi		+
E. magellanicum	+	
E. ustulatum	+	
E. albiumbilicatum	+	
Elphidiella arctica	+	
E. sibirica		+
E. hannai		+
E. prima		+
E. heteropora		+
E. subnodosum	+	

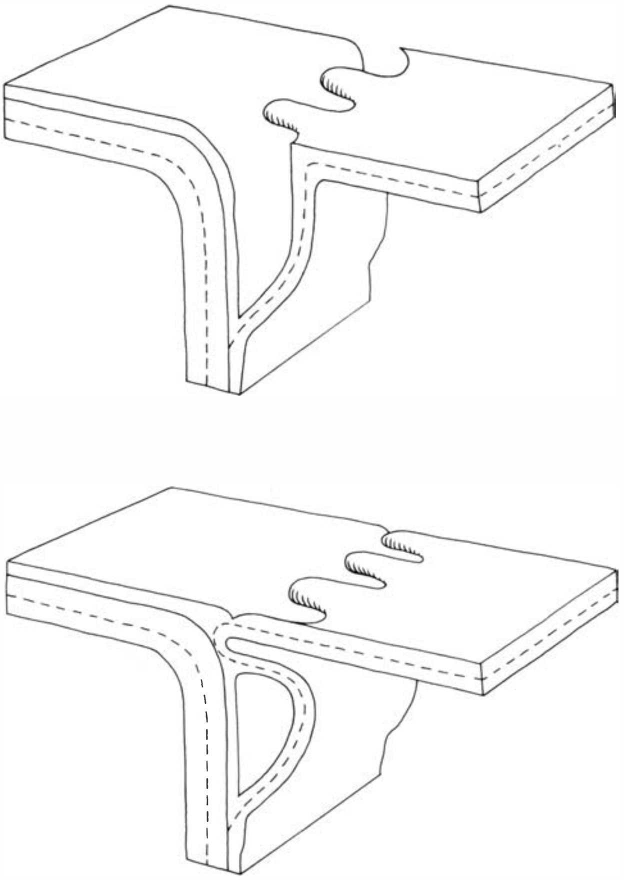


Fig. 5. Formation of an interloclar space in *Elphidium crispum* and similar forms with a deeply sunken suture, covered by the outer lamella of the new chamber (and the secondary lamellae of later formed chambers).

to have different optical wall structure. We believe that the present work reinforces the argument to such a degree, that the optical wall structure as a hierarchical character should be discredited above species level for the time being (compare Table 1).

The recent works by Bellemo (1974a, b, c, d) would indicate that more than two modes of orientation exist. However, too few forms have been studied in this respect on which to base a judgement of the utility of this discovery for systematics. Furthermore, Bellemo (1974a–d) used etching techniques and made the assumption that etch patterns and shapes of crystallites may be correlated with optical orientation. This assumption may be true but it needs confirmation by independant methods of study.

Thus one of the grounds for separating the elphidiids far from the nonionids does not appear to be well found and the two groups may again by regarded as closely related.

With respect to the interpreted principle of chamber formation in the groups concerned two different types were found. The first model is rather simple and can be arrived at from the basic bilamellar model (see Fig. 1) or modified with the addition of a septal flap (Fig. 2). In some forms (like e.g. *Elphidium crispum*) the sutures become deeply sunken and an interlocular space is formed which is covered on the side walls and bottom with the outer lamella of the respective chamber and by secondary lamellae of later formed chambers (Fig. 5).

This mode of formation of an interlocular space applies to all the nonionids here studied and to all forms allied to *Elphidium* (*sensu strictu*) (but not to *Elphidiella* and *Notorotalia*).

When the interlocular space is deep a septal flap is present, while it may only be partially developed if the interlocular space is shallow or present only for a shorter part of the suture (as in *Nonion germanicum*). However, this principle does not hold true since a septal flap is present in both *Pullenia bulloides* and in *Melonis pompilioides,* in neither of which is an interlocular space developed. It is true that when a deep interlocular space is present a septal flap is always present, while the opposite case is not true. Both the genera *Pullenia* and *Melonis* have rather long and well-documented geological histories (from Upper Cretaceous and Lower Tertiary respectively) but none of the earlier representatives show the presence of a deep interlocular space and the septal flap of the two forms in question can therefore not be explained as a relict structure.

It would thus seem that the character of the septal flap

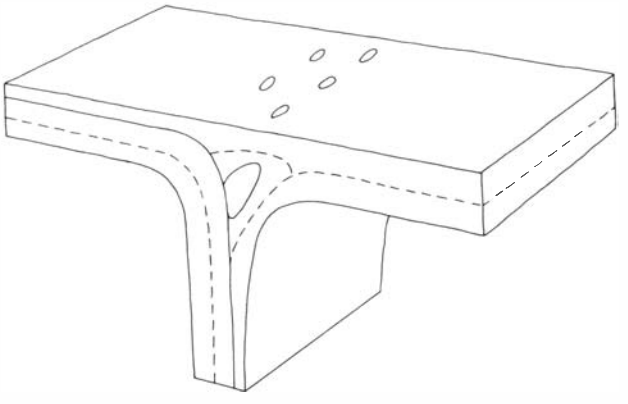


Fig. 6. Chamber formation and subsutural canal in *Elphidiella* and *Notorotalia*.

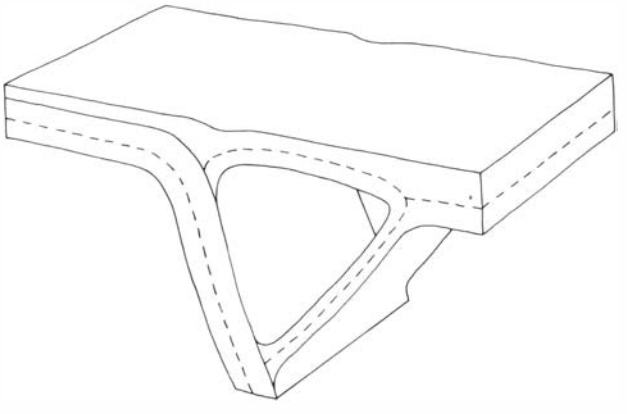


Fig. 7. Delimitation in *Amphistegina* of chamberlets by means of a wall consisting of the doubled inner calcareous layer of the shell.

is one of degree rather than presence or absence. This would render the definition of the superfamily Rotaliidae *sensu* Loeblich & Tappan (1964) inapplicable.

The forms with an interlocular space seem to compensate for the resultant mechanical weakening of the test by development of ponticuli. These often, but not always, reflect the presence of posterior marginal prolongation of the chamber lumen, i.e. retral processes. *Pseudorotalia schroeteriana,* which does not possess ponticuli, is considerably more fragile than forms with these structures. The effect is seen in washed samples, in which *Pseudorotalia* invariably lack the final chamber(s). An alternative means of solving the problem of strengthening a test with a deep interlocular space is exemplified by *Asterorotalia*; in this case strength is provided by its drawn-out umbilical part of the chambers, and therefore in washed samples these tests occur with the final chamber intact.

In the species studied all degrees of development of retral processes exist. Accordingly this is a poor character for distinguishing the *Elphidium* group from neighbouring groups.

The second principle of chamber formation that exists in the forms studied differs basically from the first one described above. It can only be arrived at with difficulty from the traditional bilamellar model and the canals below the sutures (subsutural canals) are not homologous with the interlocular space (sunken suture) developed in *Elphidium* and in some nonionids.

The chamber is primarily two-layered as in bilamellars described by Reiss, Hansen & Reiss in a series of papers (see Bibliography). The primary chamber wall consists of an outer and inner secreted calcareous layer separated by an organic layer of varying appearance and thickness. At the junction with a previous chamber the outer layer crosses the suture and forms a secondary lamel on all exposed parts of the older shell.

By contrast the inner layer continues inwards to cover the previous septum as a septal flap. Where it separated from the outer layer in the suture a doubling of the inner layer occurs so that a subsutural canal is formed. The wall of the canal in a peripheral direction (the 'roof') is composed of inner layer covered by outer lamella. In the anterior direction the wall consists of the doubled inner layer and its posterior wall is formed by the surface of the previous septum (Fig. 6). This mode of forming chambers applies both to *Elphidiella* and to *Notorotalia*.

Foraminiferida possessing a primary double inner layer delimiting a well-defined chamber-part were previously described by Hansen & Reiss (1972a). *Asterigerina, Amphistegina* and related forms delimit their umbilical chamber-parts (chamberlets) by means of a wall consisting of the doubled inner lining (inner calcareous layer) as shown in Fig. 7.

Thus the canals below the sutures in *Elphidiella* are in part analogous in their formation principle to that of the chamberlets of *Asterigerinidae.* They are basically different from the interlocular spaces discussed earlier and we prefer the term 'subsutural canal' for these structures in order not to confuse them with interlocular spaces.

The umbilical spiral canal system originally described by Carpenter et al. (1862) was found in all elphidiids (including also *Elphidiella* and *Notorotalia*) and also in *Astrononion.* There are, however, some variations in the detailed morphology although the basic structures are identical.

In *Elphidium crispum* the canal system has a rather smooth appearance and is formed by fusion of the most umbilical chamber-parts. When a new chamber is added there is an overlap between the posterior umbilical-most chamber-part of the new chamber with the previous one. The most umbilical anterior aperture of the preceeding chamber serves the purpose of communication into the newly formed chamber. Simultaneously with the formation of a new chamber a plate is deposited so as to seal off the umbilical part of the earlier chamber from the main-chamber lumen of that chamber.

In the umbilical part of the final chamber there is a posterior aperture directed into the interlocular space/subsutural canal which, when the sealing plate is deposited, will remain the communication between the sealed-off umbilical chamber-part and the interlocular space/subsutural canal. If umbilical apertures (besides the ones already mentioned) are present, some but not necessarily all will be converted with the addition of secondary lamellae into vertical umbilical canals. Since they are placed in the umbilical part of the chambers, they will also be prevented from communicating with the chamber lumina of the main chambers.

In addition to these passageways there are other canals, called herein oblique vertical canals, being nothing but the most umbilical fossettes of the previous coil which, by addition of secondary laminae, are converted into canals opening into the 'floor' of the umbilical chamber-parts (spiral canal) of the following coil. They thus correspond with the sutures of the previous coil but not with the chambers of the following coil.

Various different modifications of the system exist. If the umbilical chamber-parts are not tubular but rather are plate-like, the umbilical spiral canal may have the appearance in moulds of overlapping plates like the blades of a turbine. However, the same types of communications as described above also exist in such forms.

It is remarkable that the formation of a new chamber also involves deposition of a plate in the umbilical part of the previous chamber. This system was earlier described for *Ammonia* and associated forms by Hansen & Reiss (1971) where the addition of a new chamber also involved deposition in the umbilical part of the previous chamber of a so-called 'umbilical coverplate' (Fig. 8).

The formation of the umbilical coverplate in *Ammonia* and associated forms appears to be intimately connected also with the 'foraminal plate' (visualised as an inpush of the outer wall by Hansen & Reiss, 1971; compare also the 'gutter' of *Asterigerina* described by Hansen & Reiss, 1972a). A structure corresponding to either the foraminal plate or gutter has not been encountered in the elphidiids or nonionids. We consider the sealing-off plate in *Elphidium* analogous but not homologous with the umbilical coverplate of *Ammonia.* On the other hand, as outlined above, both time and place of formation are identical for the two structures. It should be mentioned that we have observed in *E. tranlucens* that the sealing-off plate apparently is composed of two layers. However, the very complicated and contorted morphology has precluded the possibility of producing sections in which it would be possible to follow the layers in order to establish their true nature (i.e. inner/outer layers).

The communications from the subsutural canals to the shell surface in the *Elphidiella* group are basically different from the openings in the sutures between ponticuli of *Elphidium.* In *Elphidiella* (and *Notorotalia*) the passageways from the subsutural canals to the shell surface 'cut' through the outer lamella that crosses the suture. They are generally smaller than fossettes and may have the appearance of 'a double row of sutural pores' or be arranged in an alternating series. This is, however, not always true, since e.g. one specimen of *Elphidiella sibirica* did have a single row in each suture (except one).

Communications have been described as 'bifurcating' but this is generally due to the phenomenon of superimposed neighbouring tubes when seen in thin sections under the light microscope. In the penultimate suture in *Notorotalia* we have observed a secondary lamel penetrating into the narrow openings and covering the subsutural canal on the inside. This, in our interpretation, means that after the deposition of the sealing off plate the subsutural canals can no longer be regarded as functional chamber lumen (contrary to the ultimate subsutural canal).

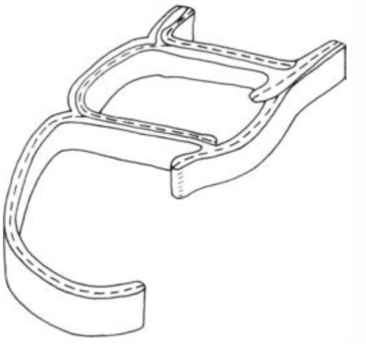


Fig. 8. Deposition of a plate in the umbilical part of the previous chamber in *Ammonia* upon the formation of a new chamber.

This further leads us to the conclusion, that the 'sutural pores' of the ultimate suture in *Elphidiella* must be interpreted as true apertures, while those of the older sutures are not.

There is thus a profound difference with respect to construction principle between on the one hand *Elphidium* and the nonionids and on the other hand *Elphidiella* and associated forms.

A survey of earlier classifications reveals a pronounced splitting into genera of the groups concerned. However, it appears that many of these genera are difficult to distinguish from neighbouring genera. The confusion as to the proper definition of the genera is evident from publications from recent years (e.g. the usage of the genera *Cribroelphidium, Cribrononion, Elphidiononion, Gavelinonion, Protelphidium, Florilus*). It therefore seems relevant to discuss the validity of some of the genera in common use in the light of the result presented above.

The genus *Cellathus* has all the characters of the genus *Elphidium.* It contains only one species namely *C. craticulatus* (Fichtel & Moll 1798). Hofker (1971:72) stated that a separation of *Cellathus* from *Elphidium* "... is only a question of taste...". Large specimens of *C. craticulatus* get a very large umbonal plug while smaller specimens show a high degree of similarity to specimens of e.g. *Elphidium crispum* (Linnaeus, 1758). Since no difference exists other than size we regard the two genera as synonymous.

Loeblich & Tappan (1964:C 635) wrote that the canal system of *Cellanthus* is more highly developed than that of *Elphidium.* The above descriptions and illustrations demonstrate that there is no difference in this character between the two genera in question. They further mentioned that the shell surface of *Cellathus* is not "highly ornamented" as in *Elphidium.* Ornamentation (i.e. ridges, pustules, tubercles etc.) cannot, however, be considered generic characters but may be used at a specific level only.

The genus *Cribroelphidium* Cushman & Brönnimann, 1948 was characterized by Loeblich & Tappan (1964: C 635) as having: sutures crossed by "solid pillars or septal bars but without retral processes"; possession of a "simplified sutural canal system"; coarsely perforated optically radiate wall; multiple aperture "with one or more pores at base of septal face and with one or more areal pores in addition".

Our study of the type species of this genus, namely *Cribroelphidium vadescens,* clearly demonstrates the presence of retral processes and hollow ponticuli. This also applies to the other species of the genus *Cribroelphidium* shown by Loeblich & Tappan, namely *C. kugleri, C. poeyanum* and *C. vulgare* (=*C. bartletti*), as described and illustrated above.

The sutural canal system in the type species as well as in the other species mentioned is not simplified as it is constructed in a way similar to that of *Elphidium.* It should be pointed out that the interlocular space (sutural canals *sensu* Loeblich & Tappan) communicates with an umbilical spiral canal system which is not mentioned by these authors.

The character of the optical wall structure i.e. optically radiate as opposed to optically granulate has been rejected as a distinguishing character above species level earlier in this paper (see also Hansen 1972). The coarsely perforated walls of the representatives of the genus *Cribroelphidium* mentioned by Loeblich & Tappan cannot be corroborated. Thus *C. vadescens* has a pore diameter of about 3.0 μm, *C. kugleri* 2.0 μm, *C. poeyanum* 2.0 μm and *C. vulgare* (=*C. bartletti*) about 0.4 μm.

With respect to apertures the figure of the type species reproduced by Loeblich & Tappan (1964) from Todd & Brönnimann (1957) does not show additional areal apertures. This is, however, seen in the second figure by Todd & Brönnimann as well as in the figure of the holotype in Cushman & Brönnimann (1948). The topotypes studied by us showed no additional areal apertures. It thus appears that the type species of the genus *Cribroelphidium* may or may not have additional areal apertures.

It should be mentioned in this context that the same phenomenon takes place in the species *Elphidium guntheri* which in many respects resembles *C. vadescens.*

Cribroelphidium was said by Loeblich & Tappan (1964: C 636) to differ from *Elphidium* by "absence of hollow retral processes, the presence of solid, non-perforate septal bridges, coarser pores in the wall, and a simple canal system, which does not connect to the chamber interior through retral processes".

The absence of retral processes and the simpler canal system in *Cribroelphidium* is shown above to be not correct. Neither can the coarser pores of *Cribroelphidium* be used as a distinctive character as is evident from the varying pore diameter of the species mentioned above.

The "canal system, which does not connect to the chamber interior through retral processes" is surprising since it implies that there should exist a communication from the chamber lumen through the retral processes into the interlocular space. Such a passageway has never been observed in any of the species studied by us.

Loeblich & Tappan (1964) placed in synonymy with the genus *Cribroelphidium* the genus *Elphidiononion* Hofker, 1951 with type species *Polystomella poeyana* d'Orbigny, 1839. Hofker (1951) characterised the genus *Elphidiononion* as different from *Elphidium* by the presence of solid pillars or bridges across the sutures and absence of retral processes. In 1971 Hofker pointed out that the solid pillars or bridges (by us called ponticuli) are without pores. As is evident from the present study the type species *Polystomella poeyana* does in fact have retral processes.

Hofker (1971) placed several species within the genus *Elphidiononion,* indicating their solid ponticuli and absence of retral processes. Some of these species i.e. *E. oregonense, E. advenum* and *E. striatopunctatum* have been studied by us and all show the presence of retral processes.

In view of the above discussion the genus *Cribroelphidium* (*sensu* Loeblich & Tappan 1964) must be considered synonymous with the genus *Elphidium.*

The genus *Cribrononion* Thalmann, 1947 was characterised by Loeblich & Tappan (1964) by the lack of retral processes; by possible occurrence of solid and imperforate septal bridges; by coarse perforation of the optically radiate wall and by lack of additional areal apertures.

It was further said to differ from the genus *Cribroelphidium* by the absence of additional areal apertures. Since the type species of the genus *Cribroelphidium* varies in this character (as mentioned above), the genus *Cribrononion* (*sensu* Loeblich & Tappan) cannot be separated from the genus *Cribroelphidium* which again cannot be separated from the genus *Elphidium* (see above).

Due to lack of material of the type species of *Cribrononion,* namely *Nonionina heteropora* Egger, 1857, Loeblich & Tappan (1964) based their concept of the genus on their study of the species *Polystomella umbilicatula* var. *incerta* Williamson, 1858 which they mention as optically radiate. Buzas (1966) however, showed that this species has an optically granulate wall structure, thereby making it obvious that the material studied by Loeblich & Tappan but not figured (except for a drawing of a vertical section reproduced from Hofker 1956) must belong to a species other than *E. incertum* (Williamson 1858). Our material of *E. incertum* shows an optically granulate structure like that found by Buzas (1966).

Topotype material of the type species *Nonionina heteropora* Egger was available to the present authors while Kristoffersen (1972) studied material of this species from Danish Miocene deposits. Both materials were found to be optically granulate.

The genus *Cribrononion* Thalmann, 1947 with the type species *Nonionina heteropora* Egger is maintained by Kristoffersen (1972), who emended the diagnosis. He characterised the genus *Cribrononion* by lack of retral processes, by optically granulate wall structure, small pores, presence of a spiral canal system and by presence of a "distinct apertural chamberlet". The aperture was described as a rather short interiomarginal slit which to a certain extent is subdivided when it is converted into a foramen. Our material shows that the aperture is already partly subdivided.

It should be pointed out, however, that particularly the presence of an 'apertural chamberlet' is a very doubtful character since, with the addition of a new chamber, it must either by resorbed or pushed off, because no trace of it is generally preserved at the foramina. We therefore regard it as an ornamental feature which should not be regarded as a character above species level. In this context it should be mentioned that an almost identical structure is developed in *Nonion graniferum* (Terquem 1882; compare illustrations in Hansen 1970b). Likewise *N. graniferum* generally does not show signs of this structure at the foramina.

On the other hand, the presence of subsutural canals formed in a way differing from that of *Elphidium* would point to identity of the genus *Elphidiella* rather than *Elphidium*. The double row of sutural openings in *Elphidiella* is not a constant character. In one of the examples shown in this work (*Elphidiella sibirica*) one row of openings was seen as well as two. Therefore the number of openings are *per se* of subordinate importance compared to the construction principle of the canals in the sutures, i.e. subsutural canals *versus* interlocular space. From the point of view of construction principle there is very little doubt indeed that the species *Nonionina heteropora* belongs to *Elphidiella* but is very different from *Elphidium*.

A series of polished and etched sections were made in order to study the nature of the 'apertural chamberlet'. The material is, however, not in a desirable state of preservation and thereby precludes definite conclusions, but it appears that the 'apertural chamberlet' is formed by the outer lamella exclusively thereby making it an ornamental feature and not a variant of some kind of apertural lip (which would also encompass the inner lining). This agrees well with the fact that such a structure generally is absent from the foramina.

It appears likely, then, that the type species of *Cribrononion* belongs to the genus *Elphidiella*.

Elphidium incertum, E. translucens, E. excavatum and *E. boreale* have been placed by authors in the genus *Cribrononion*. These forms as studied herein all show presence of retral processes, hollow ponticuli, interlocular spaces and umbilical spiral canal system as found in the genus *Elphidium*, to which genus they must be referred.

The genus *Protelphidium* Haynes, 1956 was erected with *P. hofkeri* Haynes, 1956 as type species. Haynes pointed out that the genus *Protelphidium* holds an intermediate position between elphidiids and nonionids or in other words is an optically radiate *Nonion*. Its morphological characters i.e. absence of retral processes, ponticuli, spiral canal system and interlocular space naturally places this genus among the nonionids.

Loeblich & Tappan (1964) expanded the concept of the genus *Protelphidium*, including into it also the genus *Porosononion* Putrya, 1958 with type species *Nonionina subgranosa* Egger, 1857 (=*Nonionina tuberculata* d'Orbigny, 1846).

Accordingly the genus *Protelphidium sensu* Loeblich & Tappan is characterised by radiate wall structure "no sutural pores or retral processes but vertical canals piercing umbilical plug of secondary shell material". "Primary aperture possibly interiomarginal, secondary areal foramina and umbilical pores".

We do not consider optical wall structure a character of value above species level. Neither *Nonionina tuberculata* nor *P. hofkeri* have retral processes or ponticuli. Vertical canals piercing the umbilical plug are found in *N. tuberculata* but not in *P. hofkeri*. The vertical canals originate from the umbilical spiral canal system of *N. tuberculata*. The primary aperture in *P. hofkeri* is an interiomarginal, equatorial slit confined to the central part while that of *N. tuberculata* is multiple, interiomarginal with additional multiple areal apertures. *P. hofkeri* has no secondary areal foramina.

P. hofkeri has no interlocular spaces (deeply sunken sutures) which feature is, however, present in *N. tuberculata*.

Nonionina tuberculata and thereby the genus *Porosononion* belongs to *Elphidium* in spite of the absence of retral processes. As mentioned earlier we have observed all degrees of development of retral processes and do not regard this character as distinctive for the genus *Elphidium*.

Species like *Nonion germanicum* (Ehrenberg) (=*Protelphidium anglicum* Murray) and *Nonion orbiculare* here investigated, by different authors were referred to the genus *Protelphidium*. These, like *P. hofkeri*, are placed among the nonionids since they lack a spiral canal system.

Other species referred to the genus *Protelphidium* such as *Elphidium albiumbilicatum* and *E. ustulatum* (=*Protelphidium lenticulare* Gudina) also herein studied are placed in the genus *Elphidium* since they have developed a spiral canal system.

The genus *Elphidium* Montfort, 1808 with type species *Nautilus macellus* var. β Fichtel & Moll, 1798 thus contains species that are planispiral, bilaterally symmetrical, involute or parlty evolute, with or without retral processes. With interlocular spaces between adjacent chambers constructed like sunken sutures communicating with an umbilical spiral canal system. Vertical umbilical canals may or may not be present. Aperture and foramina interiomarginal, single or multiple with or without additional areal openings. When the aperture is simple it never reaches the umbilici. Primary wall and septa bilamellar with a septal flap partly or fully covering the older septa. Optical wall structure radiate or granulate. Pore diameter variable.

With respect to inhomogeneity in optical wall structure the genus *Elphidiella* resembles *Elphidium* since *Elphidiella* also encompasses forms with radiate and granulate wall structure. *Elphidiella* was erected as a genus by Cushman 1936 because of its double row of 'sutural pores'.

All species of this genus studied by us show presence of an umbilical spiral canal system formed in a way identical to that of *Elphidium*. Moreover chamber arrangement and apertural characters strongly resemble the corresponding characters in *Elphidium*. The difference noted, i.e. the double row of 'sutural pores' in *Elphidiella* by contrast to the 'normal' single row in *Elphidium*, seems *per se* to be a poor distinguishing character. When considered solely from the point of outer morphology we do in fact find double rows of 'sutural pores' in some species of *Elphidium* (e.g. *E. striatopunctatum*) but as explained earlier these sutural openings are fossettes and parafossettes and are basically different from the double or single row of sutural openings in *Elphidiella*. In *Elphidiella sibirica* we found that all but one suture in the final whorl of one of the specimens studied carried one row of sutural openings. Furthermore species like *Elphidiella heteropora* and *Elphidiella subnodosa* have only one row of openings in each suture. Thus the character of double rows of openings in the sutures cannot be used as a distinguishing character. In *Elphidiella* the openings penetrate the outer calcareous layer of a chamber bridging the suture. The calcareous layer is not bent inwards to 'coat' the canal in the suture (subsutural canal by contrast to the interlocular space in *Elphidium*).

Elphidiella can be distinguished from *Elphidium* because of its basically different construction of the canals in the sutures. *Elphidiella* lacks ponticuli and fossettes but as shown by *E. sibirica* (and also *Notorotalia zelandica*) the construction principle of the subsutural canals of *Elphidiella* does not preclude development of retral processes.

The genus *Elphidiella* Cushman, 1936 with type species *Polystomella arctica* Parker & Jones, 1864 contains species that are planispiral, involute, bilateral symmetrical with or without retral processes. With subsutural canals formed as a cave between a septum and the following chamber where the outer lamella of the new chamber crosses the suture while the inner lining is double in the canal area. The subsutural canals communicate with an umbilical spiral canal system. Vertical umbilical canals may be present. Aperture and foramina interiomarginal, single or multiple with or without additional areal multiple openings. Primary wall and septa bilamellar with septal flaps partly or fully covering the older septa. Optical wall structure radiate or granulate. Pore diameter variable.

The genus *Nonion* Montfort 1808 was erected with *Nautilus incrassatus* Fichtel & Moll, 1798 as type species. However, recent unpublished investigations by Dr. F. Rögl, Vienna (communicated at the 1st International Conference on Benthonic Foraminifera, Halifax, Canada, 1975, by Dr. J. Saunders, Basel) show that the species *Nautilus incrassatus* has been misunderstood by Montfort (1808) and all later workers. It appears (according to Dr. F. Rögl's study of the Fichtel & Moll types) that this species should be correctly referred to the genus *Anomalinoides*. It has no relation to the genus *Nonion* as is generally understood. Thus the genus *Nonion* was erected with a misunderstood type species and either a new type species must be selected or the genus must be abandoned.

It is not desirable to erect a new genus since the name *Nonion* has been in common use for many years and since one should adhere as strictly as possible to the preamble of the rules of zoological nomenclature converning nomenclatorial stability. Our concept of the genus *Nonion* is well represented by the species *Nonion depressulum* (Walker & Jacob 1798) and until some verdict is passed by the competent body (namely ICZN) we regard this species as a 'typical' representative of the genus *Nonion*.

The genus *Florilus* Montfort, 1808 with type species *Nautilus asterizans* Fichtel & Moll, 1798 was recognized by Loeblich & Tappan (1964) in spite of the fact that this genus had not been in use since it was erected in 1808. There are in fact very serious problems involved in defining the differences between the genus *Nonion* (as here understood) and the genus *Florilus*.

Thus Loeblich & Tappan (1964: C 748) wrote that *Florilus* "differs from *Nonion* in the flaring test, due to the numerous broad low chambers ...". When the figured specimens of species of the genus *Florilus* are studied in this respect it becomes evident that great variability exists in this character. In our opinion it is impossible to keep the genera *Nonion* and *Florilus* apart and in consequence we regard them as synonymous. A further complicating fact is that according to Dr. F. Rögl's investigations (referred to above) the type species of *Florilus* has been misunderstood (as in the case of *Nonion*) and its type species, namely *Nautilus asterizans*, should correctly be referred to the genus *Hazawaia*. Often *Nonion boueanum* has been mistaken for *N. asterizans*. In spite of the fact that the genus *Florilus* is defined on an earlier page in the work of Montfort than is the genus *Nonion* there can be no doubt that the genus *Nonion* should be retained for reasons of desirability, while the (in our impression) identical genus *Florilus* (*sensu* Loeblich & Tappan 1964) should be suppressed.

The genus *Nonionellina* Voloshinova, 1958 with the type species *Nonionina labradorica* Dawson, 1860 was erected since it differs from *Nonion* in having a trochospiral initial part while the later part is planispiral and bilaterally symmetrical.

With reference to the earlier mentioned character of the type species of the genus *Elphidiella*, i.e. *Elphidiella arctica*, in which the initial part does not show any subsutural canals and accordingly no sutural openings and thereby possibly demonstrates its ancestral group, it becomes impossible by analogy to maintain a separate genus (containing so far as is known only one species) for forms showing in their initial part a supposedly relict initial trochospiral coiling. We therefore place the genus *Nonionellina* in synonymy with the genus Nonion.

By contrast we regard the genus *Nonionella* Cushman, 1926 with type species *Nonionella miocenica* Cushman, 1926 as a valid genus as it shows trochospiral coiling throughout with asymmetrical chambers.

From a phylogenetic point of view it would appear that the genus *Nonionella* forms a main stem originating somewhere in Upper Cretaceous times, developing in the Early Tertiary planispiral and bilaterally symmetrical forms and possibly again in Miocene times giving rise to planispiral (at least in the adult) coiling forms. Thus *Nonionella* can be separated taxonomically by accepting the coiling as the distinguishing character.

The consequences for the *Elphidium* group is that the genus *Faujasina* (according to published investigations), being a trochospiral *Elphidium*, must be recognised. The same is true of the genus *Notorotalia* which can be separated from the genus *Elphidiella* by its trochospiral coiling and in addition by its subsutural canal in the spiral suture on the spiral side.

The genus *Pullenia* represents a problem of its own, since it appears to have been a rather stable form-group since the Upper Cretaceous. It can be separated from the genus *Nonion* as it is not umbilicate. We therefore tentatively regard *Pullenia* as an independent genus.

The genus *Melonis* was placed by Loeblich & Tappan (1964) among forms like *Anomalina, Heterolepa* and *Gavelinella.* Its early Tertiary forms like e.g. *Melonis nobilis* (Brotzen 1948) clearly show a slightly asymmetrical coiling while the geologically younger representatives develop into planispiral bilaterally symmetrical forms.

The genus *Astrononion* Cushman & Edwards, 1937 with type species *Nonionina stelligera* d'Orbigny 1839 represents an interesting combination of characters with a simple aperture extending into the umbilici, sutures that are depressed only towards the umbilici, without septal flap and finally with an umbilical spiral canal system. *Astrononion* differs from *Elphidium* in its apertural characters where *Astrononion* has no separate umbilicalmost apertural section. This involves that the spiral canal system in *Astrononion* is analogous with that of *Elphidium* but differs in certain respects, namely that the delimitation in peripheral direction of the attachment of the umbilical chamber part at the place of overlap with the previous chamber is made by the posterior chamber wall of the younger chamber.

The representatives of the genus *Astrononion* form a morphologically well defined group with a geological history dating back to the Eocene (in New Zealand) and can be kept separate from other allied genera by their remarkable combination of characters.

The present work does not intend to represent in any way a complete picture since many important forms have been inaccessable to the authors. This is true of *Fissoelphidium, Polystomellina, Faujasina* and *Lafitteina* to mention but a few examples. However, the forms studied once more indicate the difficulty in establishing a hierarchical order of characters in the classification of the Foraminiferida. On the other hand the authors have a strong feeling that the groups here treated may very well be polyphyletic although it appears that the characters available do not suffice to make it more than a feeling.

It has struck us particularly that the presence or absence of septal flaps and their supposed close relationship with the presence of interlocular spaces or subsutural canals is one of degree rather than of kind. This is further reinforced by the discovery of septal flaps in *Pullenia* and *Melonis.* Thus, as stated earlier, a grouping of all genera or species with septal flaps within the Rotaliidae leads to groups being inhomogeneous in other respects. The presence of retral processes also seems a very doubtful character since this, too, is one of degree rather than of kind. Thus a very deep interlocular space is connected (sometimes) with retral processes as a shell reinforcement measure preventing breakage of chambers. Other forms solve this problem in a variety of different ways. Some forms do have retral processes in spite of presence of only a shallow interlocular space. However, other forms which from an architectural point of view would have no use for retral processes have such structures developed. These we may guess to be relict structures (although such a statement requires a thorough knowledge of the evolutionary lineage of the species in question).

In view of the above, which in many ways appears rather frustrating, we prefer not to follow any supra-generic classification since it will force us to make a highly subjective evaluation of the hierarchical order of the different characters.

We thus recognize here only genera and have for the time being no desire to place them in higher groupings.

References

Anderson, G. J. 1963: Distribution patterns of recent foraminifera of the Bering Sea. *Micropaleontology 9,* 305–317.

Bellemo, S. 1974a: Ultrastructures in recent radial and granular calcareous foraminifera. *Bull. Geol. Instn Univ. Upsala, N.S. 4,* 117–122.

Bellemo, S. 1974b: The compound and intermediate wall structures in Cibicidinae (foraminifera) with remarks on the radial and granular wall structures. *Bull. Geol. Instn Univ. Upsala, N.S. 6,* 1–11.

Bellemo, S. 1974c: Studies on the ultrastructures of calcareous foraminifera with hyaline perforate walls. *Acta Univ. Upsaliensis 321.* 14 pp. (Abst. Uppsala Dissert. Fac. Sci.).

[Bellemo, S. 1974d: Ultrastructure in the foraminifer *Cibicides floridanus* (Cushman), 1–10. Preprint; A-Offset, Uppsala.]

Brady, H. B. 1864: Contributions to the knowledge of the foraminifera. On the Rhizopodae fauna of the Shetlands. *Trans. Linn. Soc. London 24,* 463–476.

Brady, H. B. 1881: Notes on some of the reticularian Rhizopoda of the "Challenger" Expedition. III. *Quart. J. Micr. Sci. 21,* 31–71.

Brady, H. B. 1884: Report on the foraminifera dredged by H. M. S. Challenger during the years 1873–1876. *Rep. Sci. Results Explor. Voy. Challenger 1873–1876, Zool. 9.* 814 pp.

Brotzen, F. 1943: see Hessland, I. 1943.

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

Buzas, M. A. 1966: The discrimination of morphological groups of *Elphidium* (foraminifer) in Long Island Sound through canonical analysis and invariant characters. *J. Paleont. 40,* 585–594.

Carpenter, W. B., Parker, W. K. & Jones, T. R. 1862: Introduction to the study of the foraminifera. *Ray Soc. Publs.* 319 pp. London.

Cole, W. S. 1931: The Pliocene and Pleistocene foraminifera of Florida. *Bull. Florida State Geol. Surv. 6.* Tallahassee.

Cushman, J. A. 1922: The foraminifera of the Atlantic Ocean. *Bull. U.S. Nat. Mus. 104: 3.* 143 pp.

Cushman, J. A. 1927: Recent foraminifera from off the west coast of America. *Bull. Scripps Inst. Oceanography, Tech. 1: 10,* 119–188.

Cushman, J. A. 1930: The foraminifera of the Atlantic Ocean. *Bull. U.S. Nat. Mus. 104: 7.* 79 pp.

Cushman, J. A. 1933: New Arctic foraminifera collected by Capt. R. A. Bartlett from Fox Basin and off the northeast coast of Greenland. *Smithsonian Misc. Coll. 89: 9,* 1–8.

Cushman, J. A. 1936: Some new species of *Elphidium* and related genera. *Contr. Cushman Lab. Foram. Res. 12,* 78–91.

Cushman, J. A. 1939: A monograph of the foraminiferal family Nonionidae. *Prof. Pap. U.S. Geol. Surv. 191.* 100 pp.

Cushman, J. A. 1941: Some fossil foraminifera from Alaska. Contr. *Cushman Lab. Foram. Res. 17,* 33–38.

Cushman, J. A. 1944: Foraminifera from the shallow water at the New England coast. *Cushman Lab. Foram. Res., Spec. Publ. 12.* 37 pp.

Cushman, J. A. 1947: New species and varieties of foraminifera from off the southeastern coast of the United States. *Contr. Cushman Lab. Foram. Res. 43,* 86–92.

Cushman, J. A. & Brönnimann, P. 1948: Some new genera and species of foraminifera from brackish water at Trinidad. *Contr. Cushman Lab. Foram. Res. 24,* 15–21.

Cushman, J. A. & Edwards, P. G. 1937: Astrononion, a new genus of the Foraminifera, and its species. *Contr. Cushman Lab. Foram. Res. 13,* 29–36.

Cushman, J. A. & Grant, U. S. 1927: Late Tertiary and Quaternary Elphidiums of the west coast of North America. *Trans. San Diego Soc. Nat. Hist. 5,* 69–82.

Cushman, J. A. & Leavitt, D. H. 1929: On *Elphidium macellum* (Fichtel and Moll), *E. striato-punctatum* (Fichtel and Moll) and *E. crispum* (Linné). *Contr. Cushman Lab. Foram. Res. 5,* 18–24.

Cushman, J. A. & Todd, R. 1943: The genus *Pullenia* and its species. *Contr. Cushman Lab. Foram. Res. 19,* 1–23.

Dam, A. ten 1944: Die stratigraphische Gliederung des Niederländischen Paläozäns und Eozäns nach Foraminiferen. *Med. Geol. Sticht. C-5: 3.* 142 pp.

Daniels, C. H. von 1970: Quantitative ökologische Analyse der zeitlichen und räumlichen Verteilung rezenter Foraminiferen im Limski Kanal bei Rovinj. *Göttinger Arb. Geol. Paläont. 8.* 109 pp.

Dawson, J. W. 1860: Notice of Tertiary fossils from Labrador, Maine, etc. and remarks on the climate of Canada in the Newer Pliocene or Pleistocene period. *Canadian Nat. 5,* 188–200.

Egger, J. G. 1857: Die Foraminiferen der Miocän-Schichten bei Ortenburg in Nieder-Bayern. *Neues Jahrb. Mineral. Geogn. Geol. Petref.,* 266–311.

Ehrenberg, C. G. 1840: Das grössere Infusorienwerke. *K. Preuss Akad. Wiss. Berlin,* 198–219.

Feyling-Hanssen, R. W. 1964: Foraminifera in Late Quaternary deposits from the Oslofjord area. *Norges Geol. Unders. 225.* 383 pp.

Feyling-Hanssen, R. W. 1972: The foraminifer *Elphidium excavatum* (Terquem) and its variant forms. *Micropaleontology 18,* 337–354.

Feyling-Hanssen, R. W., Jørgensen, J. A., Knudsen, Karen L. & Andersen, Anne-Lise L. 1971: Late Quaternary foraminifera from Vendsyssel, Denmark and Sandnes, Norway. Bull. Geol. Soc. Denmark 21, 67–317.

von Fichtel, L. & von Moll, J. P. C. 1798: *Testacea microscopia aliaque minuta ex generibus* Argonauta *et* Nautilus *ad naturam picta et descripta ... cum 24 tabulis acri incisis coloratis.* Vienna.

Finlay, H. J. 1939: New Zealand foraminifera, key species in stratigraphy. *Trans. Roy. Soc. New Zealand 68,* 504–543.

Goës, A. 1894: A synopsis of the Arctic and Scandinavian recent foraminifera hitherto discovered. *Handl. Kgl. Svenska Vet.-Akad. 25,* 9.

[Gudina, Valentina I. 1966: Foraminifera and stratigraphy of the northwest Siberian Quaternary. *Akad. Nauk SSSR Siberian Dept., Inst. Geol. and Geoph.* 132 pp. (In Russian.)]

[Gudina, Valentina I. 1969: The marine Pleistocene of Siberian lowlands. Foraminifera of the north part Ienisei's lowland. *Akad. Nauk SSSR, Siberian Dept., Inst. Geol. and Geoph. 63.* 80 pp. (In Russian.)]

Haake, F.-W. 1962: Untersuchungen an der Foraminiferen-Fauna im Wattgebiet zwischen Langeoog und dem Festland. *Meyniana 12,* 25–64.

Hansen, H. J. 1968: X-ray diffractometer investigations of a radiate and a granulate foraminifera. *Meddr Dansk Geol. Foren. 18,* 345–348.

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

Hansen, H. J. 1970b: Danian foraminifera from Nûgssuaq, West Greenland. *Meddr Grønland 193: 2.* 132 pp.

Hansen, H. J. 1972: Two species of foraminifera of the genus *Turrilina* with different wall structure. *Lethaia 5,* 39–45.

Hansen, H. J. & Reiss, Z. 1971: Electron microscopy of Rotaliacean wall structures. *Bull. Geol. Soc. Denmark 20,* 329–346.

Hansen, H. J. & Reiss, Z. 1972a: Scanning electron microscopy of some asterigerinid foraminiferida. *Journ. Foram. Res. 2,* 191–199.

Hansen, H. J. & Reiss, Z. 1972b: Scanning electron microscopy of wall structures in some benthonic and planktonic Foraminiferida. *Rev. Española Micropal. 4,* 169–179.

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

Haynes, J. 1956: Certain smaller British Paleocene foraminifera. Part I. *Contr. Cushman Fdn. Foram. Res. 7,* 79–61.

Haynes, J. R. 1973: Cardigan Bay recent foraminifera. *Bull. British Mus. (Nat. Hist.), Zool. Suppl. 4.* 245 pp.

Heron-Allen, E. & Earland, A. 1932: Foraminifera. Part I. The icefree area of the Falkland Islands and adjacent seas. *Discovery Rep. 4,* 291–460.

Hessland, I. 1943: Marine Schalenablagerungen Nord-Bohusläns. *Bull. Geol. Inst. Upsala 31.* 348 pp.

Hofker, J. 1951: The foraminifera of the Siboga Expedition. Part III. *Siboga Exped. Monogr. 4b(3).* 513 pp.

Hofker, J. 1956: Foraminifera Dentata-Foraminifera of Santa Cruz and Thatch-Island Virginia-Archipelago, West Indies. *Spolia Zool. Musei Hanniensis XV.* 237 pp.

Hofker, J. 1969: An analysis of the subfamily Notorotaliinae (foraminifera) Hornibrook, 1961. *Jour. Geol. Geophys. New Zealand 12,* 460–483.

Hofker, J. 1971: Studies of foraminifera. Part III. Systematic Problems. *Publ. Natuurhist. Genootsch. Limburg* XXI. 202 pp.

Kristoffersen, F. N. 1972: Studies on some Elphidiidae (foraminifera) from the Miocene of Denmark. *Geol. Surv. Denmark. Yearbook,* 25–35.

Lamarck, J. B. 1822: *Histoire naturelle des animaux sans vertèbres. 7.* 711 pp.

Lévy, A., Mathieu, R., Momeni, I., Poignant, A., Rosset-Moulinier, M., Rouvillois, A. & Ubaldo, M. 1969: Les réprésentants de la famille des Elphidiidae (foraminifères) dans les sables des plages des environs de Dunkerque. Remarques sur les espèces de *Polystomella* signalées par O. Terquem. *Rev. Micropaléont. 2,* 92–98.

Linnaeus, C. 1758: *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, ed. 10: 1.* 824 pp. G. Engelman (Lipsiae).

Loeblich, A. R. & Tappan, Helen 1953: Studies of Arctic foraminifera. *Smithsonian Misc. Coll. 121.* 150 pp.

Loeblich, A. R. & Tappan, Helen 1964: Sarcodina, chiefly "Thecamoebians" and Foraminiferida. In Moore, R. C. (editor): *Treatise on Invertebrate Paleontology. C, Protista 2, I–II.* Geol. Soc. Amer. and Univ. Kansas Press. 900 pp.

Loeblich, A. R. & Tappan, Helen 1974: Recent advances in the classification of the Foraminiferida. In *Foraminifera 1* (ed. Hedley and Adams), 1–54. Academic Press, London and New York.

Lutze, G. F. 1965: Zur Foraminiferen-Fauna der Ostsee. *Meyniana 15,* 75–147.

Lutze, G. F. 1968: Jahresgang der Foraminiferen-Fauna in der Bottsand-Lagune (westliche Ostsee). *Meyniana 18,* 13–30.

Marks, P. 1951: A revision of the smaller foraminifera from the Miocene of the Vienna Basin. *Contr. Cushman Fdn. Foram. Res. 2,* 33–73.

de Montfort, D. 1808: *Conchyliologie systématique et classification méthodique des conquilles 1.* 409 pp.

von Münster, A. 1838: *In* Roemer, F. A.: Die Cephalopoden des Nord-Deutschen tertiären Meeres-Sandes. *Neues Jb. Miner.,* 381–394.

Murray, J. W. 1965: Two species of British recent Foraminiferida. *Contr. Cushman Fdn. Foram. Res. 16,* 148–150.

Murray, J. W. 1971: *An atlas of British recent foraminiferids XII.* 244 pp. Heinemann Educational Books: London.

Natland, M. L. 1938: New species of foraminifera from off the west coast of North America and from the later Tertiary of the Los Angeles basin. *Bull. Scripps Inst. Oceanography, Tech. Ser. 4: 5,* 137–164.

Nørvang, A. 1959: On *Nonion pombilioides* (Fichtel and Moll). *Meddr Dansk Geol. Foren. 14,* 141–150.

d'Orbigny, A. D. 1826: Tableau méthodique de la Classe des Céphalopodes. *Ann. Sci. Nat. Paris 1: 7,* 245–314.

d'Orbigny, A. D. 1839: Foraminifères. In de la Sagra, R.: *Histoire physique, politique et naturelle de l'île de Cuba,* 1–224. Paris.

d'Orbigny, A. D. 1846: *Foraminifères fossiles du Bassin Tertiaire de Vienne.* Gide et Comp., 312 pp. Paris.

Parker, W. K. & Jones, T. R. 1862: see Carpenter, W. B. et al. 1862.

Parker, W. K. & Jones, T. R. 1864: see Brady, H. B. 1864.

Putrya, 1958: see Voloshinova 1958.

Reiss, Z. 1963: Reclassification of perforate foraminifera. *Bull. Geol. Surv. Israel 35.* 111 pp.

Reuss, A. E. 1855: Ein Beitrag zur genaueren Kenntniss der Kreidegebilde Mecklenburgs. *Deutsch. Geol. Gesell., Zeitschr. 7: 1,* 261–292.

[Stschedrina, Z. G. 1946: New species of foraminifera from the Arctic Ocean. Transaction of the Arctic Scientific Research Institute, Northern Sea Route Board Drifting Expedition on the Icebreaker "G. Sedov" in 1937–1940. *Trudy Moscow-Leningrad 3 (Biology).* 147 pp. (In Russian.)]

Tappan, Helen 1951: Northern Alaska index foraminifera. Contr. Cushman Fdn. foram. Res. 2, 1–8.

Terquem, O. 1876: *Essai sur le classement des animaux qui vivent sur la plage et dans les environs de Dunkerque 2,* 55–100.

Terquem, O. 1882: Les foraminifères de l'Éocène des environs de Paris. *Mém. Soc. Géol. Fr. 3.* 193 pp.

Thalmann, H. E. 1947: Mitteilungen über Foraminiferen. *Eclogae geol. Helv.* 39, 309–314.

Todd, Ruth 1957: Foraminifera from Carter Creek, northern Alaska. A report on the discovery of a late Tertiary foraminifera fauna from the northeastern coast of Alaska. *Prof. Pap. U.S. Geol. Surv. 294-F,* 223–235.

Todd, Ruth & Brönnimann, P. 1957: Recent Foraminifera and Thecamoebina from the eastern Gulf of Paria. *Cushman Fdn. Foram. Res. Spec. Publ. 3,* 1–43.

Todd, Ruth & Low, Dorris 1967: Recent foraminifera from the Gulf of Alaska and southeastern Alaska. *Prof. Pap. U.S. Geol. Surv. 573-A,* 1–46.

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

Ujiié, H. 1956: The internal structures of some Elphidiidae. *Tokyo Kyoiku Daigaku, Sci. Repts. C: 4,* 267–282.

Voloshinova, N. A. 1952: see Voloshinova, N. A. & Dain, L. G. 1952.

[Voloshinova, N. A. & Dain, L. G. 1952: Nonionidy, Kassidulinidy i Khilostomellidy. Iskopaemye foraminifery SSSR. *Trudy VNIGRI N.S. 63.* 151 pp.]

[Voloshinova, N. A. 1958: O novoy sistematike Nonionid. Mikrofauna SSSR, Sbornik 9. *Trudy VNIGRI 115,* 117–191.]

van Voorthuysen, J. H. 1951: Recent (and derived Upper Cretaceous) foraminifera of the Netherlands Wadden Sea (tidal flats). *Med. Geol. Sticht. N.S. 11,* 27–39.

van Voorthuysen, J. H. 1957: Foraminiferen aus dem Eemien (Riss-Würm-Interglacial) in der Bohrung Amersfoort I (Locus typicus). *Med. Geol. Sticht. N.S. 11,* 27–39.

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

Walker, G. & Jacob, E. 1798: *In* Adams, G.: *Essays on the Microscope* (2nd ed.). F. Kanmacker, London.

Weiss, L. 1954: Foraminifera and origin of the Cardiners Clay (Pleistocene), eastern Long Island, New York. *Prof. Pap. U.S. Geol. Surv. 254-G,* 139–163.

Williamson, W. C. 1858: On the recent foraminifera of Great Britain. *Roy. Soc. Publs. XX.* 107 pp. London.

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.

Explanations of plates

Plate 1

Figs. 1–9. *Elphidium macellum* (Fichtel & Moll). Recent, off Cyprus, Mediterranean Sea.

☐ Fig. 1. Side view, ×128. ☐ Fig. 2. Edge view, ×122. ☐ Fig. 3. Oblique edge view showing depressed tuberculate umbilicus, ×120. ☐ Fig. 4. Etched horisontal section, ×69. ☐ Fig. 5. Detail of Fig. 4 showing bilamellar final chamber wall, ×1725. ☐ Fig. 6. Etched horisontal section (at a level higher than that in Fig. 4), ×87. ☐ Fig. 7. Detail of Fig. 6 showing sealing off plates in the region of the umbilical spiral canal, ×844. ☐ Fig. 8. Plastic mould showing retral processes and umbilical spiral canal system, ×154. ☐ Fig. 9. Detail of Fig. 8 showing communications from the umbilical spiral canal into the interlocular spaces along with vertical umbilical canals, fossettes and retral processes, ×378.

Figs. 10–12. *Elphidium crispum* (Linnaeus). Recent, Gulf of Naples, Mediterranean Sea.

☐ Fig. 10. Side view, ×43. ☐ Fig. 11. Oblique apertural view, ×131. ☐ Fig. 12. Plastic mould showing retral processes, fossettes, umbilical spiral canal system, vertical umbilical canals and oblique vertical canals, ×130.

The following code of letters has been used in the plates

A Aperture
B Foramen
C Ponticulus
D Fossette
E Parafossette
F Interlocular space
G Subsutural canal
H Connecting canals from subsutural canal to shell surface
I Inner lining
J Retral process
K Most umbilical interiomarginal apertural part
L Umbilical aperture
M Median layer
O Outer lamella
P Vertical umbilical canal
R Oblique vertical canal
S Secondary lamination
T Umbilical spiral canal
U Sealing off plate
V Septum
X Fracture (artificial)

Plate 2

Figs. 1–2. *Elphidium crispum* (Linnaeus). Recent, Gulf of Naples, Mediterranean Sea.

☐ Fig. 1. Deeply etched vertical section showing interlocular space, retral processes, fossettes, umbilical spiral canal system, vertical umbilical canals and strongly developed secondary lamination, ×61. ☐ Fig. 2. Detail of Fig. 1, ×367.

Figs. 3–9. *Elphidium craticulatum* (Fichtel & Moll). Recent, Kei Islands, Banda Sea.

☐ Fig. 3. Side view, ×56. ☐ Fig. 4. Edge view, ×42. ☐ Fig. 5. Apertural detail of Fig. 4, ×157. ☐ Fig. 6. Detail of Fig. 3, showing fossettes and ponticuli. Note the anteriorly directed umbilical chamber parts as well as umbilical apertures, ×384. ☐ Fig. 7. Detail of ultimate suture showing fossettes, ponticuli and position of parafosettes, ×667. ☐ Fig. 8. Plastic mould showing spiral canal, vertical umbilical canals and oblique vertical canals, ×171. ☐ Fig. 9. Detail of Fig. 8, showing continuity of chamber lumen of final chamber with umbilical spiral canal and position of the sealing off plate in the earlier chambers. Note position of umbilical aperture and communication with interlocular spaces, ×759.

Figs. 10–12. *Elphidium advenum* (Cushman). Recent, off Banyuls, Mediterranean Sea.

☐ Fig. 10. Side view, ×119. ☐ Fig. 11. Edge view, ×153. ☐ Fig. 12. Detail of fractured specimen showing aperture, foramina, retral processes, ponticuli, fossettes and parafossettes, ×340.

Plate 3

Fig. 1. *Elphidium advenum* (Cushman). Recent off Banyuls, Mediterranean Sea. ☐ Plastic mould showing umbilical spiral canal system, oblique vertical canals, retral processes, fossettes and communications from the spiral canal into the interlocular spaces, ×185.

Figs. 2–6. *Elphidium margaritaceum* (Cushman). Recent, Kattegat, Denmark.

☐ Fig. 2. Side view, ×171. ☐ Fig. 3. Oblique edge view, ×489. ☐ Fig. 4. Fractured specimen showing aperture, ×383. ☐ Fig. 5. Fractured specimen showing retral processes as well as partly covered multiple foramen, ×497. ☐ Fig. 6. Plastic mould showing retral processes and umbilical spiral canal system. Note the absence of sealing off plate in the final chamber, ×400.

Figs. 7–10. *Elphidium sagrum* (d'Orbigny). Recent, Jamaica.

☐ Fig. 7. Side view, ×193. ☐ Fig. 8. Oblique edge view, ×175. ☐ Fig. 9. Detail showing aperture, foramen and retral processes, ×381. ☐ Fig. 10. Plastic mould showing umbilical spiral canal system, vertical umbilical canals, retral processes and fossettes. The final chamber is missing, ×351.

Figs. 11–12. *Elphidium striatopunctatum* (Fichtel & Moll). Recent, Nabek, Gulf of Elat.

☐ Fig. 11. Side view, ×43. ☐ Fig. 12. Edge view, ×44.

Plate 4

Figs. 1–7. *Elphidium striatopunctatum* (Fichtel & Moll). Recent, Nabek, Gulf of Elat.

□ Fig. 1. Edge view, ×124. □ Fig. 2. Detail of etched, vertical section showing foramina, retral processes as well as secondary lamination, ×391. □ Fig. 3. Detail of ultimate suture showing fossettes, parafossettes and ponticuli, ×327. □ Fig. 4. Detail of ultimate but three suture showing fossettes, parafossettes and ponticuli, ×301. □ Fig. 5. Detail of etched horisontal section close to retral process showing bilamellar septum with septal flap and interlocular space with secondary lamellae, ×1424. □ Fig. 6. Plastic mould showing retral processes, interlocular spaces and their communication with umbilical spiral canal, ×354. □ Fig. 7. Plastic mould showing umbilical spiral canal, vertical umbilical canals and oblique vertical canals, ×224.

Figs. 8–12. *Elphidium voorthuyseni* Haake. Eemian, Meetkerke, Belgium.

□ Fig. 8. Side view, ×192. □ Fig. 9. Oblique edge view, ×295. □ Fig. 10. Fractured specimen showing aperture, ×798. □ Fig. 11. Detail of etched horisontal section showing attachment of septum to previous coil demonstrating bilamellar septum and septal flap, ×1864. □ Fig. 12. Plastic mould showing part of umbilical spiral canal system and retral processes, ×384.

Plate 5

Figs. 1–6. *Elphidium williamsoni* Haynes. Recent, Roskilde Fjord, Denmark.

□ Fig. 1. Side view, ×115. □ Fig. 2. Edge view, ×101. □ Fig. 3. Detail of etched horisontal section showing bilamellar septum with septal flap, ×2565. □ Fig. 4. Detail of etched horisontal section at the level of a fossette showing secondary lamination on the sides of the interlocular space, ×1312. □ Fig. 5. Detail of plastic mould showing retral processes and fossettes, ×792. □ Fig. 6. Vertically sectioned plastic mould showing umbilical spiral canal system as well as vertical umbilical canals, ×382.

Figs. 7–12. *Elphidium gerthi* van Voorthuysen. Recent, Kattegat, Denmark.

□ Fig. 7. Side view, ×231. □ Fig. 8. Edge view, ×203. □ Fig. 9. Detail showing multiple aperture, ×997. □ Fig. 10. Ultimate suture showing ponticuli, fossettes and parafossettes, ×847. □ Fig. 11. Plastic mould showing umbilical spiral canal system, ×490. □ Fig. 12. Preparation of plastic mould in the area of the proloculus showing umbilical spiral canal system and vertical umbilical canals as well as retral processes, ×489.

Plate 6

Figs. 1–6. *Elphidium excavatum* (Terquem). Quaternary, Hirtshals, Denmark.

□ Fig. 1. Side view, ×156. □ Fig. 2. Edge view, ×164. □ Fig. 3. Detail of etched horisontal section showing bilamellar septum with septal flap, ×1420. □ Fig. 4. Plastic mould showing retral processes, ×178. □ Fig. 5. Detail of Fig. 4 showing contorted umbilical chamber parts, vertical umbilical canals as well as sites of sealing off plates, ×265. □ Fig. 6. Detail of preparation of plastic mould showing deep-seated umbilical spiral canal and foramina, ×351.

Figs. 7–12. *Elphidium groenlandicum* Cushman. Quaternary, Hirtshals, Denmark.

□ Fig. 7. Side view, ×62. □ Fig. 8. Edge view, ×63. □ Fig. 9. Detail of etched horisontal section at the level of a retral process showing septum, interlocular space, retral process and secondary lamination, ×866. □ Fig. 10. Detail of section shown in Fig. 9 at the side of a retral process showing bilamellar septum with septal flap and various layers, ×860. □ Figs. 11–12. Plastic mould showing the very delicate umbilical spiral canal system, vertical umbilical canals as well as communication from interlocular spaces into the umbilical spiral canal system. Fig. 11, ×153. Fig. 12, ×170.

Plate 7

Figs. 1–11. *Elphidium translucens* Natland. Recent, Rimini, Italy.

□ Fig. 1. Side view, ×113. □ Fig. 2. Edge view, ×96. □ Fig. 3. Ultimate suture demonstrating distinct but small ponticuli, ×515. □ Fig. 4. Detail of etched horisontal section at the level of a fossette showing bilamellar septum and configuration of various layers, ×72. □ Fig. 5. Detail of plastic mould showing small but distinct retral processes, ×519. □ Figs. 6–7. Plastic mould showing umbilical spiral canal system along with vertical umbilical canals. Note absence of sealing off plate in the final chamber. Fig. 6, ×279. Fig. 7, ×331. □ Figs. 8–11. Details of etched vertical section showing configuration of layers in the sealing off plate between the chamber lumen and the sealed off umbilical spiral canal. Fig. 8, ×813. Fig. 9, ×1644. Fig. 10, ×4077. Fig. 11, ×1634.

Fig. 12. *Elphidium vadescens* (Cushman & Brönnimann). Recent, Gulf of Paria, Trinidad. □ Side view, ×295.

Plate 8

Figs. 1–9. *Elphidium vadescens* (Cushman & Brönnimann). Recent, Gulf of Paria, Trinidad.

□ Fig. 1. Side view, ×292. □ Fig. 2. Edge view, ×314. □ Fig. 3. Apertural view showing veiling tuberculation and imperforate septal face, ×482. □ Fig. 4. Detail of fractured specimen showing multiple foramen, ×736. □ Fig. 5. Etched horisontal section showing position of the details in Figs. 6–7, ×234. □ Fig. 6. Detail showing bilamellar septum, interlocular space and secondary lamination, ×2132. □ Fig. 7. Detail of bilamellar septum with septal flap. Note that no interlocular space is developed at this early stage, ×1736. □ Figs. 8–9. Plastic moulds demonstrating retral processes as well as presence of an umbilical spiral canal system in spite of the rather poor state of the preparations. The moulds of the interlocular spaces have been lost but their communication sites with the umbilical canal are observed. Fig. 8, ×364. Fig. 9, ×885.

Figs. 10–12. *Elphidium guntheri* Cole. Eemian, Meetkerke, Belgium.

Fig. 10. Side view, ×140. □ Fig. 11. Edge view, ×239. □ Fig. 12. Edge view of specimen missing the final chamber showing multiple foramen and retral processes as well as presence of septal flap, ×134.

Plate 9

Figs. 1–3. *Elphidium guntheri* Cole. Eemian, Meetkerke, Belgium.

□ Fig. 1. Detail of opened specimen showing multiple aperture, ×351. □ Fig. 2. Plastic mould showing retral processes, ×630. □ Fig. 3. Detail of plastic mould showing umbilical spiral canal system as well as vertical umbilical canals, ×342.

Figs. 4–8. *Elphidium kugleri* (Cushman & Brönnimann). Recent, Gulf of Paria, Trinidad.

□ Fig. 4. Side view, ×180. □ Fig. 5. Edge view, ×166. □ Fig. 6. Detail of fractured specimen showing multiple foramen and retral processes, ×403. □ Fig. 7. Detail of etched horisontal section at the level of a retral process showing bilamellar septum and septal flap as well as interlocular space, ×2824. ☐ Fig. 8. Plastic mould showing umbilical spiral canal system, ×467.

Figs. 9–12. *Elphidium poeyanum* (d'Orbigny). Recent, off Florida.

☐ Fig. 9. Side view, ×106. ☐ Fig. 10. Edge view, ×83. ☐ Fig. 11. Detail showing aperture, ×292. ☐ Fig. 12. Fractured specimen showing foramen, ×736.

Plate 10

Figs. 1–5. *Elphidium poeyanum* (d'Orbigny). Recent, off Florida.

☐ Fig. 1. Ultimate suture showing small but distinct ponticuli, ×585. ☐ Fig. 2. Plastic mould details of which are shown in Figs. 3–5, ×110. ☐ Fig. 3. Detail showing retral processes and fossettes, ×712. ☐ Fig. 4. Detail showing connection from interlocular space into spiral canal, ×695. ☐ Fig. 5. Detail showing umbilical spiral canal system and vertical umbilical canals, ×696.

Figs. 6–12. *Elphidium bartletti* Cushman. Quaternary, Hirtshals, Denmark.

☐ Fig. 6. Side view, ×83. ☐ Fig. 7, Edge view, ×77. ☐ Fig. 8. Detail showing apertural region, ×247. ☐ Fig. 9. Detail of fractured specimen showing aperture, ×470. ☐ Fig. 10. Edge view of specimen missing final chamber showing foramen as well as septal flap smoothing former pustulose apertural face, ×1012. ☐ Fig. 11. Detail of ultimate suture showing fossettes and ponticuli along with pustules on the lateral chamber wall of penultimate chamber, ×614. ☐ Fig. 12. Plastic mould showing retral processes, plate-like elements of the umbilical spiral canal system. Note fracture in the final chamber being an artefact, ×170.

Plate 11

Figs. 1–7. *Elphidium hallandense* Brotzen. Quaternary, Hirtshals, Denmark.

☐ Fig. 1. Side view, ×103. ☐ Fig. 2. Side view of specimen with distinct fossettes, ×66. ☐ Fig. 3. Edge view, ×92. ☐ Fig. 4. Detail of fractured specimen showing aperture, ×420. ☐ Fig. 5. Detail of fractured specimen showing foramina and retral processes, ×234. ☐ Fig. 6. Detail of etched horisontal section showing irregular boundary between bilamellar septum and the partly developed septal flap, ×854. ☐ Fig. 7. Plastic mould showing retral processes, umbilical spiral canal system as well as vertical umbilical canals. Note absence of sealing off plate in the final chamber as well as continuity of interlocular spaces with the umbilical spiral canal, ×216.

Figs. 8–13. *Elphidium oregonense* Cushman & Grant. Quaternary, North Sea basin.

☐ Fig. 8. Side view. Complete specimen, ×28. ☐ Fig. 9. Side view. Specimen lacking final chamber, ×41. ☐ Fig. 10. Edge view. Specimen lacking final chamber, ×25. ☐ Fig. 11. Edge view of specimen lacking half a coil, ×31. ☐ Fig. 12. Detail of fractured specimen showing foramen and apparent agglutinated surface layer, ×672. ☐ Fig. 13. Plastic mould showing retral processes, umbilical spiral canal system and its communication with the interlocular spaces. Note vertical umbilical canals, ×102.

Plate 12

Figs. 1–4. *Elphidium tuberculatum* (d'Orbigny). Miocene, Marienhof, Germany.

☐ Fig. 1. Side view, ×126. ☐ Fig. 2. Edge view of specimen showing aperture and foramen, ×342. ☐ Fig. 3. Plastic mould showing absence of retral processes, ×83. ☐ Fig. 4. Detail of Fig. 3 showing fractured parts of the umbilical spiral canal system, ×176.

Figs. 5–9. *Elphidium incertum* (Williamson). Recent, Kattegat, Denmark.

☐ Fig. 5. Side view, ×85. ☐ Fig. 6. Edge view, ×75. ☐ Fig. 7. Detail of opened specimen showing aperture and foramina, ×366. ☐ Fig. 8. Detail of plastic mould showing small but distinct retral processes, ×365. ☐ Fig. 9. Detail of plastic mould showing umbilical spiral canal system as well as the communication from the interlocular spaces into the spiral canal, ×354.

Figs. 10–12. *Elphidium asklundi* Brotzen. Quaternary, Hirtshals, Denmark.

☐ Fig. 10. Side view, ×59. ☐ Fig. 11. Edge view, ×62. ☐ Fig. 12. Detail of etched horisontal section showing attachment of bilamellar septum to previous coil. Note the septal flap, ×1083.

Plate 13

Fig. 1. *Elphidium asklundi* Brotzen. Quaternary, Hirtshals, Denmark. ☐ Plastic mould showing umbilical spiral canal system slightly veiled by pore tubules, ×167.

Figs. 2–6. *Elphidium magellanicum* Heron-Allen & Earland. Recent, Kattegat, Denmark.

☐ Fig. 2. Side view, ×137. ☐ Fig. 3. Edge view, ×153. ☐ Fig. 4. Detail of etched horisontal section showing bilamellar septum and septal flap. Note irregular boundary with septal flap due to tuberculation on the former apertural face, ×3570. ☐ Fig. 5. Detail of plastic mould showing rather small retral processes, ×755. ☐ Fig. 6. Detail of plastic mould showing umbilical spiral canal system and its communication with the interlocular spaces. Note absence of sealing off plate in the final chamber, ×303.

Figs. 7–12. *Elphidium ustulatum* Todd. Quaternary, Lundergaard, Denmark.

☐ Fig. 7. Side view, ×175. ☐ Fig. 8. Edge view, ×117. ☐ Fig. 9. Detail of embedded and opened specimen showing aperture viewed from the inside. Apertural openings filled with embedding material, ×738. ☐ Fig. 10. Plastic mould showing long openings from the interlocular space to the outside (fossette?), ×136. ☐ Fig. 11. Detail of plastic mould showing umbilical spiral canal system. Note absence of sealing off plate in the final chamber, ×769. ☐ Fig. 12. Plastic mould of specimen sectioned tangentially in the umbilical region showing communication from the umbilical canal into the deep-seated interlocular spaces, ×295.

Plate 14

Figs. 1–6. *Elphidium albiumbilicatum* (Weiss). Quaternary, Hirtshals, Denmark.

☐ Fig. 1. Side view, ×107. ☐ Fig. 2. Edge view, ×97. ☐ Fig. 3. Detail of opened specimen showing aperture, ×278. ☐ Fig. 4. Detail of etched horisontal section showing bilamellar septum and septal flap, ×3340. ☐ Fig. ·5. Detail of plastic mould showing absence of retral processes, ×200. ☐ Fig. 6. Detail of plastic mould showing umbilical spiral canal system, ×435.

Figs. 7–12. *Elphidiella arctica* (Parker & Jones). Recent, off West Greenland.

☐ Fig. 7. Side view, ×47. ☐ Fig. 8. Edge view, ×47. ☐ Fig. 9. Detail of suture showing grooves connected with canals leading into the subsutural canal, ×139. ☐ Fig. 10. Detail of suture with smooth band between the canals leading into the subsutural canal, ×332. □ Fig. 11. Detail of opened specimen showing aperture. Note the partial subdivision, ×171. □ Fig. 12. Detail of opened specimen showing foramen, ×81.

Plate 15

Figs. 1–7. *Elphidiella arctica* (Parker & Jones). Recent, off West Greenland.

□ Fig. 1. Etched horisontal section, ×52. □ Fig. 2. Detail of section (Fig. 1) showing bilamellar wall of final chamber, ×894. □ Fig. 3. Detail of section (Fig. 1) showing bilamellar septum and septal flap, ×915. □ Fig. 4. Detail of section (Fig. 1) showing ultimate suture with doubled inner lining in the region of the subsutural canal, ×906. □ Fig. 5. Detail of plastic mould showing lack of retral processes, ×224. □ Fig. 6. Detail of plastic mould showing subsutural canal and arrangement of canals leading to the shell surface, ×566. □ Fig. 7. Detail of plastic mould showing umbilical spiral canal system, vertical umbilical canals as well as communication from the subsutural canals into the spiral canal. Note absence of sealing off plate in the final chamber, ×92.

Figs. 8–12. *Elphidiella sibirica* (Goës). Quaternary, Alaska.

□ Fig. 8. Side view, ×38. □ Fig. 9. Detail of Fig. 11 showing doubled inner lining, ×3614. □ Fig. 10. Edge view. Opened specimen showing foramen, ×17. □ Fig. 11. Detail of etched horisontal section showing final suture, ×708. □ Fig. 12. Composite picture. Detail of Fig. 10. Note the configuration of the various layers, ×1448.

Plate 16

Figs. 1–4. *Elphidiella sibirica* (Goës). Quaternary, Alaska.

□ Fig. 1. Side view. Note double row of openings leading into the subsutural canals, ×14. □ Fig. 2. Detail of plastic mould showing retral processes, ×221. □ Fig. 3. Detail of plastic mould showing subsutural canal and position of canals to the exterior, ×151. □ Fig. 4. Detail of plastic mould showing umbilical spiral canal system as well as vertical umbilical canals. Note the foramina, ×110.

Figs. 5–10. *Elphidiella hannai* (Cushman & Grant). Quaternary, Antwerp, Belgium.

□ Fig. 5. Side view, ×74. □ Fig. 6. Edge view, ×102. □ Fig. 7. Detail of etched horisontal section in the sutural region showing bilamellar septum and septal flap as well as doubling of inner lining around the subsutural canal, ×1570. □ Fig. 8. Detail of plastic mould showing subsutural canal and associated canals, ×923. □ Fig. 9. Detail of plastic mould showing umbilical spiral canal system and vertical umbilical canals, ×251. □ Fig. 10. Detail of plastic mould showing final chamber and the absence of a sealing off plate, ×414.

Figs. 11–12. *Elphidiella prima* (ten Dam). Danian, Copenhagen, Denmark.

□ Fig. 11. Side view, ×92. □ Fig. 12. Edge view, ×98.

Plate 17

Figs. 1–3. *Elphidiella prima* (ten Dam). Danian, Copenhagen, Denmark.

□ Fig. 1. Fractured specimen showing foramen, ×143. □ Fig. 2. Detail of etched tangential vertical section showing traces of lamination in the sutural region, ×1274. □ Fig. 3. Plastic mould showing umbilical spiral canal system, vertical umbilical canals as well as communication with the subsutural canals. Note configuration of canals from the subsutural canal to the shell exterior as well as absence of sealing off plate in the final chamber, ×109.

Figs. 4–10. *Elphidiella heteropora* (Egger). Miocene, Marienhof, Germany.

□ Fig. 4. Side view, ×150. □ Fig. 5. Edge view, ×166. □ Fig. 6. Detail of opened specimen showing aperture and so-called apertural chamberlet, ×451. □ Fig. 7. Detail of opened specimen showing foramen and absence of apertural chamberlet, ×684. □ Fig. 8. Detail of etched horisontal section in the sutural region showing bilamellar septum and septal flap, ×1350. □ Fig. 9. Detail of plastic mould showing subsutural canal and arrangement of canals to the shell surface, ×393. □ Fig. 10. Detail of plastic mould showing part of the umbilical spiral canal system, ×455.

Figs. 11–12. *Elphidiella subnodosa* (Münster). Oligocene, Sophienlund, Denmark.

□ Fig. 11. Side view, ×62. □ Fig. 12. Edge view, ×77.

Plate 18

Figs. 1–3. *Elphidiella subnodosa* (Münster). Oligocene, Sophienlund, Denmark.

□ Fig. 1. Detail of apertural area showing dense tuberculation, ×252. □ Fig. 2. Detail of etched horisontal section showing bilamellar septum and configuration of layers in the region of the subsutural canal, ×730. □ Fig. 3. Plastic mould showing umbilical spiral canal system as well as vertical umbilical canals. Note absence of sealing off plate in the final chamber, ×143.

Figs. 4–12. *Notorotalia zelandica* Finlay. Recent, off New Zealand.

□ Fig. 4. Fig. 4. Side view. Umbilical side, ×62. □ Fig. 5. Edge view, ×61. □ Fig. 6. Side view. Spiral side, ×104. □ Fig. 7. View of margin showing elevated rims around the exits of the canals in the sutures leading into the subsutural canals, ×121. □ Fig. 8. Edge view of fractured specimen showing foramen, ×112. □ Figs. 9–10. Details of etched vertical section showing bilamellar septa, septal flap and doubling of inner lining around subsutural canals. Fig. 9, ×1687. Fig. 10, ×1687. □ Fig. 11. Plastic mould showing umbilical side with retral processes, umbilical spiral canal system, ×68. □ Fig. 12. Detail of plastic mould (spiral side) showing subsutural canal and the canals connecting it to the shell surface. Note one example of a bifurcating canal, ×405.

Plate 19

Figs. 1–2. *Notorotalia zelandica* Finlay. Recent, off New Zealand.

□ Fig. 1. Detail of plastic mould (spiral side) showing subsutural canal in the spiral suture, ×348. □ Fig. 2. Detail of etched out vertical section showing umbilical spiral canal system made of plate-like umbilical chamber parts, ×142.

Figs. 3–6. *Nonion depressulum* (Walker & Jacob). Recent, Kattegat, Denmark.

□ Fig. 3. Side view, ×218. □ Fig. 4. Edge view, ×265. □ Fig. 5. Detail of opened specimen showing aperture, ×710. □ Fig. 6. Detail of etched horisontal section showing bilamellar septum as well as partly developed septal flap, ×4500.

Figs. 7–12. *Nonion germanicum* (Ehrenberg). Recent, Kattegat, Denmark.

□ Fig. 7. Side view, ×128. □ Fig. 8. Edge view, ×137. □ Fig. 9. Detail of opened specimen showing aperture, ×280. □ Fig. 10.

Detail showing tuberculate sutures, ×298. ☐ Fig. 11. Detail of etched horisontal section showing bilamellar septum and septal flap, ×632. ☐ Fig. 12. Plastic mould demonstrating the absence of umbilical spiral canal system, ×144.

Plate 20

Figs. 1–4. *Nonion graniferum* (Terquem). Danian, Nugssuaq, West Greenland.

☐ Fig. 1. Side view, ×200. ☐ Fig. 2. Edge view, ×220. ☐ Fig. 3. Detail of etched horisontal section showing bilamellar septum and septal flap, ×3737. ☐ Fig. 4. Detail of plastic mould showing absence of umbilical spiral canal system. The umbilical chamber parts are overlapping the umbilical tuberculation, ×443.

Figs. 5–9. *Nonion hofkeri* (Haynes). Thanetian, Reculver, England.

☐ Fig. 5. Side view, ×270. ☐ Fig. 6. Edge view, ×245. ☐ Fig. 7. Detail of opened specimen showing foramen, ×816. ☐ Fig. 8. Detail of plastic mould demonstrating absence of umbilical spiral canal system, ×704. ☐ Fig. 9. Detail of cast of the specimen shown in Fig. 8 demonstrating that all communications in the umbilical region takes place between the tubercles, ×590.

Figs. 10–13. *Nonion orbiculare* (Brady). Quaternary, Hirtshals, Denmark.

☐ Fig. 10. Side view, ×79. ☐ Fig. 11. Edge view, ×65. ☐ Fig. 12. Detail of opened specimen showing aperture and foramen, ×329. ☐ Fig. 13. Detail of etched horisontal section showing bilamellar septum and septal flap, ×1000.

Plate 21

Fig. 1. *Nonion orbiculare* (Brady). Quaternary, Hirtshals, Denmark. ☐ Plastic mould showing very small and indistinct retral processes, ×164.

Figs. 2–4. *Nonion boueanum* (d'Orbigny). Pliocene, France.

☐ Fig. 2. Side view, ×71. ☐ Fig. 3. Edge view, ×60. ☐ Fig. 4. Detail of etched horisontal section, showing the junction between the ultimate and penultimate chamber demonstrating bilamellar wall and a partial covering of the septal face by the inner lining of the ultimate chamber, ×1912.

Figs. 5–8. *Nonion labradoricum* (Dawson). Recent, off East Greenland.

☐ Fig. 5. Side view, ×157. ☐ Fig. 6. Edge view, ×131. ☐ Fig. 7. Etched horisontal section, ×136. ☐ Fig. 8. Detail of Fig. 7, showing bilamellar final chamber, ×2014.

Figs. 9–12. Nonionella atlantica Cushman. Recent, off Brazil.

☐ Fig. 9. Side view. Spiral side, ×130. ☐ Fig. 10. Side view. Umbilical side, ×81. ☐ Fig. 11. Edge view, ×105. ☐ Fig. 12. Detail of etched horisontal section showing bilamellar septum as septal flap, ×1350.

Plate 22

Figs. 1–4. *Pullenia bulloides* (d'Orbigny). Miocene, Soos, Baden.

☐ Fig. 1. Oblique side view, ×153. ☐ Fig. 2. Apertural view, ×145. ☐ Fig. 3. Etched horisontal section, ×130. ☐ Fig. 4. Detail of Fig. 3, showing bilamellar septum as well as septal flap. Note median layer with irregular larger crystals, ×890.

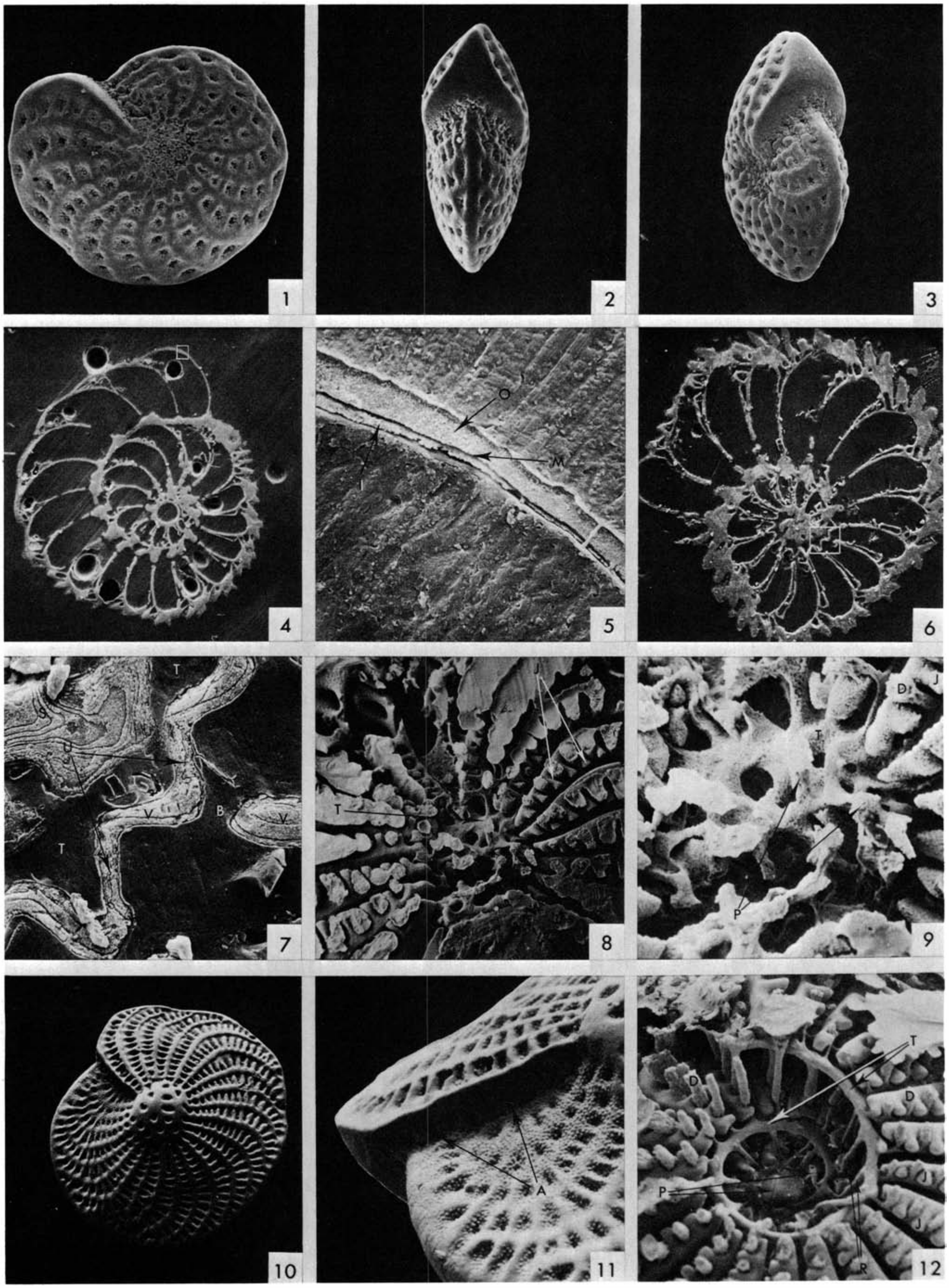
Figs. 5–9. *Astrononion gallowayi* Loeblich & Tappan. Quaternary, Hirtshals, Denmark.

☐ Fig. 5. Side view, ×150. ☐ Fig. 6. Edge view, ×175. ☐ Fig. 7. Detail of etched vertical tangential section showing bilamellar septum and depressed suture covered by secondary lamination, ×804. ☐ Fig. 8. Plastic mould showing umbilical spiral canal system. Note absence of sealing off plate in the final chamber, ×194. ☐ Fig. 9. Detail of etched tangential horisontal section showing configuration in the umbilical spiral canal area, ×255.

Figs. 10–13. *Melonis pompilioides* (Fichtel & Moll). Recent, off Banyuls, France.

☐ Fig. 10. Side view, ×130. ☐ Fig. 11. Apertural view, ×118. ☐ Figs. 12–13. Details of etched horisontal section showing bilamellar septum and septal flap. Fig. 12, ×598. Fig. 13, ×1373.

Plates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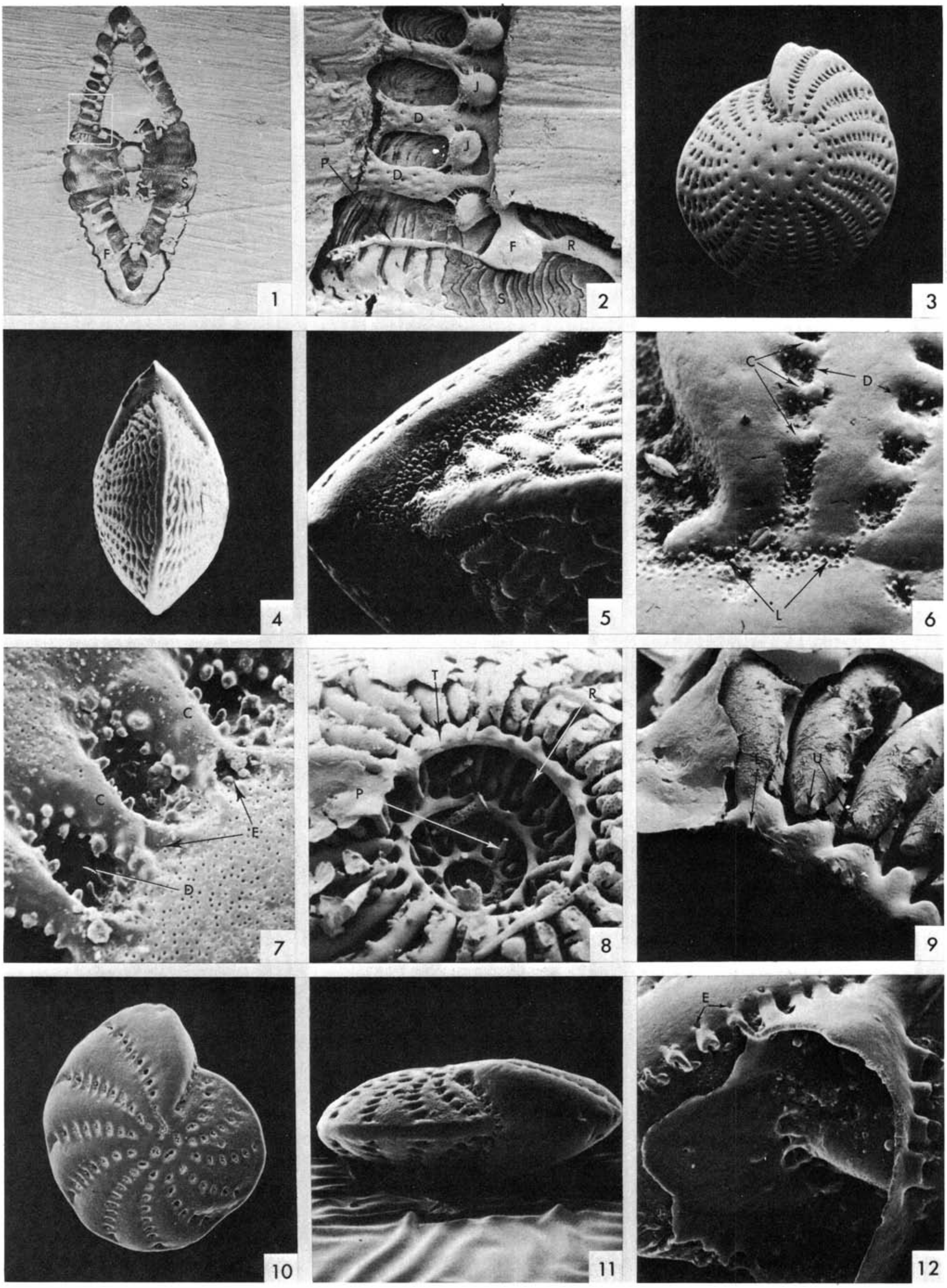
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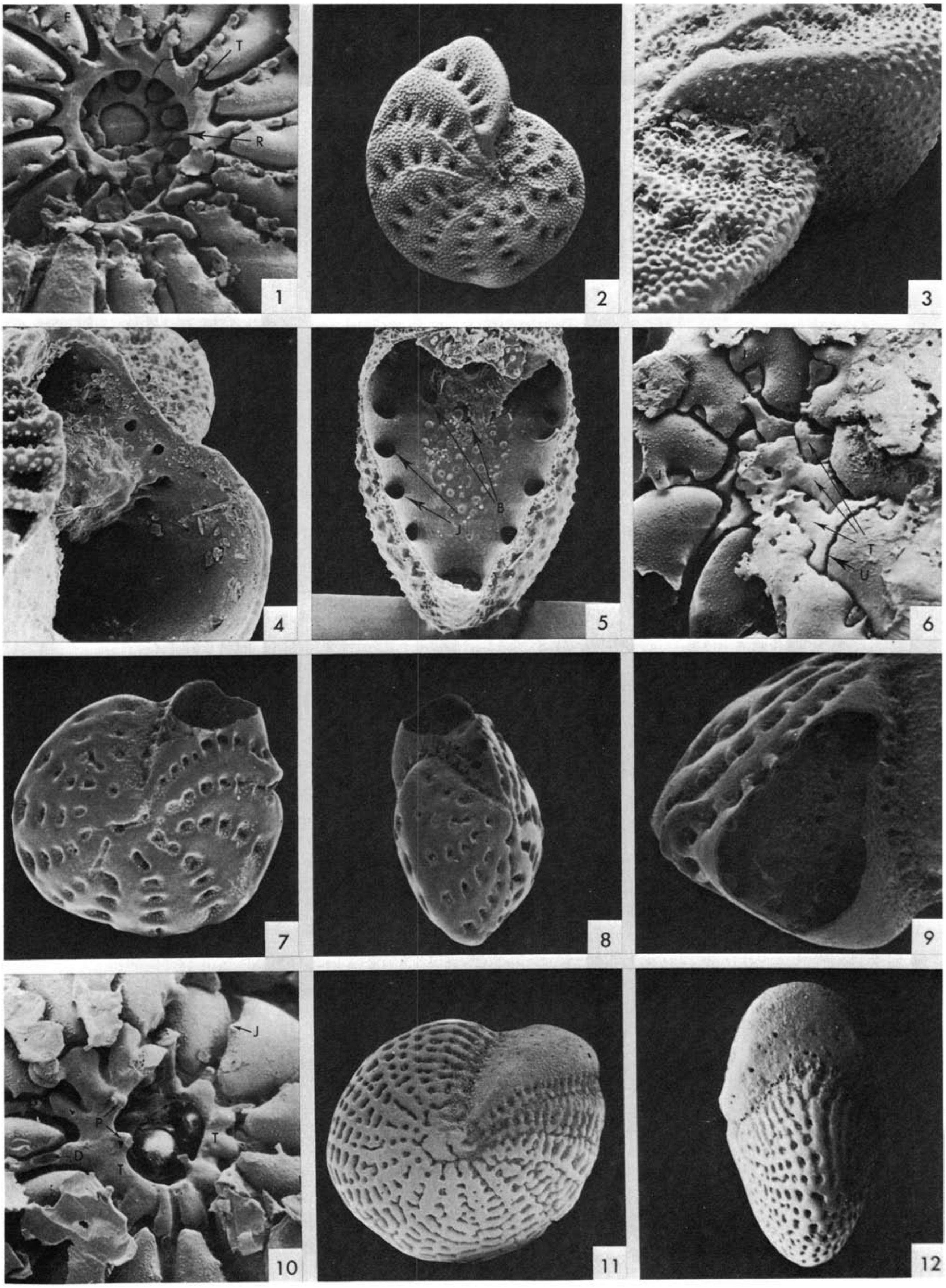
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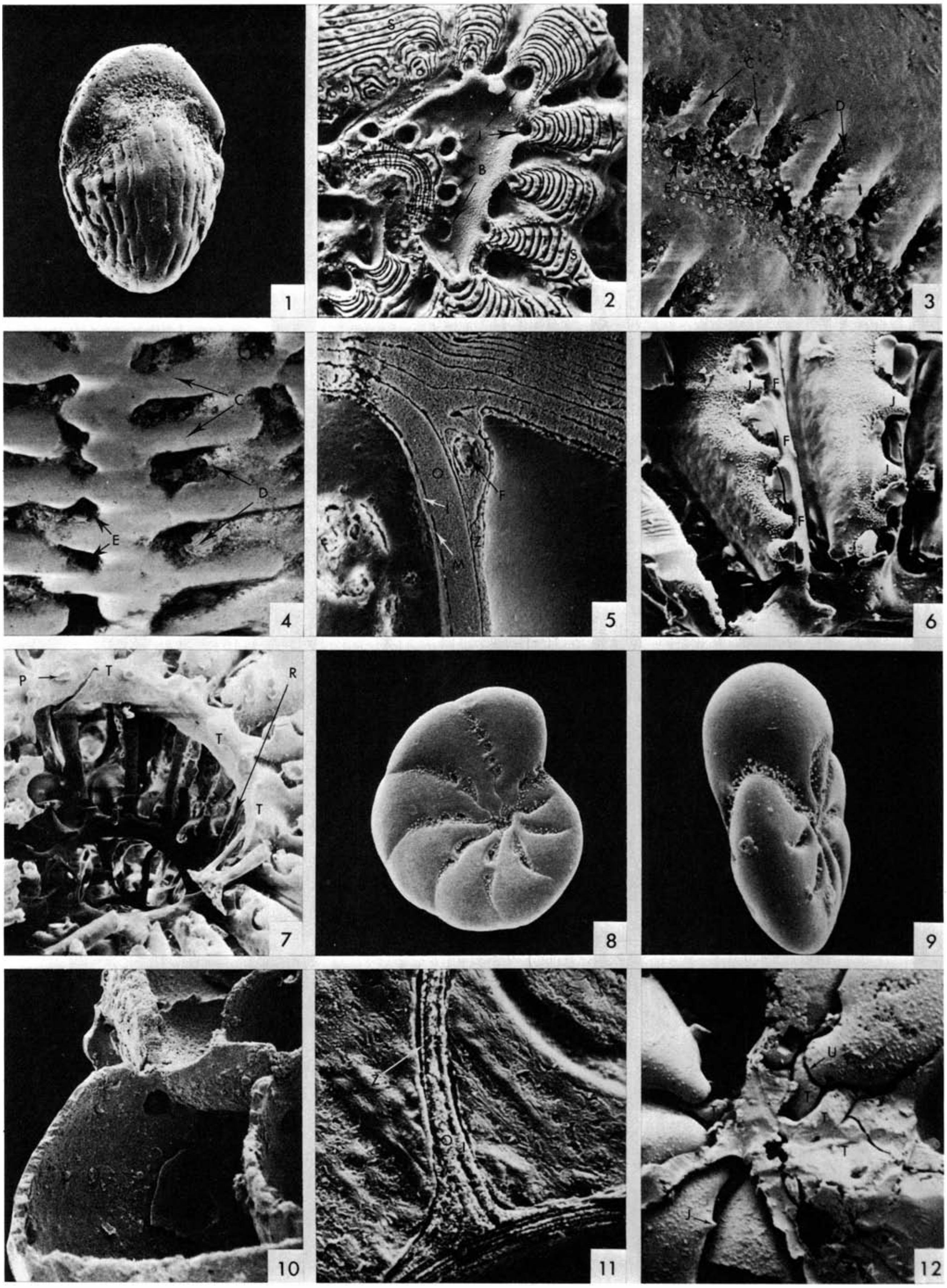
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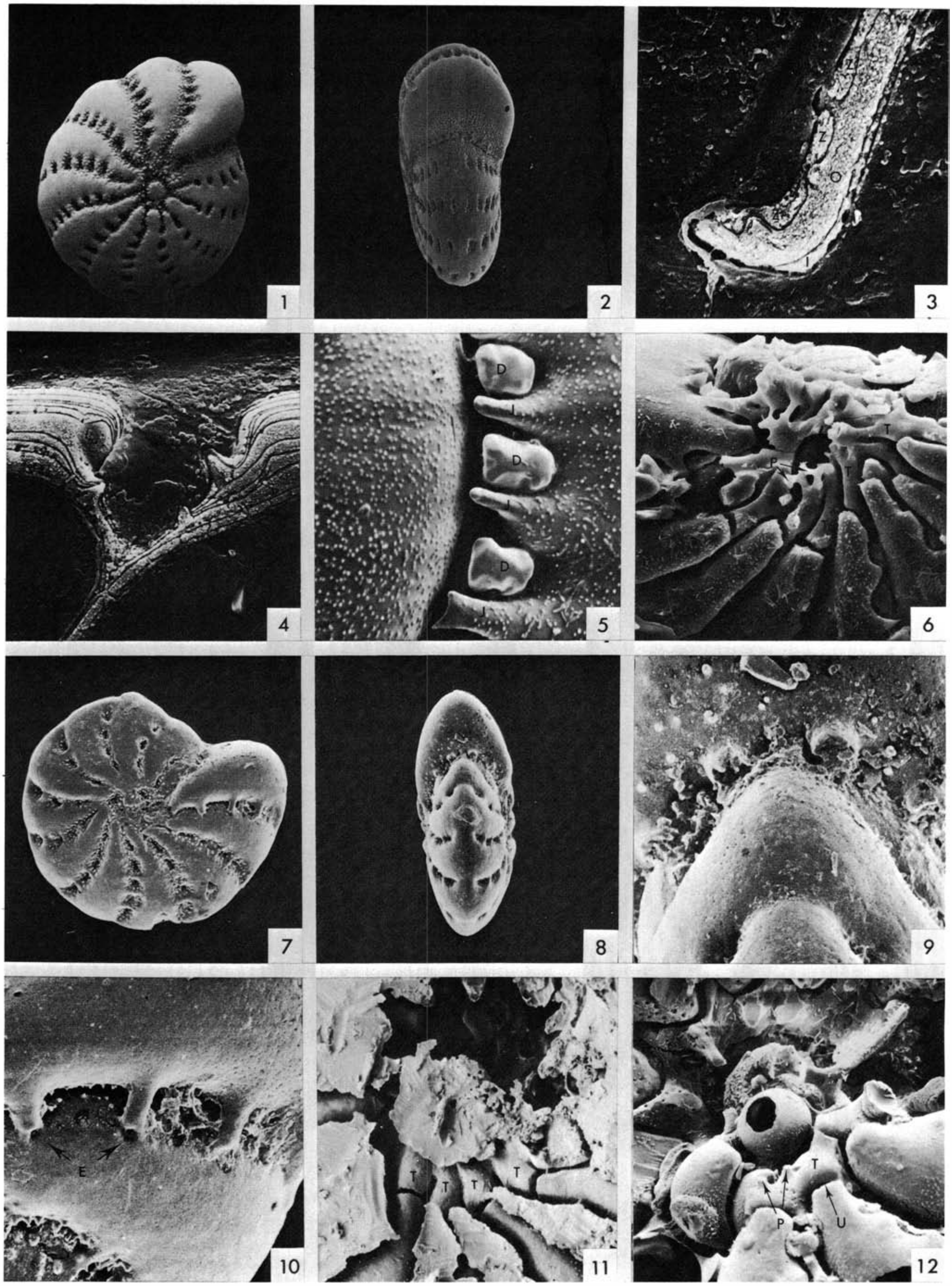
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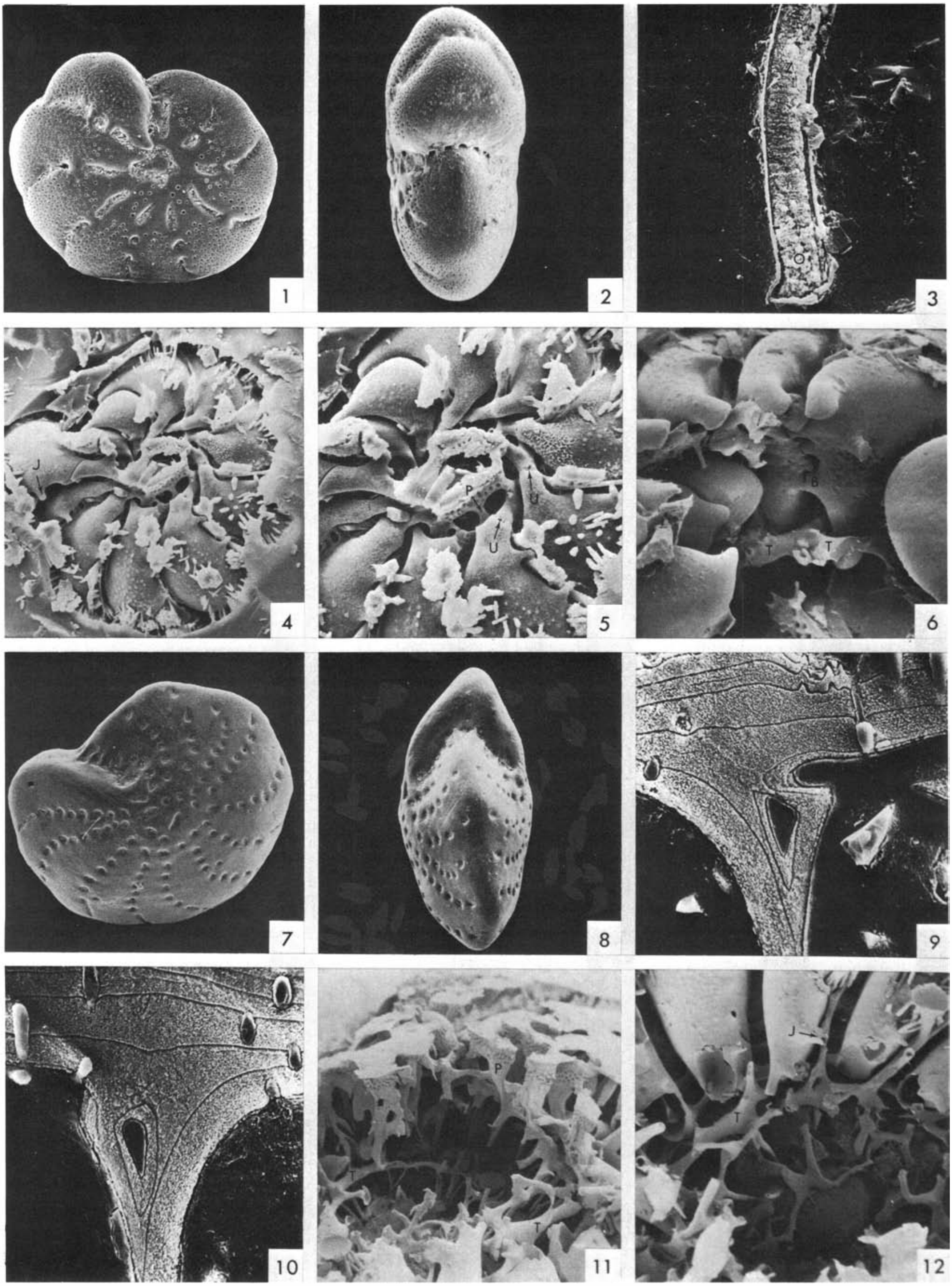
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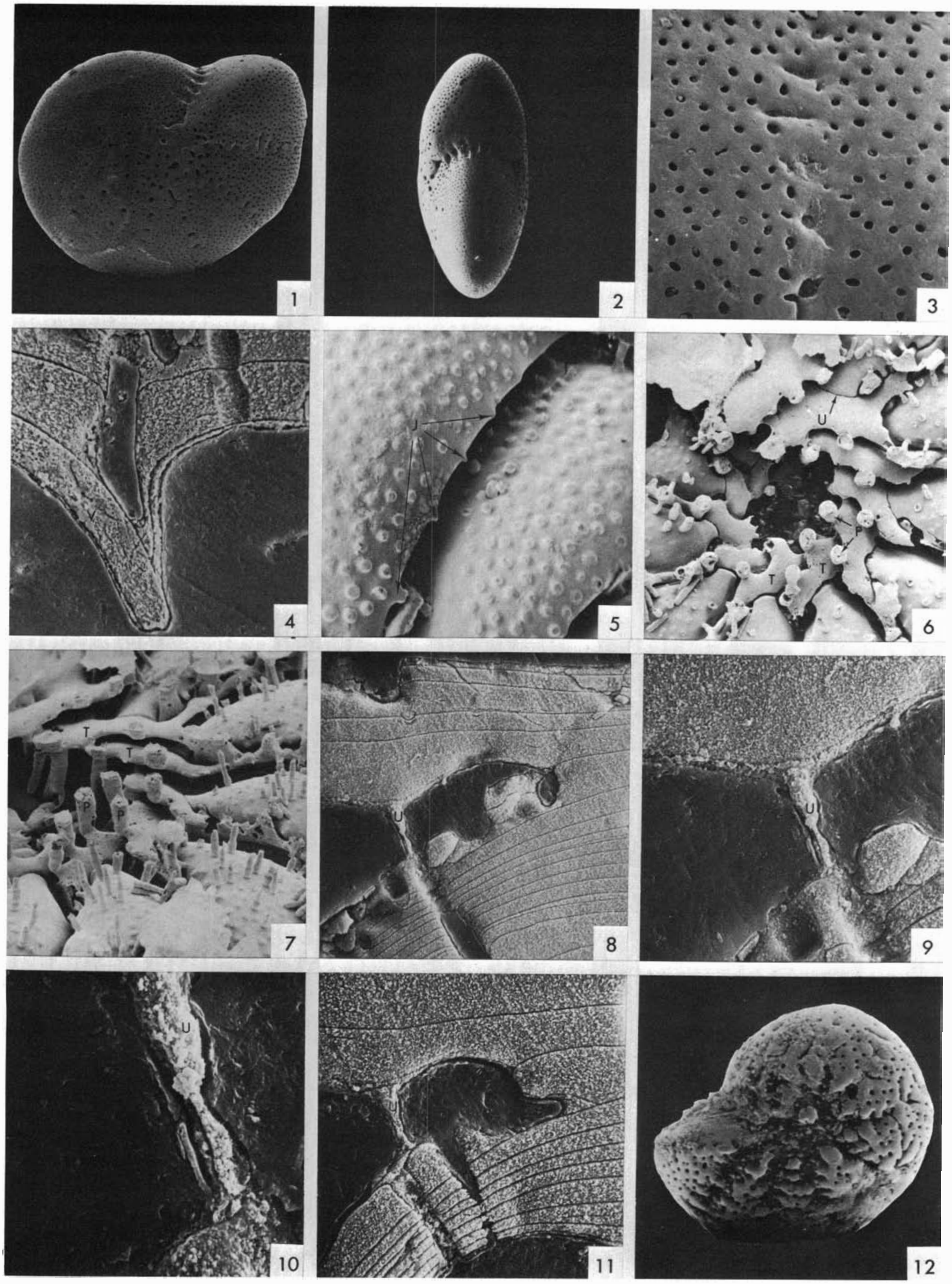
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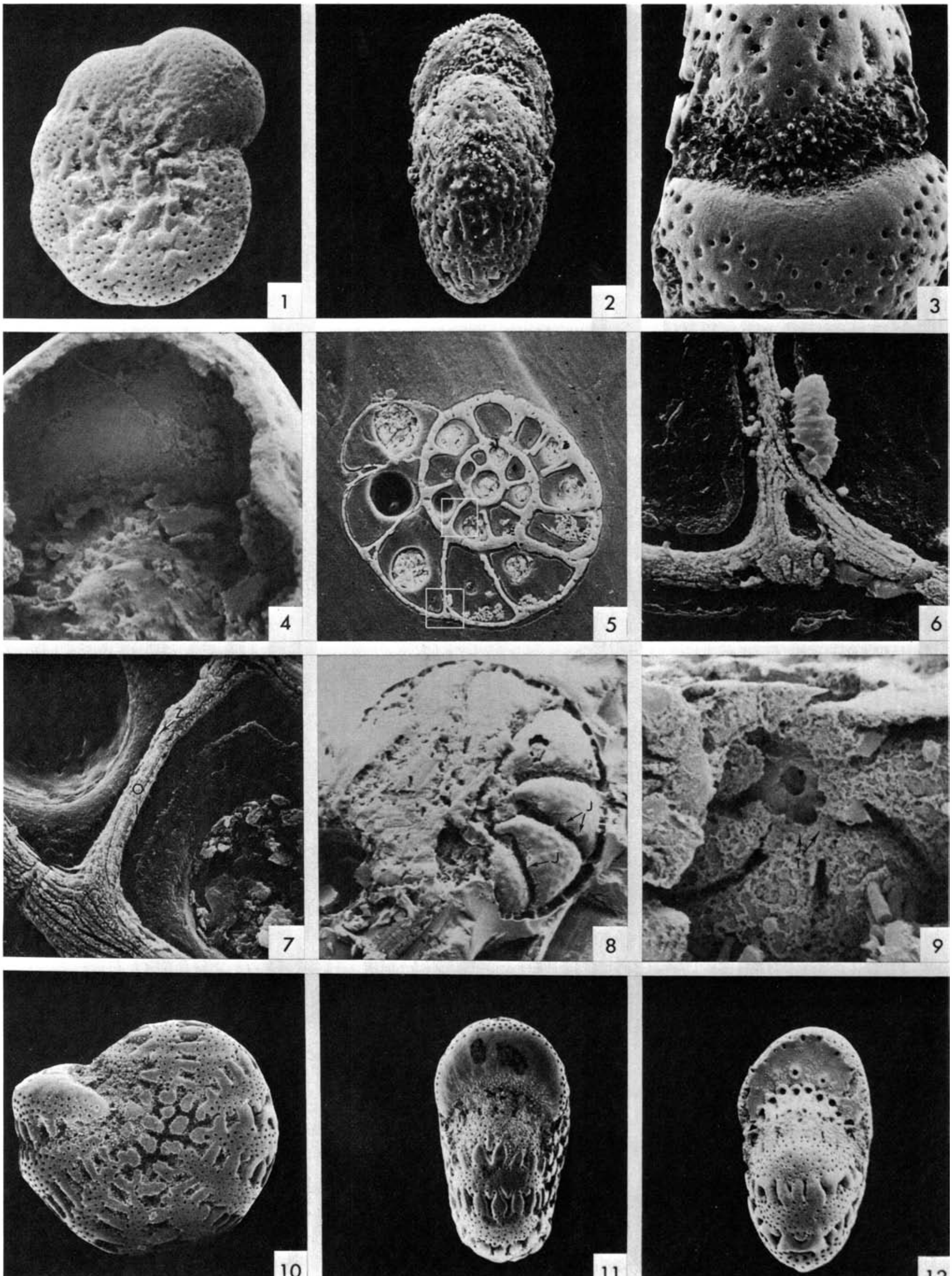
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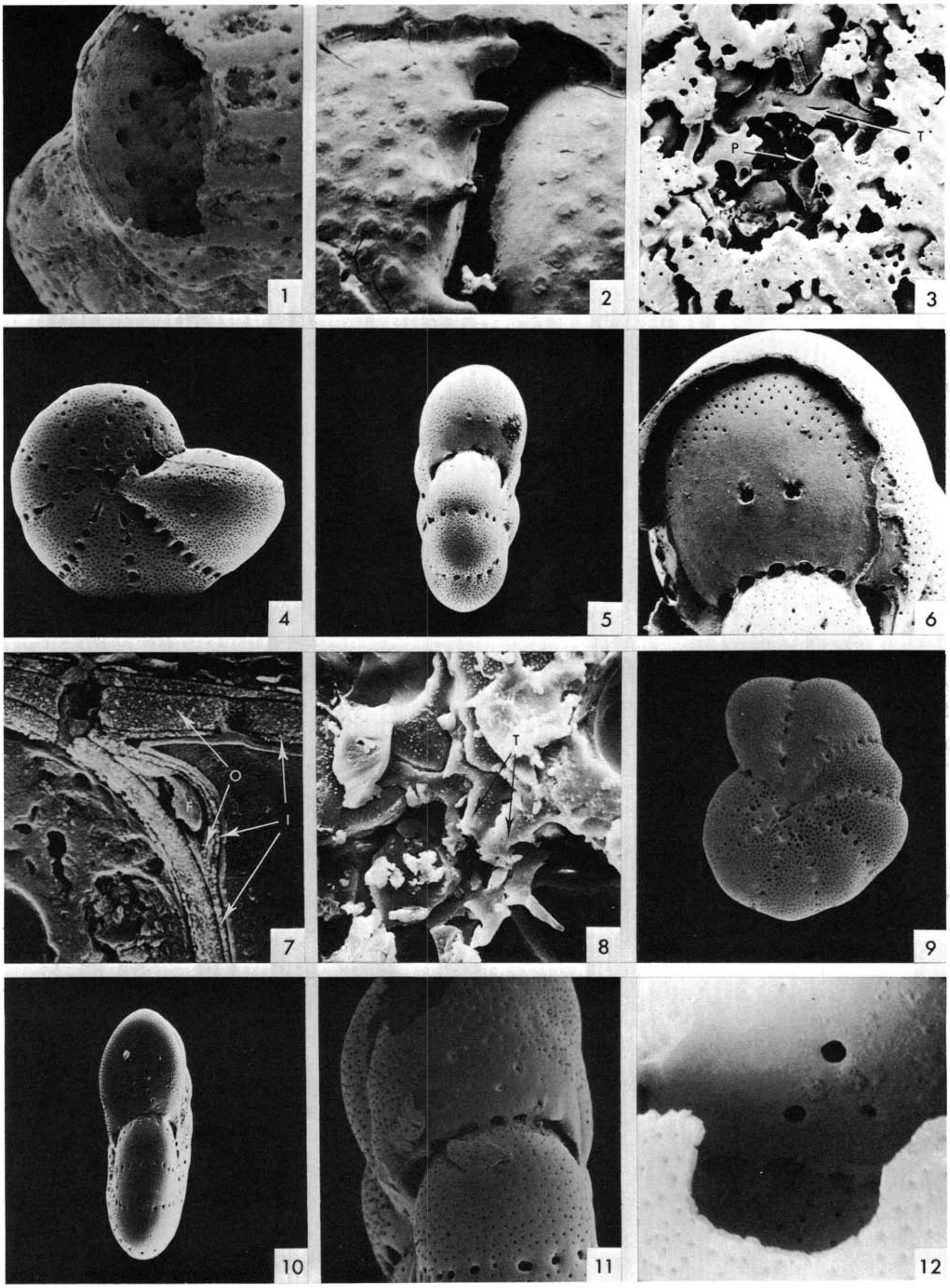
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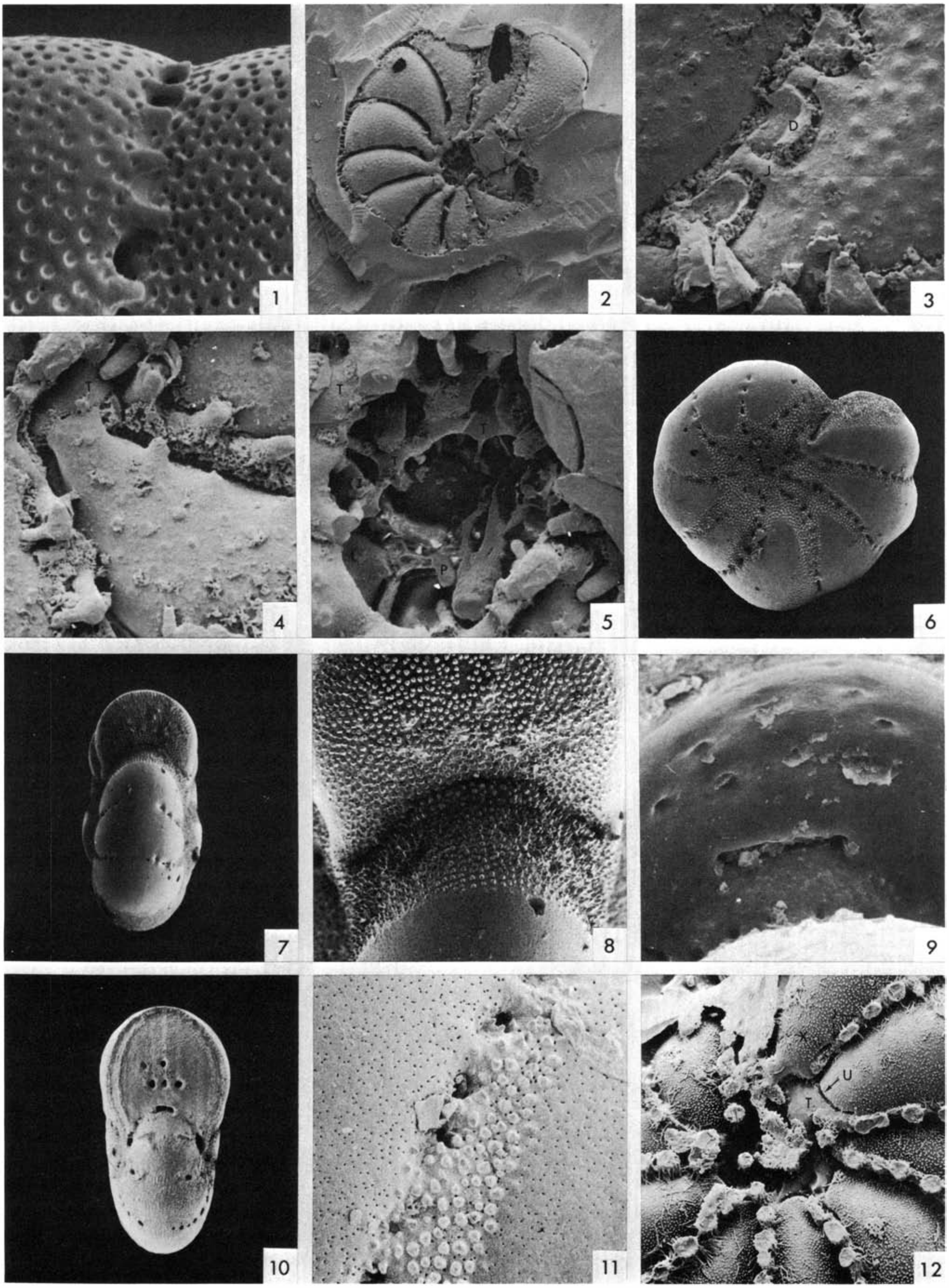
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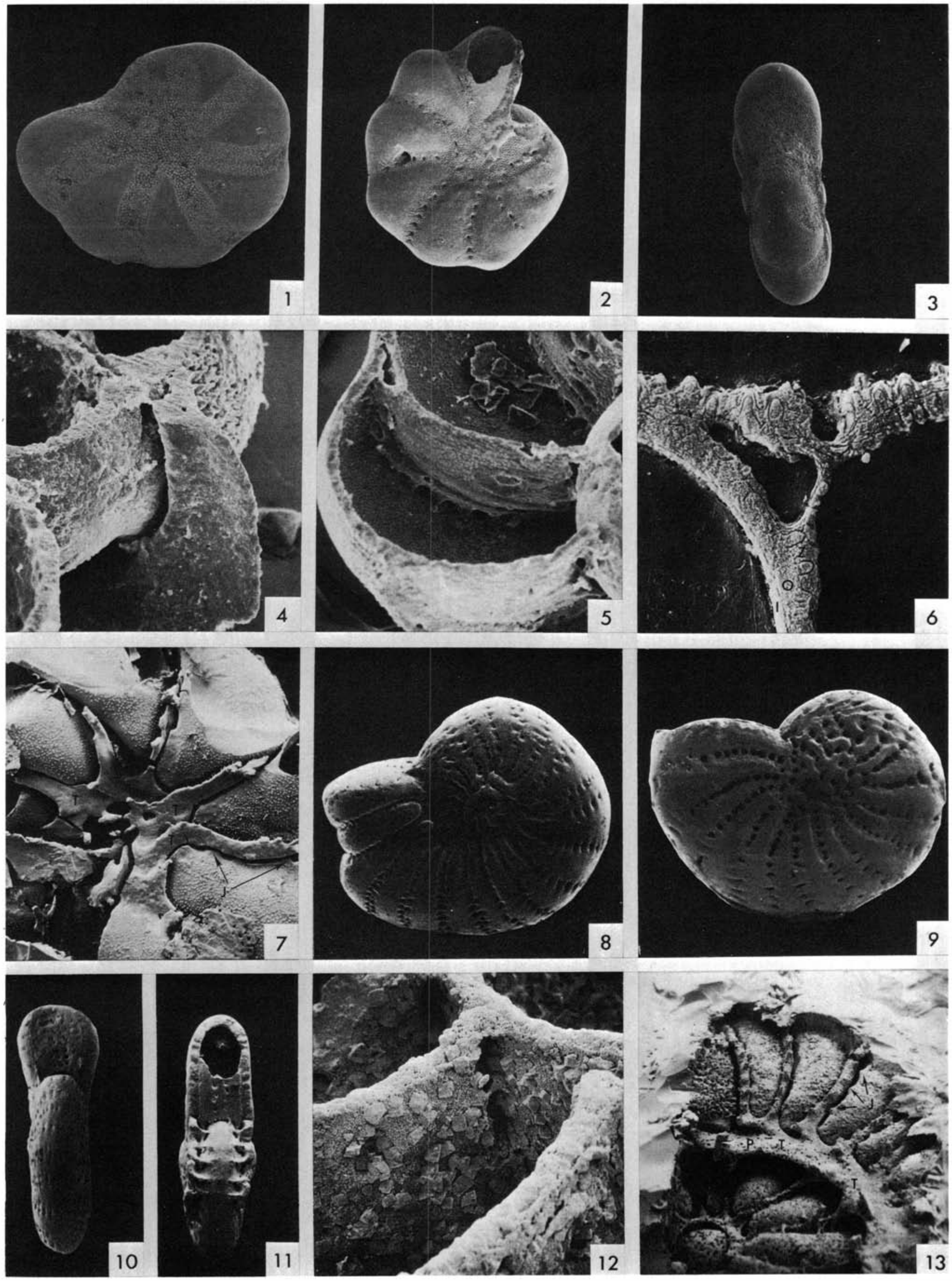
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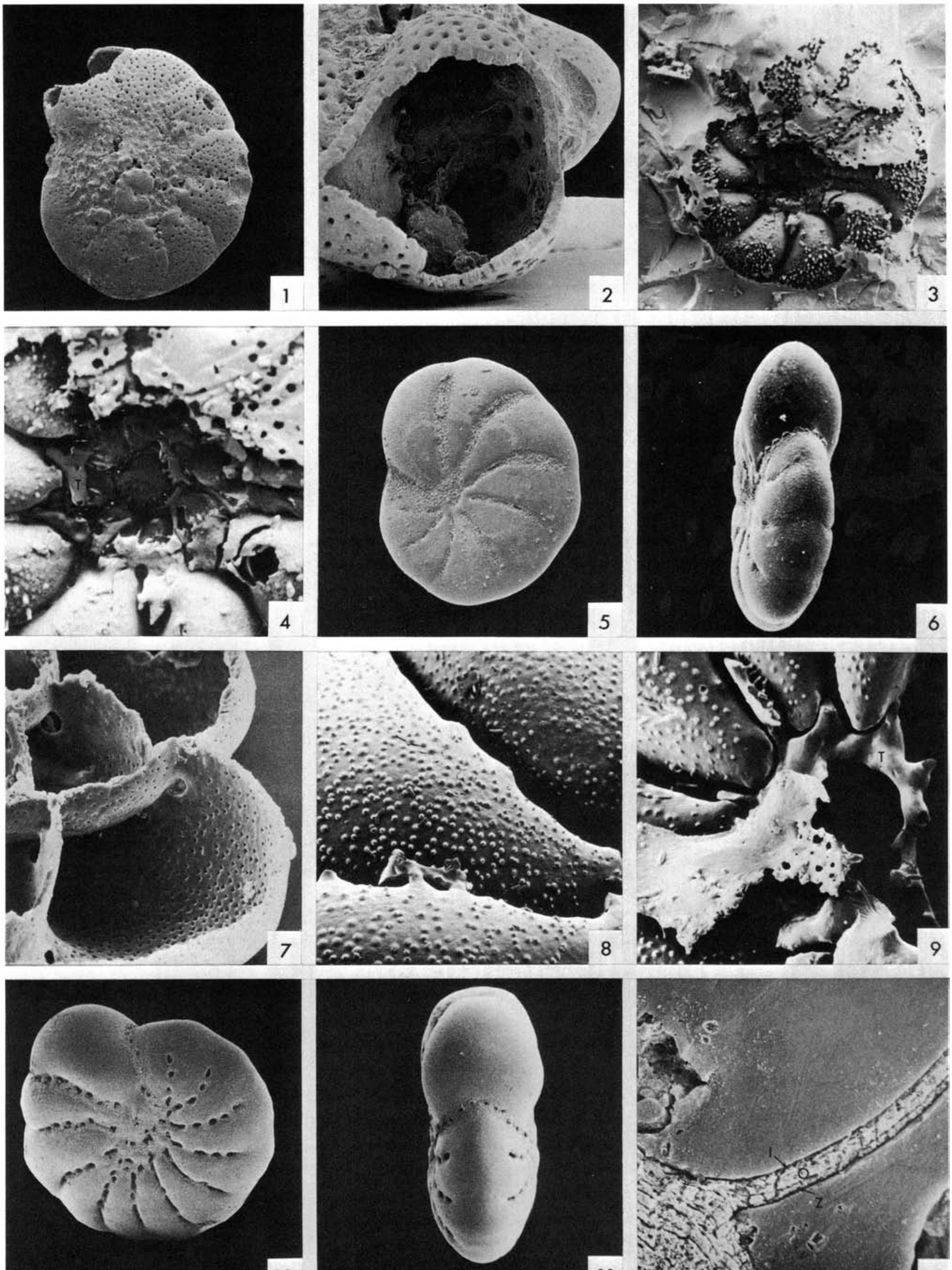
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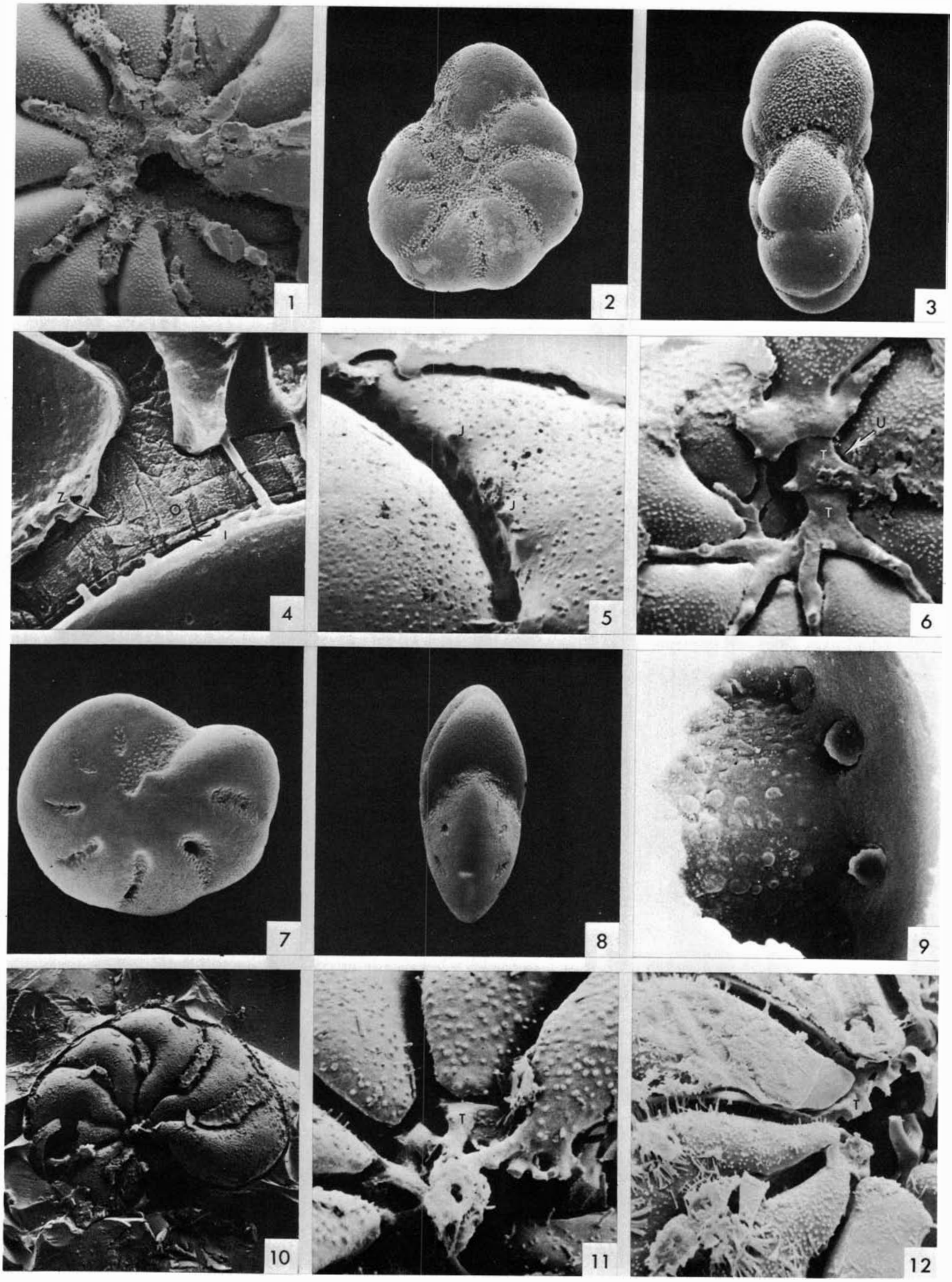
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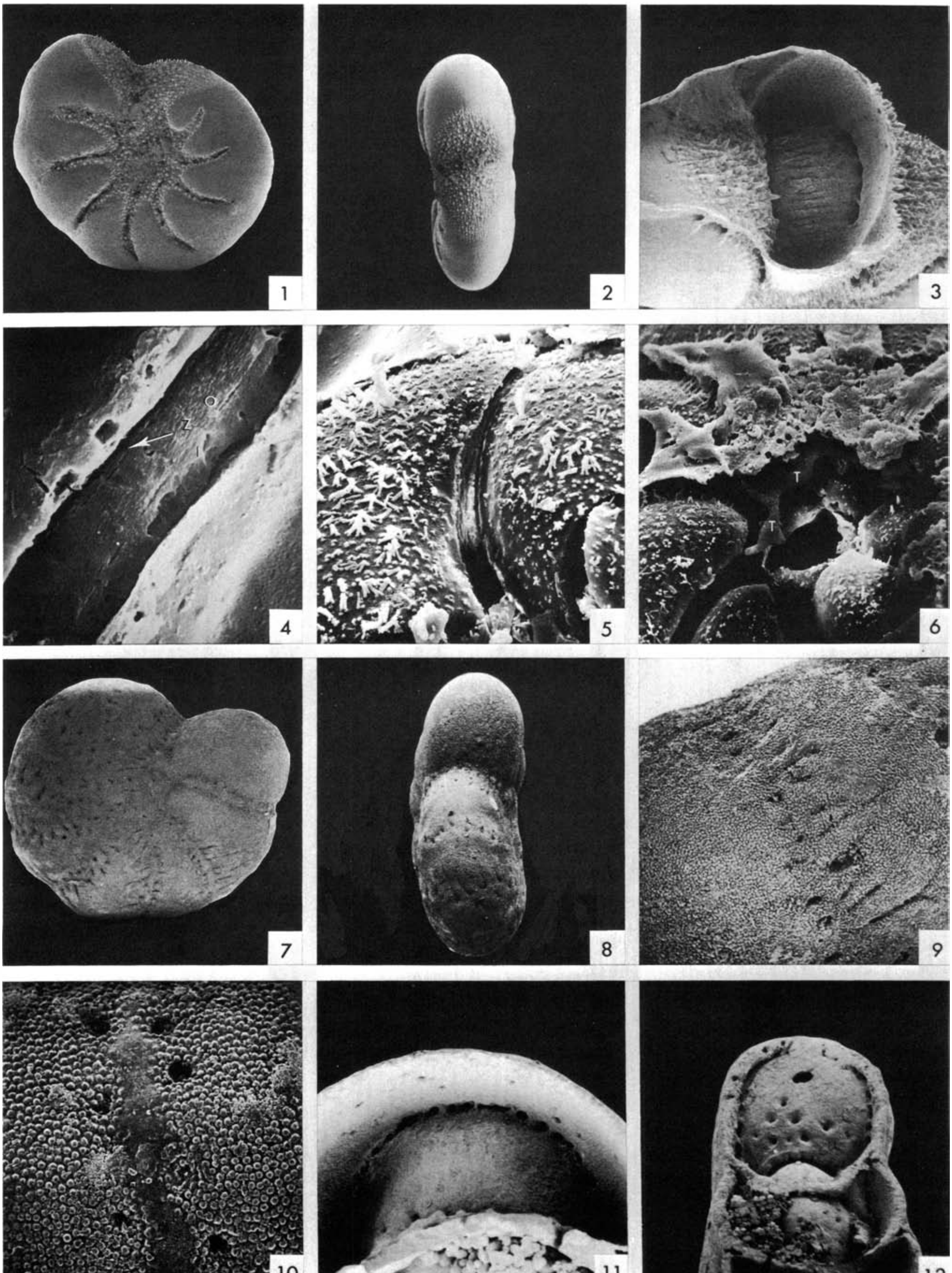
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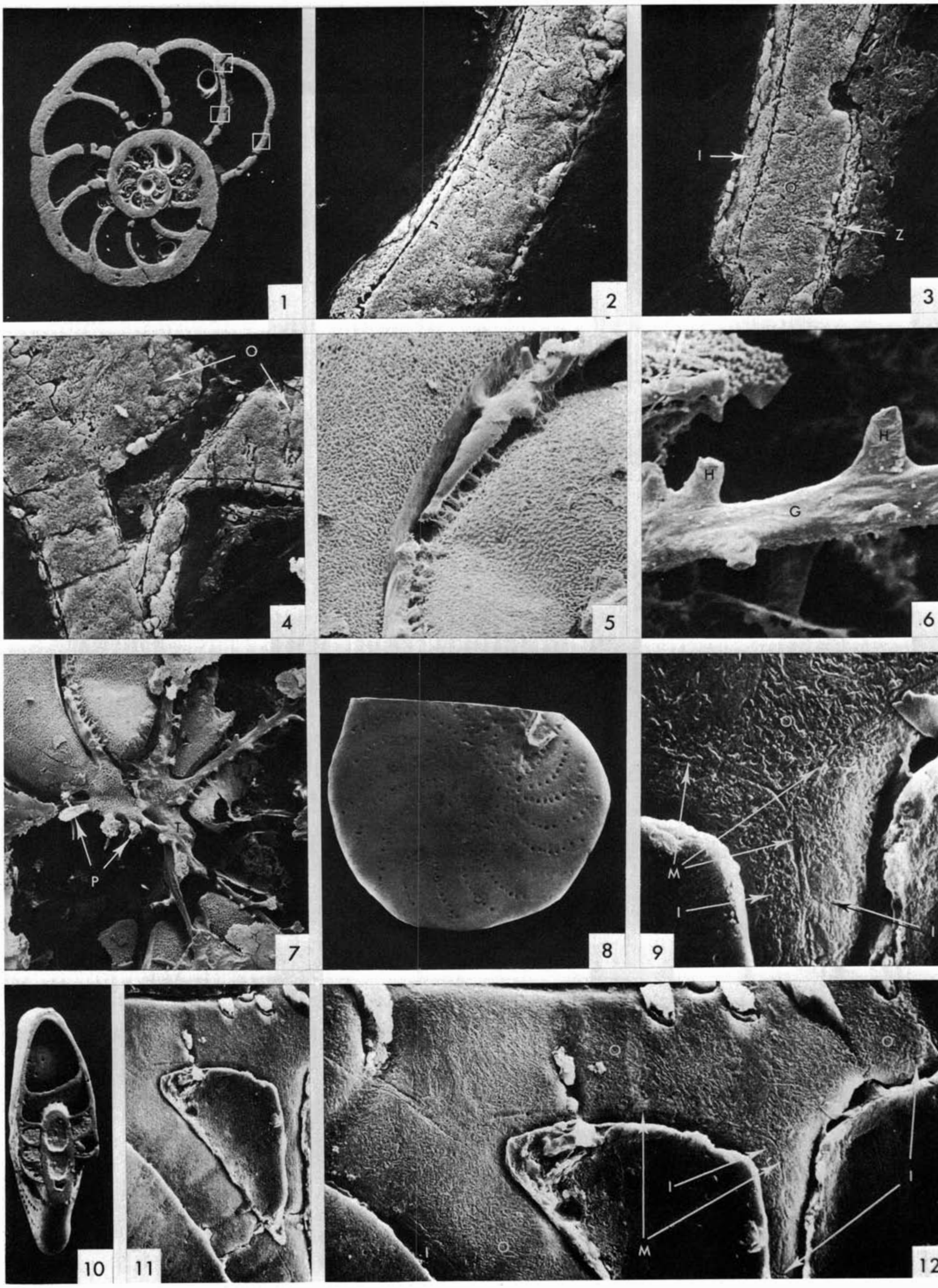
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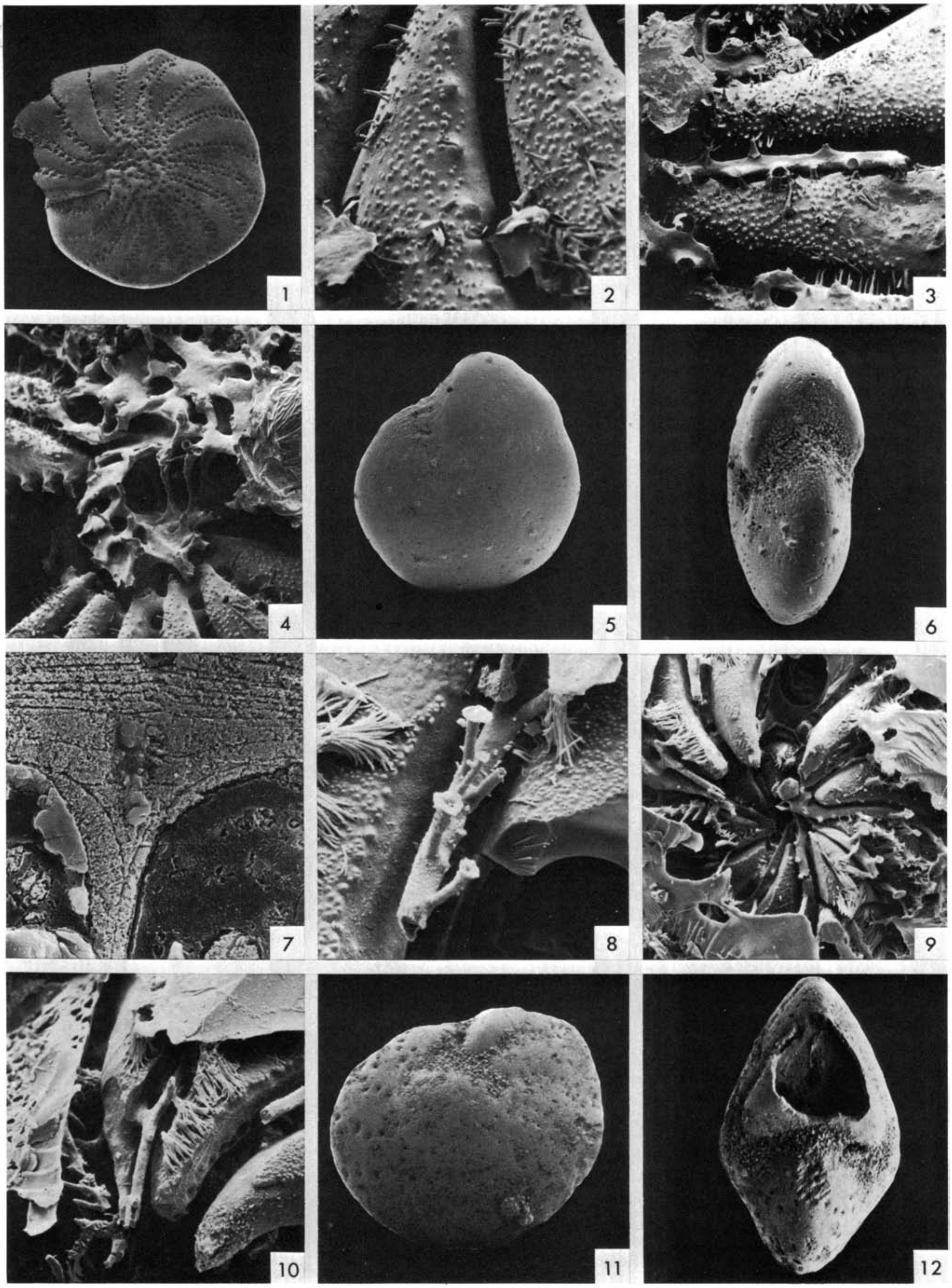
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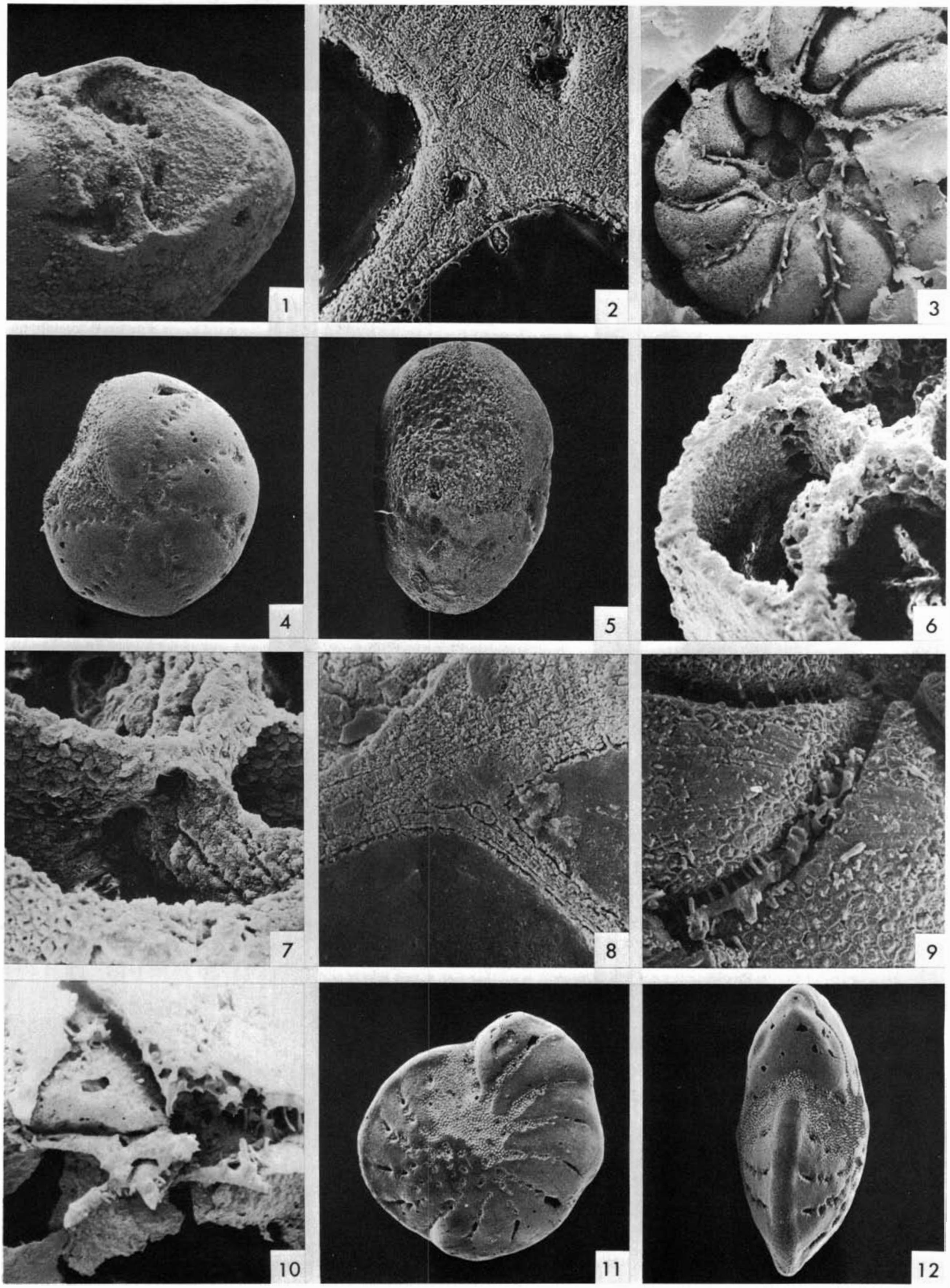
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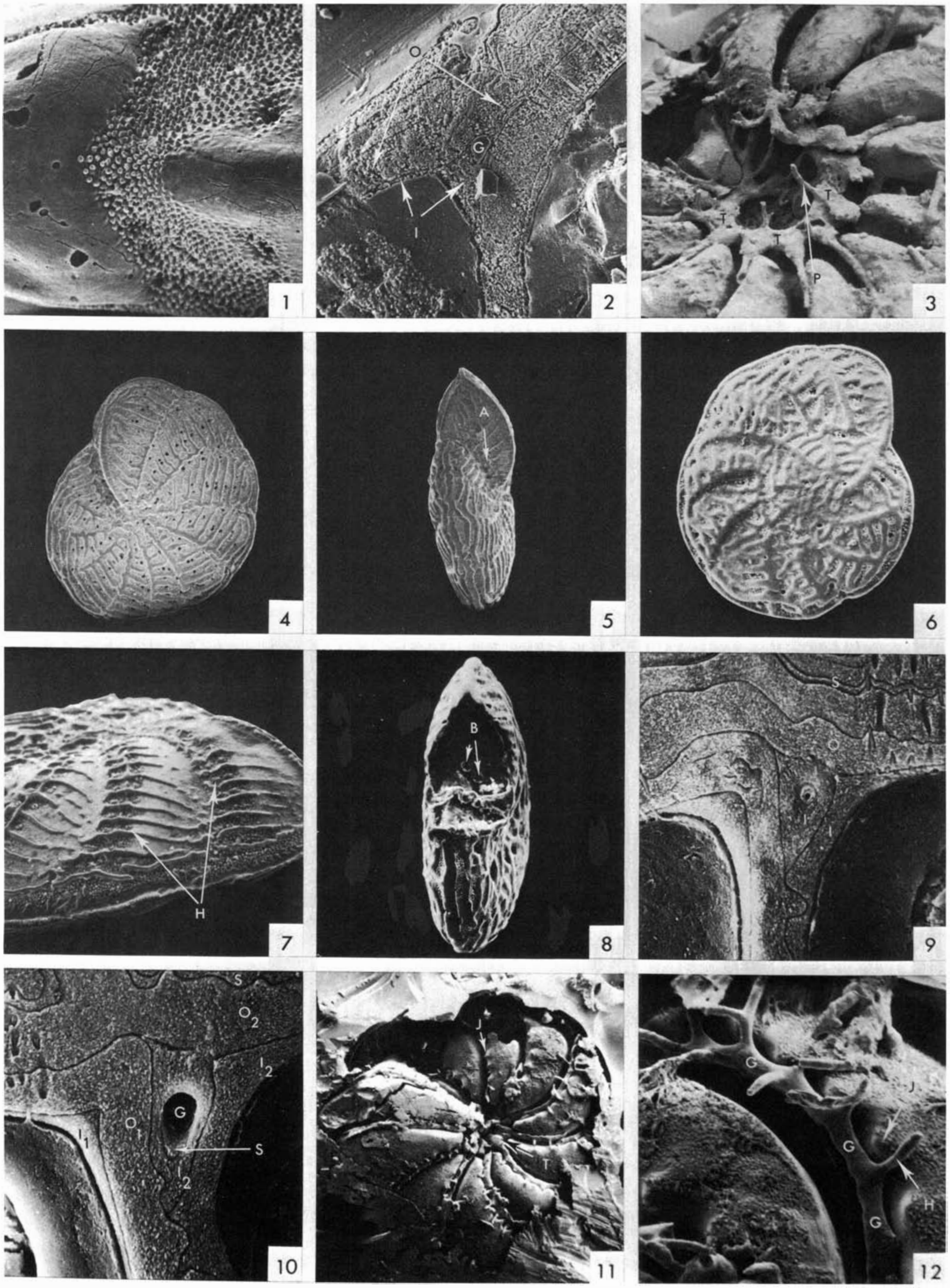
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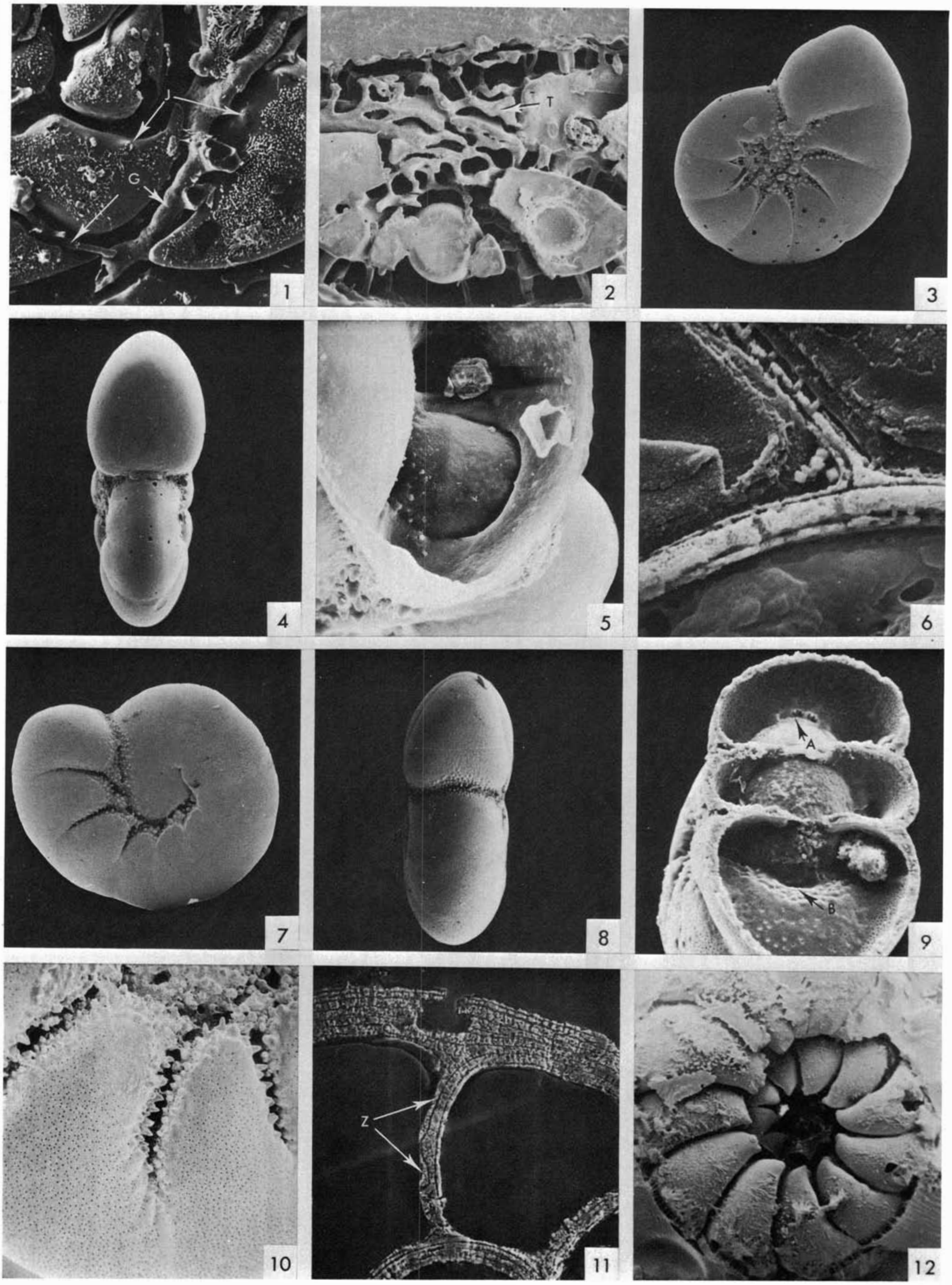
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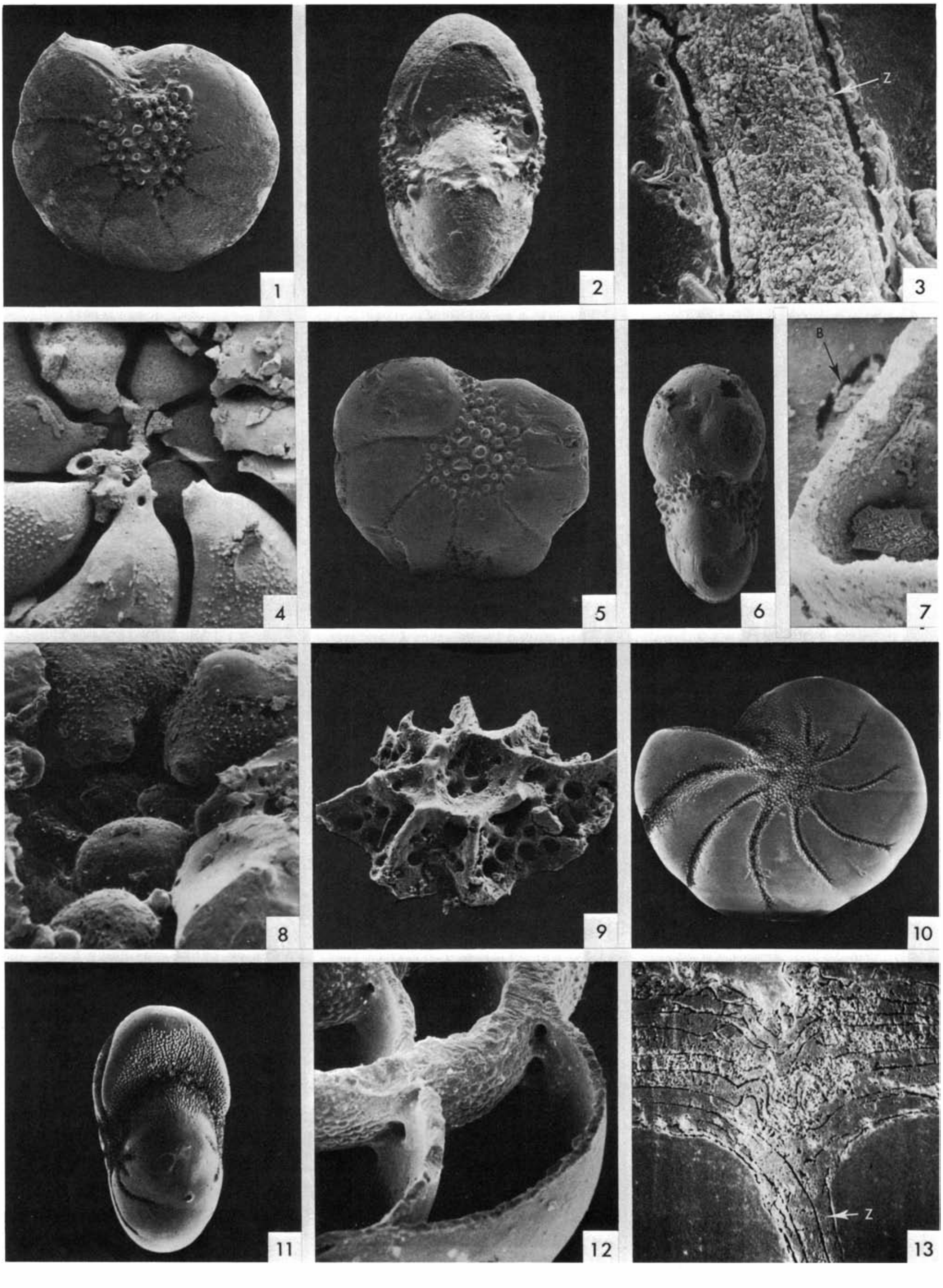
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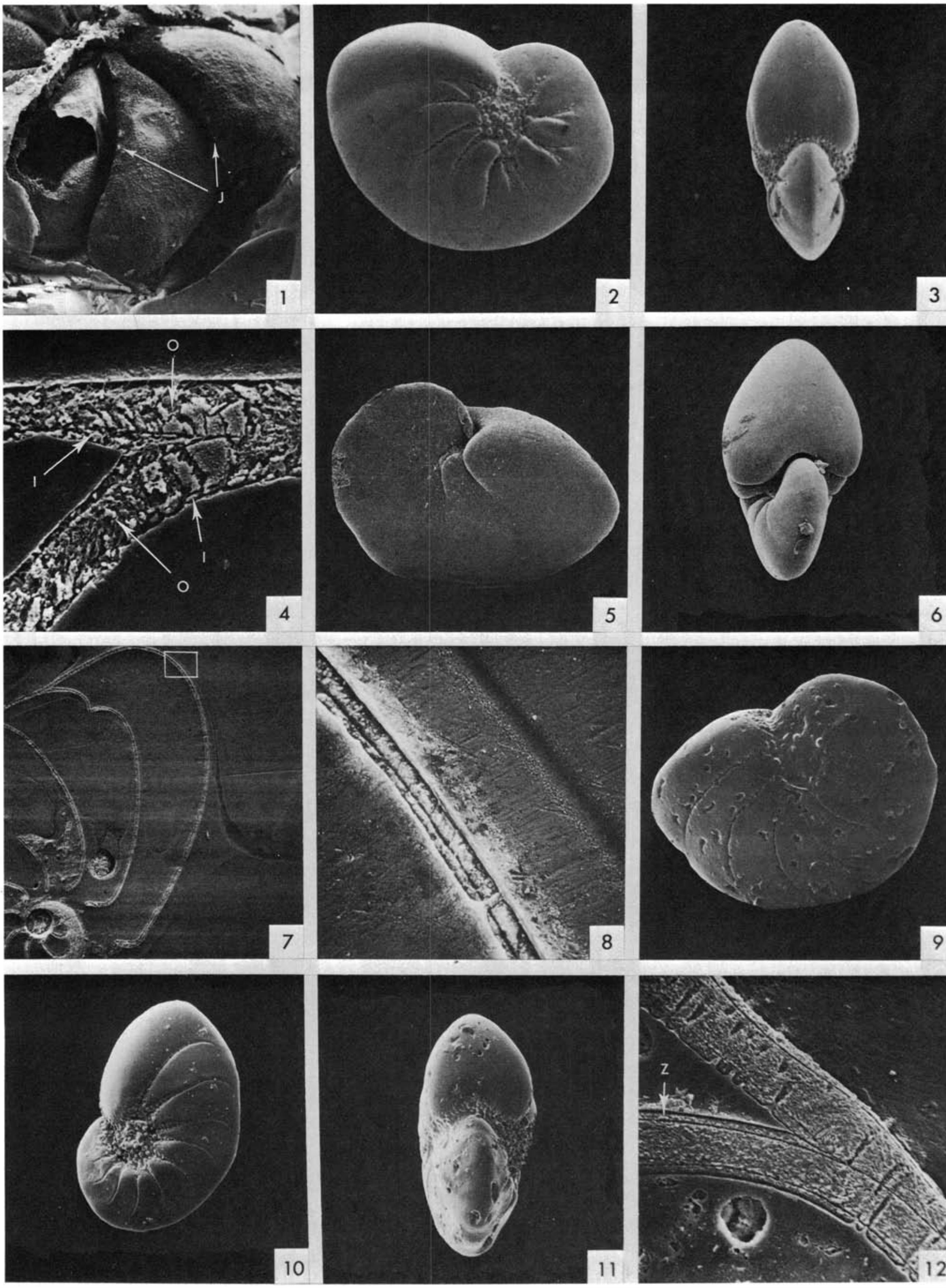
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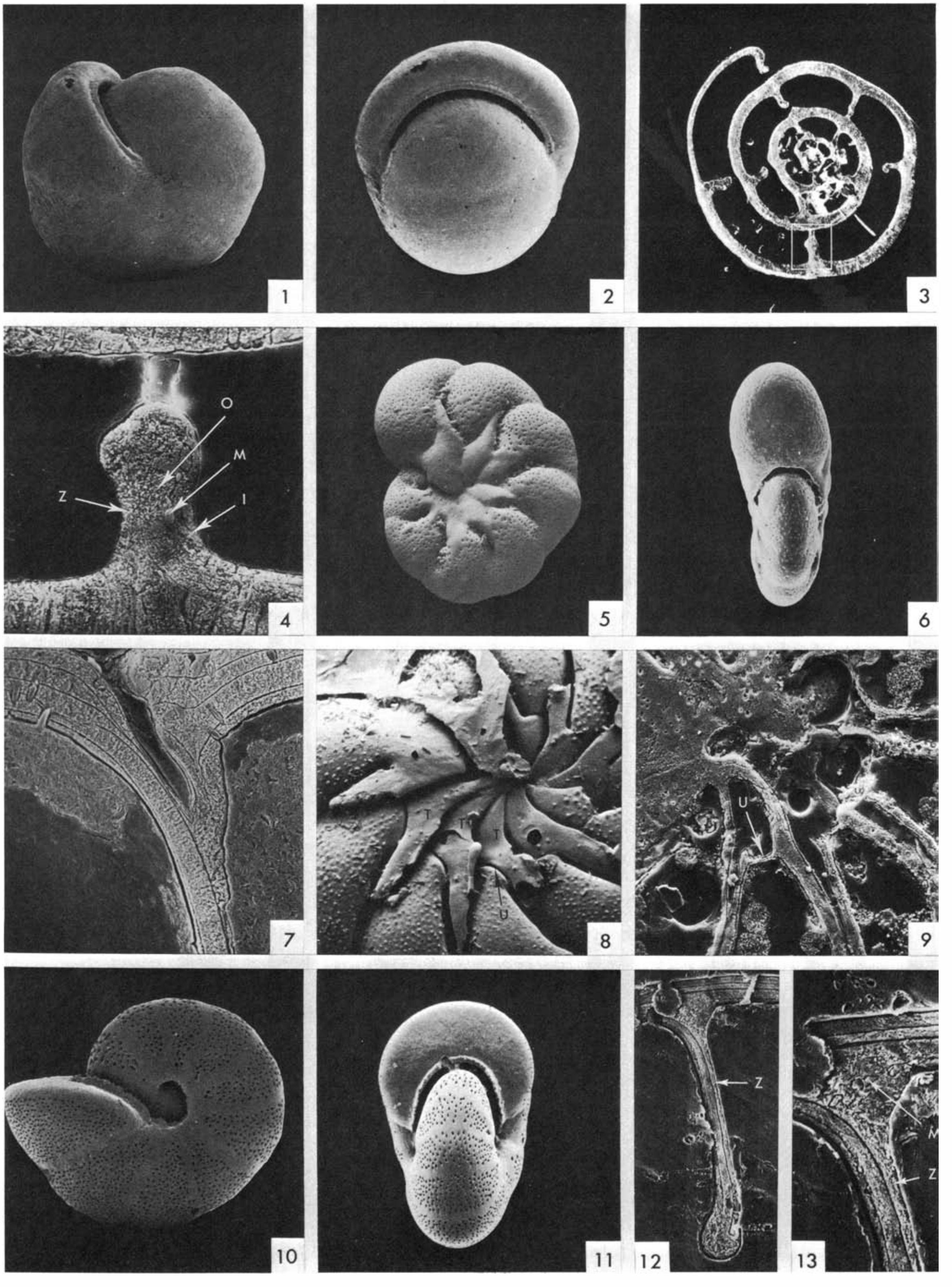
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The manuscript must be typewritten (carbon copy not acceptable) on one side of standardized paper, double spaced, and with an ample left margin. The text must be clear and concise, and written preferably in English; German or French manuscripts may be submitted. Manuscripts should be arranged in the following order: (1) Informative but brief title. Avoid titles with interrogative form, abbreviations, formulae, and brackets. (2) Author's name; one or more of his forenames unabbreviated. (3) A *short* abstract, always in English, not exceeding 12 lines (910 letters and spaces), and starting with a repetition of 2 and 1, with a translation in parentheses of non-English titles. (4) The author's professional address and a dating of the manuscript. (5) The main text. Use three or fewer grades of headings. Indicate in the left hand margin the approximate position of figures and tables. The words "Fig." ("Figs."), "Pl." ("Pls."), and "Table" (unabbreviated) are to be written with capital initials in the text. In the main text, Fossils and Strata does not use small capitals, bold-face, or letter-spacing. Instead of footnotes, insert paragraphs which can be composed in smaller type or use parentheses. (6) References shall conform to the examples given below. Abbreviations used should be consistent; necessary editorial changes will adhere to the usage in *International List of Periodical Title Word Abbreviations* (UNISIST/ICSU AB 1970). (7) Captions of illustrations, if any. Add an English caption below captions in other languages. *Figure captions and tables must be submitted on separate sheets.* (8) Tables, if any, with captions, numbered with arabic numerals. When possible, try to simplify table material so that it can be run in with the text. (9) Explanations of plates, if any.

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Figures in the text should be reducible to a maximum size of 17.1 × 25.3 cm or less. It is recommended that figures be constructed *either* for the entire width of the type area (17.1 cm) *or* for the column width (8.1 cm). Line drawings (maps, sections, etc.) may occasionally be allowed to extend into the inner margin of the page by an additional 2 cm. On all figures should be the author's name and the figure number. Do not attach captions to the figure. Photographs are to be clear, sharply contrasted, and printed on white paper with glossy finish. Photographs of fossils, however, should be made without very pronounced light areas or very heavy shadows; the shadows are to fall consistently towards the lower right corner of the figure. Figures may be composed of several quadrangular units separated by 1 mm broad spaces. The items in composite figures should be similar to each other in tone. If the natural background is to be deleted, blackening is preferred.

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REFERENCES

Ballance, P. F. 1964: Streaked-out mud ripples below Miocene turbidites, Puriri Formation. New Zealand. *Jour. Sed. Petrology 34,* 91—101. Menasha, Wisconsin.

Hecker, R.F. (Геккер, Р. Ф.) 1957: *Введение в палеоэкологию.* [*Introduction to Palaeoecology.*] 83 pp. Госгеолтехиздат, Москва.

Pettijohn, F. J. & Potter, P. E. 1964: *Atlas and Glossary of Primary Sedimentary Structures.* 370 pp. Springer-Verlag, Berlin, Göttingen, Heidelberg, New York.

Seilacher, A. 1963: Lebensspuren und Salinitätsfazies. *In* Unterscheidungsmöglichkeiten mariner und nichtmariner Sedimente. *Fortschr. Geol. Rheinl. Westf. 10,* 81—94. Krefeld.

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