

# THE GENUS PSEUDEDOMIA AND ITS PHYLETIC RELATIONSHIPS, WITH REMARKS ON ORBITOLITES AND OTHER COMPLEX FORAMINIFERA

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## GENERAL

*Pseudedomia* HENSON 1948 is the only genus known to occur stratigraphically to form a link between the older Cretaceous Alveolinidae and the Tertiary genera of that family. Although showing similarities to the Cretaceous genera, *Pseudedomia* has characters suggestive of closer relationship to complex Miliolidae such as *Fabularia* and *Raadshoovenia*. Tertiary Alveolinidae are more probably derived from Miliolidae than from *Pseudedomia*. The tracing of phyletic links between larger Foraminifera is very difficult because most species present themselves as quite isolated, or as members of a very small group of obviously related species. This can be partly ascribed to imperfections of the geological record, but is in part due to their stability for considerable periods of geological time.

The justification for regarding *Pseudedomia* as a genus of the family Alveolinidae involves an accurate knowledge of the morphology of other larger Foraminifera and some appreciation of their possible phylogeny. In some cases, the distinctions can be summarily stated; in others there have been confusions about the morphology and a redescription has had to be made. In a number of cases, the taxonomy has been gravely confused and it has not been possible to refer to genera and species without taxonomic revision. Where possible, this is definitive but in a number of cases there are further investigations to be made and a summary of the present position is given. It is hoped that this will provide a useful point of departure for further taxonomic and phyletic work. The writer attaches great importance to the rigorous application of taxonomy in phyletic discussions, for two reasons. The first is the danger of misunderstanding. The second is because the taxonomy should be closely related to phyletic theory. Of course, it can not conform to it in every detail for this would be logically impossible and in practice too nomenclaturally disturbing. It will be noted that there is a great deal in common between the writer's opinions on the phylogeny of the Alveolinidae and those of GALLOWAY (1933). However, much has been learnt about the Alveolinidae since then and the generic changes affect the statement of relationships as well as their assessment.

The diagnosis and description of the foraminiferal family Alveolinidae was placed on a firm basis by REICHEL (1937) in his monograph "Étude sur les Alveolines". This

has been widely accepted, excepting for the usage of the genera *Alveolina*, *Borelis* and *Flosculina* by American authors, who usually prefer the classification suggested by CUSHMAN (1927) and the family name "Alveolinellidae". REICHEL's system is in better accord with European usage before 1937 and is normally followed by European workers at present. Alveolinidae are much more common in the Old World than in the New World and, accordingly, REICHEL's classification has a substantial preponderance of usage over CUSHMAN's. The use of "Alveolinidae" in preference to "Alveolinellidae" is clearly correct but minor taxonomic doubts about REICHEL's use of *Alveolina* and *Neoalveolina* do exist. However, their descriptions are clear and unambiguous while the alternative classification (CUSHMAN, 1955) is confused by inadequate descriptions of the morphology of the genera. This is particularly true of *Flosculina*, which is presumably the genus to which *Alveolina* as defined by REICHEL (1937) would be assigned. It is obviously desirable that REICHEL's system should be stabilised by appropriate designation of types or even by plenary decision if necessary. GLAESSNER (1945) provided an adequate account in English of the generic definitions given by REICHEL (1937) but textbooks in English do not yet include the genera *Cisalveolina* REICHEL 1941 and *Multispirina* REICHEL 1947. EAMES and SMOUT (1955) recognised that *Pseudedomia* HENSON 1948 is a complanate genus of the Alveolinidae and emended its description, but the type species *P. multistriata* HENSON 1948 has not yet been fully described. The holotype is still the only microspheric specimen known and the description given below is still incomplete, but the megalospheric generation has now been identified and is here described. REICHEL (1937, p. 136, footnote) mentioned specimens from Istria that had received the manuscript name "*Cosinella*" SCHLUMBERGER and stated that *Borelis cardenasensis* BARKER and GRIMSDALE 1937 was similar. "*Cosinella*" has never been validly named, figured or described and no more can be said about it. *B. cardenasensis*, according to the original description, has a globular, streptospiral test, except for a single terminal planispiral whorl, but REICHEL stated that a uniserial stage was developed in the largest individuals. If this is correct, and GRIMSDALE (verbal communication) has informed me that it is possibly so, *B. cardenasensis* should be regarded as a species of *Raadshoovenia* VAN DEN BOLD 1946 and formally excluded from the Alveolinidae. Some doubt must be attached to any record of uniserial habit that is not fully substantiated by illustrations, because a globular test with a thin complanate flange developed terminally will appear terminally uniserial in most random sections and only the globular early part of the test can normally be separated from the rock matrix.

There are a considerable number of species of larger Foraminifera that have a superficial resemblance to *Pseudedomia* and an investigation has been made into the basis of classification of such forms to determine whether any known species require to be transferred to the family Alveolinidae. Foraminiferal tests of globular or fusiform shape are readily separated from rock matrix and the loss of one or two of the outer whorls does not materially change their appearance or affect their description. In the case of compressed lenticular and discoidal tests, it is usually impossible to separate specimens from the rock matrix without serious damage. The general appearance

therefore has to be reconstructed from sections, often random in direction, and the interpretation of the structure can be very difficult. The problem is further aggravated by gross homeomorphy between genera of several families of the porcellaneous Foraminifera, so that an accurate knowledge of their comparative morphology is necessary. Further difficulties are introduced because the porcellaneous shell material often alters in fossilisation to a microgranular texture. Tests of the Lituolidea have a microgranular texture that cannot be distinguished from the altered porcellaneous texture unless there are agglutinated grains incorporated in it. There are, however, many species of the Lituolidea, scattered among many genera, that do not have agglutinated grains. Conversely, porcellaneous Foraminifera may have agglutinated grains attached to the outside of the chamber walls, although this is not recorded in any of the complex species with which we are concerned here. It follows that, although there is no intention to alter REICHEL's description of the Alveolinidae, it is necessary to discuss the characters of relevant genera of the families Peneroplidae, Miliolidae, Ophthalmitidae and the superfamily Lituolidea to establish the criteria on which the differential diagnosis rests.

REICHEL (1937, p. 17), defined the family Alveolinidae as follows:

- (1) Nature of test... porcellaneous.
- (2) Mode of coiling: (a) nepionic stage: streptospiral or planispiral, (b) adult stage: planispiral (symmetrical-spiral).
- (3) Division of chambers... into tubular chamberlets in the direction of coiling.
- (4) The number of chambers per whorl... progressive, more than two per whorl in the adult.

REICHEL explicitly included any species that might be found with an outer agglutinated layer of the chamber wall or with only the last whorl planispiral. He regarded the tubular chamberlets as a fundamental character and noted that all known species have a preseptal canal. The guiding principle is exclusiveness; the Alveolinidae can only be distinguished from the Miliolidae that have endoskeleton by arbitrary definition and in practice it is found that a species that does not conform in all ways to the alveolinid structure differs in more than one character and is best regarded as miliolid. To REICHEL's definition we may add that all known species are strictly involute and that no case of cyclical growth is known. It is still true that all species have a preseptal canal and this is probably an essential character. REICHEL excluded species with a uniserial termination by implication. The only difficult case is that of *B. cardenasensis*, but information on this species is inadequate for treatment at present.

Under the headings of various families, their validity is discussed when in doubt, and the characters by which their complex genera can be recognised are demonstrated. LOEBLICH and TAPPAN (1961) have recently revived the family Meandropsinidae, abolished by HENSON (1950), and this is shown to be inadvisable. The classification of the family Peneroplidae by HENSON (1950) has long been regarded by him as obsolescent; he proposed it as a necessary but interim step towards a final assessment. The present work was instigated by him and carried out with his help, although the writer takes sole responsibility for the observations and opinions recorded. HOFKER (1950,

1951 a, b, 1952 a, b, 1953) reclassified the living species of the Peneroplidae, but omitted some of the more complex living forms and did not consider fossil species, so that his work has little direct bearing on the present investigation. MARIE (1940, 1958) has published important notes on the identity of certain species. LACROIX (1959) has made a similar contribution but this cannot be accepted without reservations.

The morphology and classification of the family Peneroplidae has been discussed at some length because the existing summaries on the subject provide an inadequate basis on which to discuss the differential diagnosis of the Peneroplidae from the Alveolinidae. In order to give meaning to many common names, it has been necessary to redescribe some species and nominate types for them, particularly for Orbitolitinae, which may resemble *Pseudedomia* when seen in fragmentary condition.

Careful scrutiny of the published species of larger Foraminifera, especially those classified by HENSON (1948) in the obsolete family Meandropsinidae, has not yielded any more that should be transferred to the family Alveolinidae. *Pseudedomia multi-striata* has been fully described, including the megalospheric generation, and *P. globularis* nov. sp. has been described.

#### COMPARATIVE ANATOMY OF THE ENDOSKELETON IN SELECTED GENERA OF THE SUPER-FAMILIES MILIOLIDEA AND LITUOLIDEA

In many complex Foraminifera of the superfamilies Miliolidea and Lituolidea, the chambers are partly infilled by shell material that was formed at the same time as the formation of the chamber wall. This endoskeleton usually consists of a subepidermal part and a part in the central zone of the chamber, the structure of the two being independent, although often the two zones are fused together. In the special case of the Alveolinidae, it is more convenient to regard the chamber as entirely filled with endoskeleton excepting for more or less tubular "canals" and "chamberlets". The greater degree of development of endoskeleton usually enables the Alveolinidae to be distinguished from other families without hesitation, but in some species the proportion of lumen is great enough to make the endoskeleton appear as either general infilling or as partitions of a general space, according to the prejudice of the viewer. Similarly, the endoskeleton of the other families can be thick enough in some species to approach the condition in Alveolinidae. It is therefore desirable to have additional criteria to resolve cases of doubt.

Some Peneroplidae develop subepidermal partitions which run from septum to septum and are of constant thickness. They are only approximately constant in spacing and are randomly arranged from chamber to chamber, and on opposite sides of the same chamber in cases where the chamber is compressed or equitant. The apertures always lie in the central zone of the chamber, not in the subepidermal zone. Partitions may occur in this central zone and these may be extensions of the subepidermal partition or fused with them, but there are nevertheless recognisable subepidermal and central zones of the chamber.

Some Lituolidea have primary subepidermal partitions like those of the Peneroplidae, with the addition of transverse secondary and tertiary plates, dividing the subepidermal zone into cellules. When the endoskeleton is particularly heavy, these may be reduced to tubules and the structure can be described as a thick wall with quadrichotomous alveoles. As in the Peneroplidae, apertures never appear in the part of the apertural face corresponding to the subepidermal zone. When lituolid subepidermal partitions are reduced to the primary plates, they are closely similar to the condition in the Peneroplidae and have the same possibilities of confusion with the internal structures of Alveolinidae.

Complex species of both Peneroplidae and Lituolidea often have characters of the central zone of the chamber which immediately distinguish them from the Alveolinidae, but there are cases where the central zone is too reduced to be distinctive.

Some Alveolinidae, particularly Cretaceous species, have a "continuous" layer of chamberlets and the apertures are in alignment with these. In a number of species, this chamberlet layer is subepidermal and a more solid endoskeleton, in which more scattered chamberlets lie, occupies the central zone of the chamber. The preseptal canal lies more in the central than in the subepidermal zone of the chamber and in the complex species the primary chamberlets open into it but it does not intervene between each and its corresponding aperture. In other cases, the preseptal canal intervenes but the apertures are still mostly aligned with the chamberlets. The primary chamber layer can appear very similar to the subepidermal layer of a peneroplid or even lituolid species, but the "continuous" alignment of chamberlets from chamber to chamber, caused by the continuity of the apertures with them, serves as a diagnostic character. In yet other alveolines the apertures regularly alternate with the chamberlets, again a character not paralleled in other families. The increase of the number of chamberlets from chamber to chamber in Alveolinidae necessarily causes some disturbance of the regular "continuous" or "alternating" chamberlets. In many species this is negligible but in some it causes sufficient irregularity to make the simple statement that the apertures are regularly arranged with respect to the chamberlets open to objection. However, the Alveolinidae often have a single layer of chamberlets and there is no question of subepidermal zones being present in such cases, this only arises when there is more than one layer of chamberlets.

REICHEL (1952) raised the question of the resemblance of *Meandropsina* to the Alveolinidae and similar queries could arise with *Edomia* and other peneroplids. For this reason, a considerable digression on selected Peneroplidae is made below. It is concluded that the structure of the endoskeleton in these genera is not homologous with that of alveolinids.

#### Family Peneroplidae REUSS 1860.

The family Peneroplidae (Soritidae, Orbitolitidae auct.) is in use for planispiral, porcellaneous Foraminifera and related genera with uniserial or cyclical terminal stages, provided the chambers are without endoskeleton, or the endoskeleton takes the form of subepidermal partitions, with or without fusions and with or without

interseptal buttresses in the central region. The apertures are sometimes single but usually cribrate and always in the central part of the apertural face, avoiding the subepidermal zone. When subepidermal partitions are present, their spacing tends to be roughly equal, but they are otherwise aligned at random in consecutive chambers and, when the chambers are compressed, they are also randomly arranged on the two sides of the chamber. The random arrangement necessarily includes the two cases; alternating and continuous alignment. These are normally observed in sections of the test and, rarely, one mode may be found throughout the test of an individual, simulating the regularity of an alveoline. In such cases the presence or absence of apertures in the subepidermal zone becomes critical evidence of family affinities. The Peneroplidae typically have discoidal, lenticular, cylindrical or flabelliform tests while the Alveolinidae typically have fusiform or globular tests, but REICHEL (1937, 1952) has made it quite clear that the shape of the test is not diagnostic. The chambers of Peneroplidae are usually involute in spiral tests, but they may be evolute, especially at late stages of ontogeny, in which case they contrast with the strictly involute alveolinid chamber. The cyclical genera have no parallel in the Alveolinidae, nor have those in which the later chambers show shortening of the alar prolongations and progressive ontogenetic change from the spiral to the uniserial chamber arrangement.

The peneroplid test has a more or less spherical proloculus, followed in the microspheric generation by a spire of chambers and in the megalospheric generation by a "canal flexostyle" or elongate deuteroconch that may coil for 90° to nearly 360° around the proloculus, in the equatorial plane. In simple species, this is followed by a single spire of simple chambers, but even in such species, the aperture is often cribrate in the ephebic chambers. In species which have cyclical chambers in the later stages of growth, the initial spire becomes flaring or aduncate and the chambers are recurved; the next stage is reniform and the cyclical habit follows. In some species a similar initial spire is succeeded by uniserial chambers which may be cylindrical or may be compressed so that the uniserial part of the test is flabelliform. The early chambers are often involute, with alar prolongations that reach the poles. The alar prolongations may be shorter in the later chambers and the cyclical and uniserial chambers are always evolute.

In some cyclical species the megalospheric nepiont has a very abbreviated spire, making less than one whorl. Further abbreviation leads to a three-chambered nucleconch that looks as if it were formed as a single unit; the third chamber is large and embraces the proloculus and deuteroconch almost completely. It has no endoskeleton, which distinguishes it from the ephebic chambers in many species, but it has the ephebic type of multiple, marginal, aperture and gives rise to a reniform or cyclical chamber of ephebic type. The ultimate reduction leaves only the proloculus and deuteroconch, the third chamber being reniform or cyclical and of ephebic type.

Some Peneroplidae have no endoskeleton in the chambers but in most, including most of the cyclical species, endoskeleton is present. The interior of each chamber can be thought of as consisting of two parts; the subepidermal zone and the central zone. All the apertures are marginal or areal and open into the central zone. The subepider-

mal zone, if it has endoskeleton at all, is occupied by subepidermal partitions, which are thin laminae that run from septum to septum. Endoskeleton may be present in the central zone, independantly of its presence in the subepidermal zone. It may consist of extensions of the subepidermal partitions, or of labyrinthic partitions fused with the edges of the subepidermal partitions, or of inter-septal buttresses (pillars).

In *Praerhapydionina* and *Rhapydionina* the cylindrical uniserial chambers have radially directed subepidermal partitions at approximately equal spacing. In *Rhipidionina* the cross-section of the uniserial chambers is oval and in the more compressed specimens it is evident that there is no correspondence between partitions on opposite sides of the same chamber. Cyclical chambers are analogous and also lack correspondance between partitions on opposite sides of the same chamber. Since the spacing between partitions is only roughly equal, considerable variation may occur, from virtual correspondence to complete irregularity or approximate alternation. In those species which have the partitions extended across the central zone, their course is not, in general, straight. Where the arrangement is least regular, two partitions of one side may fuse with one or more of the other side, or two from the same side may fuse. These irregularities are additional to the irregularities of position of the subepidermal partitions in successive chambers. HENSON (1948, 1950) and others have described species of the Peneroplidae as having "continuous" and "alternating" subepidermal partitions. In the Peneroplidae, these are limiting conditions of a fundamentally random arrangement and this must be contrasted with the fundamentally ordered arrangement of the Alveolinidae, which may be disturbed into a random arrangement in special cases.

The Peneroplidae are represented in the Cretaceous, from the Cenomanian onwards, by a number of large and complex genera but the family has only few records of simple forms in the Cretaceous. These do not become widespread and abundant until the Eocene. It is therefore reasonable to speculate whether the Aveolinidae and Peneroplidae of the Cretaceous have a common origin, especially as there is a resemblance between *Meandropsina*, *Edomia* and *Pseudedomia*. However, the detailed phyletic relationships of all these genera are obscure and no evolutionary pattern for the Peneroplidae as a whole can be discerned. The tendency of the Alveolinidae to reduction of the milioline coiling in favour of planispiral coiling could logically lead to the peneroplid spire but the apertural characters and those of the endoskeleton do not seem to be related.

Subfamily Peneroplinae (SCHULTZE, 1854, pro subfamily Peneroplida) nomen corr.

From those species which HENSON (1950) placed in the family Peneroplidae implicitly or explicitly, it is possible to state that the following belong to the subfamily Peneroplinae as here recognised, differentiated from the subfamily Orbitolitinae by the absence of a cyclical terminal stage of growth or by a substantial spiral stage occurring even in the megalospheric generation before the cyclical habit begins.

*Archaias kirkukensis* HENSON 1950.

*A. operculiniformis* HENSON 1950.

*Nautilus angulatus* FICHTEL and MOLL 1798 (type species of *Archaias* MONTFORT 1808 and, by substitution, of *Helenis* MONTFORT 1808, *Ilotes* MONTFORT 1808 and *Orbiculina* LAMARCK 1816).

Synonyms:

*Nautilus aduncus* FICHTEL and MOLL 1798; subjective synonym.

*N. orbiculus* FICHTEL and MOLL 1798; junior homonym of *N. orbiculus* FORSKAL 1775; subjective synonym.

*Orbiculina nummata* LAMARCK 1816; type species of *Orbiculina*; new name for *N. orbiculus* FICHTEL and MOLL 1798.

*O. numismalis* LAMARCK 1822; new name for *N. orbiculus* FICHTEL and MOLL 1798.

*Ilotes rotalitus* MONTFORT 1808; new name for *N. orbiculus* FICHTEL and MOLL 1798.

*Helenis spatosus* MONTFORT 1808; new name for *N. aduncus*.

*Archaias spirans* MONTFORT 1808; new name for *N. angulatus*.

*Orbiculina uncinata* LAMARCK 1822; new name for *N. aduncus*.

*Orbiculina compressa* D'ORBIGNY 1839 (type species of *Cyclorbiculina* SILVESTRI 1937).

*Orbitolites malabarica* CARTER 1853 (*Taberina* auct.).

*Pavonina liburnica* STACHE 1889 (type species of *Rhipidionina* STACHE 1913).

*Peneroplis liburnica* STACHE 1889 (type species of *Rhapydionina* STACHE 1913).

*Praerhapydionina cubana* VAN WESSEM 1943 (type species of *Praerhapydionina* VAN WESSEM 1943).

*P. delicata* HENSON 1950.

*P. huberi* HENSON 1950.

*Rhapydionina urensis* HENSON 1948.

*R. urensis* var. *minima* HENSON 1948.

*Rhipidionina macfadyeni* HENSON 1948.

*R. williamsoni* HENSON 1948.

*Sorites hofkeri* LACROIX 1940 (*Cyclorbiculina* auct.).

*Taberina cubana* KEIJZER 1945 (type species of *Taberina* KEIJZER 1945).

*Orbitolinella depressa* HENSON 1948 is also included here in the Peneroplinae, although its strictly uniserial habit makes its affinities problematical (Plate III, Plate IV, 1, 2).

Genera in which the chambers do not develop endoskeleton can be omitted from the present discussion as there is no possibility of confusing them with Alveolinidae. Genera that have endoskeleton are particularly liable to confusion with Alveolinidae, for the planispiral, involute, adult habit is common and the external shape, although usually different, is not diagnostic.

Genus *Meandropsina* SCHLUMBERGER 1898 (attributed to MUNIER-CHALMAS). (Type species *Meandropsina vidali* SCHLUMBERGER 1898, designated by CUSHMAN, 1928).

Most specimens are lenticular and strictly involute with a tightly coiled spire and curved alar prolongations of the chambers. In this they closely parallel *Pseudedomia*,



but in very large microspheric specimens the last few chambers are cyclical and evolute, with meandrine lateral chambers developed; a character alien to the Alveolinidae. The endoskeleton consists of subepidermal plates which run interseptally at their insertions but are not extended as far into the central zone of the chamber distally as proximally. REICHEL (1951) suggested that this might be an indication that the species *M. vidali* has affinities with the Alveolinidae, the distal void in the chamber corresponding to the alveolinid preseptal canal and the partitions to incomplete walls of primary chamberlets. This interpretation of the homologies is not accepted because the apertures lie in the central zone of the chamber and do not place the subepidermal cellules in continuity from chamber to chamber directly. A further discussion of this genus will be found under the heading of the obsolete family Meandropsinidae.

Genus *Taberina* KEIJZER 1945. (Type species *Taberina cubana* KEIJZER 1945, by original designation, monotypic).

Synonym: vide HENSON (1950): *Edomia* HENSON 1948; type species *Edomia reicheli* HENSON 1948.

The type species has a mainly spiral, involute, habit but is terminally uniserial, evolute. The chambers have interseptal subepidermal partitions and there are buttresses between the septa in the central zone of the chamber. The latter feature distinguishes this genus from *Meandropsina*, *Rhapydionina*, *Rhipidionina* and *Praerhapydionina*. *Edomia* is subjectively synonymous only; its species are Cretaceous rather than Tertiary and have no uniserial termination. *E. reicheli* has a superficial resemblance to *Pseudedomia*, as the names would indicate. One could suggest that the whole central zone of the chamber of *Edomia* is homologous with the preseptal canal of *Pseudedomia*, but this would imply that the subepidermal cellules are incompletely enclosed primary chamberlets and in that case they should be associated with apertures and be continuous or alternating from chamber to chamber. The point is very difficult to observe as the specimens are embedded and impregnated by sparitic calcite, but scattered apertures of peneroplid type in the central part of the apertural face seem to be the only ones present. The Cretaceous species *Taberina bingistani* HENSON 1948 agrees formally with the characters of *Taberina*, and so does *Orbitolites malabarica* CARTER 1853, referred to *Taberina* by HENSON (1950), excepting that its termination is aduncate, not uniserial. The varied appearance and occurrence of species of *Taberina* makes it likely that the genus is polyphyletic.

*Taberina daviesi* HENSON 1950 is so strongly cyclical and evolute that it must be regarded as belonging to the subfamily Orbitolitinae. It conforms to "*Orbitolites*" s.l. and might be regarded as a species of *Marginopora*.

Genus *Fusarchaias* REICHEL 1952 (for 1951). (Type species *Fusarchaias bermudezi* REICHEL 1952 (for 1951), original designation, monotypic).

This genus is very liable to confusion with Alveolinidae for it is fusiform in shape. Interseptal buttresses are present but no subepidermal partitions or other endoskeleton, which is considered by REICHEL to be incompatible with alveolinid affinities.

Genus *Archaias* MONTFORT 1808. (Type species *Archaias spirans* MONTFORT 1808 = *Nautilus angulatus* FICHEL and MOLL 1798, original designation).

This genus is lenticular or discoidal, sometimes with cyclical chambers terminally. Interseptal buttresses are present in the chambers but no other endoskeleton.

Genus *Praerhapydionina* VAN WESSEM 1943. (Type species *Praerhapydionina cubana* VAN WESSEM 1943, original designation).

The chambers have subepidermal partitions and no other endoskeleton. The test is initially spiral with a large uniserial, cylindrical, termination and one aperture per chamber. There is therefore no resemblance to alveolinids.

Genus *Rhapydionina* STACHE 1913. (Type species *Peneroplis liburnica* STACHE 1889, monotypic).

This genus differs from *Praerhapydionina* only in having several apertures per chamber.

Genus *Rhipidionina* STACHE 1913. (Type species *Pavonina liburnica* STACHE 1889, monotypic).

There are subepidermal partitions in the chambers, which are initially spiral but mainly uniserial, flattened in a plane at right-angles to the equatorial plane of the spire. The entire test is therefore strikingly different from anything seen in the subfamily Orbitolitinae or family Alveolinidae. However, a broken portion of the flange looks much like "*Orbitolites*" s.l. and has the same chance of confusion with alveolinids.

Genus *Cyclorbiculina* SILVESTRI 1937. (Type species *Orbiculina compressa* D'ORBIGNY 1839).

The chambers have subepidermal partitions but no other endoskeleton. The apertures are confined to the central zone of the chambers. The involute, spiral, nepiont is very large, but the ephebic chambers are cyclical and evolute. This genus could equally well be placed in the Orbitolitinae and it is doubtful if its separation from *Amphisorus* is justified.

Genus *Orbitolinella* HENSON 1948. (Type species *Orbitolinella depressa* HENSON 1948, monotypic).

The shell material was probably porcellaneous but the preservation is defective and a mistake might have been made. The megalospheric form only is known, the proloculus being large and spherical. The nature of the first chamber is uncertain but all chambers that can be seen clearly are in straight uniserial series, forming a low cone. The dorsal surface has serried subepidermal partitions. As the species is known only in random section, it is difficult to be sure of their arrangement; probably they are randomly arranged from chamber to chamber. At first sight they seem to have corresponding apertures, but this is probably not so, the appearance being due to intersection of the

open inner ends of the subepidermal cellules. Only "primary" partitions in the direction of growth are present. Within this layer, every second or third partition is produced to the ventral side of the chamber. These walls thicken and the central parts of the chambers have reticulate passages in them. Narrow, obliquely directed, pores serve as apertures on the ventral surface. They are comparatively widely spaced and open in a more marginal position externally than internally. The origin of this peculiar structure may have been from that of *Taberina bingistani*. Most of the differences of appearance in the uniserial chambers can be ascribed to the distortion to a low conical instead of a cylindrical shape. The reticulate passages of the central zone could be derived from the buttressed central zone of *Taberina* by thickening of the endoskeleton at the expense of the lumen. A somewhat similar change is known to occur in reverse in the ontogeny of *Marginopora vertebralis*. If an attempt is made to describe the structure of *Orbitolinella* in terms of an alveolinid origin, the general appearance of the axial section is at first sight encouraging, but on consideration, no homologue for the preseptal canal can be found. This is such a constant feature of alveolinid anatomy that its absence is regarded as highly significant. As no species of the Alveolinidae has a uniserial stage, this habit is suggestive of peneroplid origin in preference to alveolinid.

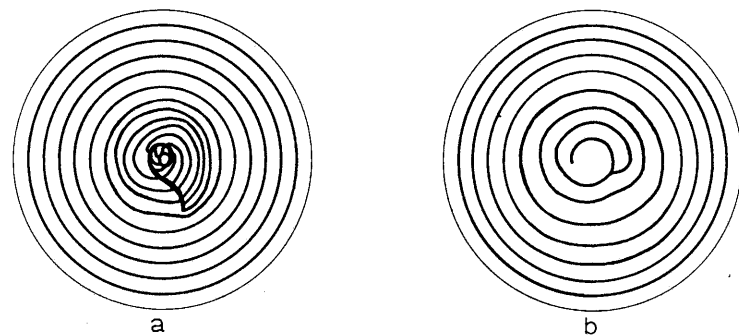


Fig. 1. Diagrams to show the chambering of the test in Orbitolitinae. Endoskeleton has been omitted. The megalospheric nucleoconch is only one of the three possible types. a. "*Orbitolites*" s.l., *Somalina* and *Opertorbitolites*, microspheric form, equatorial; b. "*Orbitolites*" s.l., *Somalina* and *Opertorbitolites*, megalospheric form, equatorial.

#### Subfamily Orbitolitinae BRADY 1881.

All genera of this subfamily have most of the chambers of the test cyclical and evolute, the nepiont being spiral in the microspheric form at least but rarely completing one whorl of divided chambers. The apertures are numerous and confined to the central zone of the chamber; they are arranged in one or two rows, in a band, or in transverse rows. Endoskeleton is normally present. Subepidermal plates are usual and may be the only endoskeleton. When endoskeleton is present in the central zone, it may be extensions of the subepidermal partitions, or independent partitions that may partly fuse with the subepidermal ones, or buttresses.

Formal distinction of members of this subfamily from the Alveolinidae is theoretically very simple; their apertures are confined to the central zone instead of having

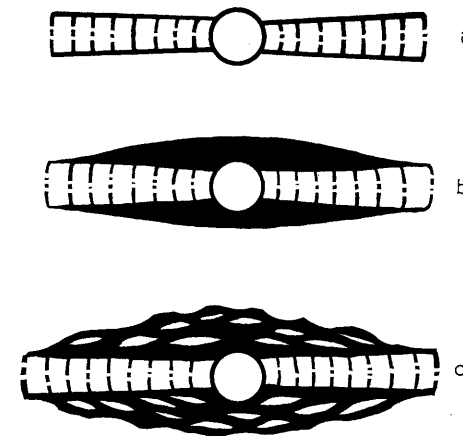


Fig. 2. Diagrams to show the chambering of the test in Orbitolitinae. Endoskeleton has been omitted. The megalospheric nucleoconch is only one of the three possible types. a. "*Orbitolites*" s.l., megalospheric form, axial; b. *Opertorbitolites*, megalospheric form, axial; c. *Somalina*, megalospheric form, axial.

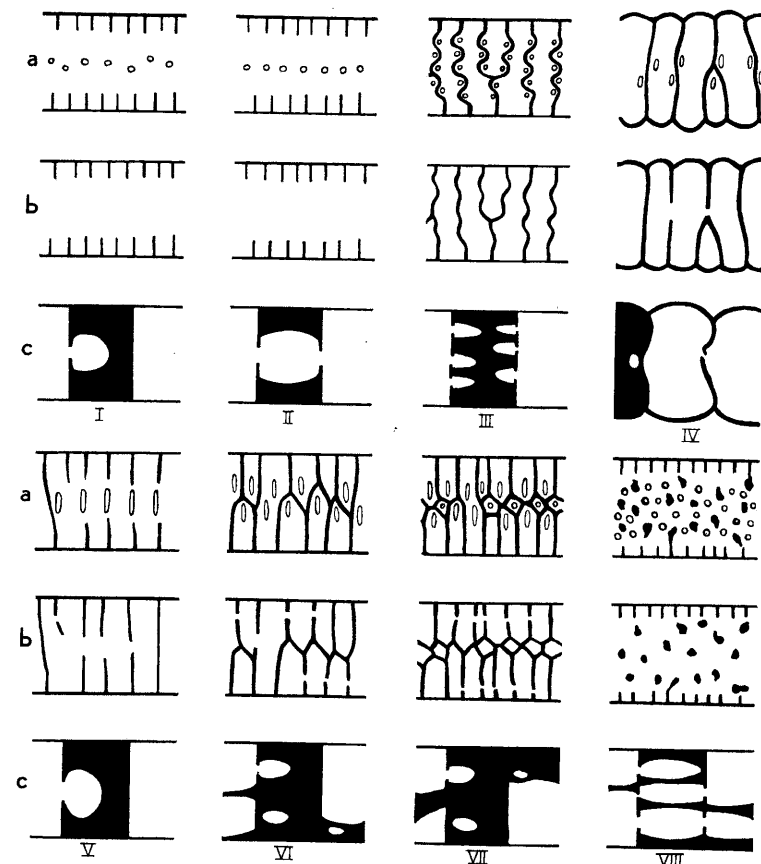


Fig. 3. Diagrams to show: a. apertural face; b. tangential section through one chamber; c. axial section through three chambers. The species represented are: I. "*O.*" *mouretti*; II. "*O.*" *anahensis*, *O. iranica*, *O. martini*; III. "*O.*" *carpenteri*; IV. "*O.*" *duplex*; V. "*O.*" *duplex* (transitional to another species?); VI. *O. complanata*; VII. "*O.*" *orbiculus*; VIII. "*O.*" *vertebralis plicata*.

some correspondence to chamberlets, and the endoskeleton is organised as subepidermal plates and partitions or buttresses, instead of a tubulated mass. In practice, particularly in fossil specimens, the distinction is less easy and a good working knowledge of the orbitolitid organisation is a great help. Unfortunately there are wide differences of opinion current about the interpretation of the structure; for instance, HENSON (1950) described cycles of small chambers instead of subdivided annular chambers. Generic nomenclature is in a very confused state and the recognition of a number of species is open to debate. Some species, *e.g.*, *Orbulites marginalis* LAMARCK 1816, have two current interpretations. To refer to Orbitolitinae without close definition of names would merely add to confusion. For this reason, notes have been made on all critical species and type specimens have been designated where this is desirable. Application of generic names to the type species is of course easily done, and some of these genera are ostensibly worth separation, but their definition to include species other than the types is a problem that cannot be completely solved at present; more observation of the remaining species is necessary. The only practical course is to use the genus "*Orbitolites*" s.l. for such species, pending further generic revision. Generic distinctions will cut across lineages and stratigraphical associations if crudely based on some of the characters traditionally cited. The use of genera so defined would be disadvantageous compared to the use of a single genus.

Variation in the Orbitolitinae occurs in the megalospheric nucleococonch; some species having proloculus and deuterococonch followed by chambers arranged spirally but of normal type, sometimes without endoskeleton. Other species have reniform or cyclical chambers formed directly after the deuterococonch and some have a third chamber of the nucleococonch, distinguished from later chambers by the wall thickness and texture and without endoskeleton, directly followed by cyclical chambers of normal type.

Variations in the endoskeleton rarely suppress the subepidermal partitions, although their extension towards the centre of the chamber is variable. In the simplest case, the central zone of the chamber is quite empty. In others, the subepidermal partitions may extend across the central zone, leaving a central hole, which in some species has a distal situation but in others is central. Complete fusion in twos and threes, leaving no hole, is possible. Yet other species do not show extension of the subepidermal partitions but develop partitions in the central zone that may fuse with the subepidermal partitions, leaving holes at their junction. Such partitions may be simple or reticulate. Partitions in the central zone may have holes and if these are large, the partitions may be reduced to buttresses. The ultimate reduction is to slender interseptal pillars.

Variations in apertural pattern are confined to arrangements on the apertural face over the central zone of the chamber and are often associated with particular arrangements of endoskeleton. In some species the shape of the apertures varies with their arrangement. In some, the apertures alternate with partitions but in others the pores are aligned along partitions, which are then fluted, and the apertures inclined, to avoid them.

Inflation of the chamber walls between the sutures of the partitions occurs to a small degree in many species, but when it is conspicuous it changes the general appearance profoundly, particularly when it is greatest at the angles of the margin. Combination of this with fusion of subepidermal partitions across the central zone of the chambers can result in an appearance of cycles of chambers that resemble those of *Lepidocyclina* in many ways. The insistence here on regarding the chambers as annular is justified by close observation; there is continuity of gradation of character with specimens in which the chambers are more obviously annular, sometimes in the same specimen. In a number of species, a perfectly equatorial section will make the chambers appear annular, while sections slightly to either side will intersect the partitions and look as though cycles of small chambers had been intersected. In all Orbitolitinae, observation of the margin will show that the insertion of subepidermal partitions on either side of the chamber is random. The extensions of the partitions into the central zone may meet naturally but in some parts it will be found that the partitions bend in order to meet, or even fuse in threes, two from one side and one from the other, or two from the same side of the chamber fuse.

With a random arrangement of subepidermal partitions from chamber to chamber, definite alignment or alternation must be found sporadically by chance. In addition, the spacing between the subepidermal partitions conforms to an average value. If the deviation from this is small, the partitions will tend to appear regularly arranged.

The Orbitolitinae often tend to have supplementary flanges and other irregularities of growth, particularly in association with plastogamy in the megalospheric generation. This variability is accentuated by the possibility of regeneration of a complete test from a broken fragment and of continuation of growth after the margin has been severely worn. Morphogenetic principles are difficult to formulate to take care of such complexities.

Genus *Orbitolites* LAMARCK 1801. (Type species *Orbitolites complanata* LAMARCK 1801, virtually designated by DOUVILLÉ, 1902, explicitly designated by CUSHMAN, 1927).

DOUVILLÉ (1902) effectively reduced this genus to monotypy by emending the description to include only species with complete partitions across the chambers. Many authors have used *Orbitolites* in a much less restricted sense and most porcellaneous, cyclical, peneroplid species with subepidermal partitions have been referred to *Orbitolites* unless they have lateral chamber or shell layers. There are a number of nominally valid genera into which *Orbitolites* s.l. can be divided, but the correct basis on which species other than the types can be allocated to genera is not clear at the moment. For immediate purposes *Orbitolites* s.str. will be used with DOUVILLÉ's definition, characterised by partitions completely fused in twos and threes across the central zone leaving no holes. "*Orbitolites*" s.l. will be used for most species of the Orbitolitinae, reflecting the writer's opinion that the extant generic names and descriptions have arisen piecemeal as individuals have been impressed by the differences between pairs of species, without sufficient knowledge of the problem as a whole. Even

HENSON's classification, which attempted to create an empirical classification based strictly on morphology, is thrown into confusion if it is admitted that the Orbitolitinae have annular chambers, with complexities not considered in his system.

The identity of *Orbitolites complanata* LAMARCK 1801 is fortunately in no doubt although it must be noted that CARPENTER (1883) described *Marginopora vertebralis* under this name.

Genus "*Orbitolites*" s.l.

The following list of species comprises all those belonging to the subfamily Orbitolitinae that lack lateral layers of shell material. A number of species that are the types of their genera have been included for consistency but there can be little objection to using these as monotypic genera if desired, other than that the genera so used are tautonymous with their type species. The problem of assignment of the remaining species to genera cannot be satisfactorily resolved on the information immediately available and it is for this reason that it is proposed to use "*Orbitolites*" s.l. for the present. *Orbitolites americanus* CUSHMAN 1918.

*Meandropsina anahensis* HENSON 1950 (= ? *O. martini*).

*Orbitolites complanata* LAMARCK 1801 (type species of *Orbitolites* s.str.).

*O. complanata d'archiaci* DE GREGORIO 1894.

*O. complanata gigantea* SACCO 1922.

*O. complanata minima* HENSON 1950.

*O. complanata perundata* SACCO 1922.

*Taberina daviesi* HENSON 1950.

*Orbitolites disculus* LEYMERIE 1851 (= ? *O. complanata*).

*Qataria dukhani* HENSON 1948 (type species of *Qataria*).

*Orbitolites duplex* CARPENTER 1883 (type species of *Bradyella*).

*Orbitolites elliptica* MICHELIN 1846 (= ? *O. complanata*).

*Sorites grecoensis* HENSON 1950.

*Amphisorus hemprichii* EHRENBERG 1840 (type species of *Amphisorus*).

*Meandropsina iranica* HENSON 1950.

*Orbitolites laciniatus* BRADY 1881 (= "*O.* *vertebralis plicata*").

*Orbulites marginalis* LAMARCK 1816.

*Orbitolites martini* VERBEEK 1896 (*Sorites* auct.).

*Praesorites moureti* DOUVILLÉ 1902 (type species of *Praesorites*).

*Nautilus orbiculus* FORSKÅL 1775 (not FICHEL and MOLL 1798).

*Dohaia planata* HENSON 1948 (type species of *Dohaia*).

*Marginopora vertebralis plicata* DANA 1846.

*Orbitolites tonga* WILLIAMSON 1856 (= "*O.* *vertebralis*").

*Marginopora vertebralis* QUOY and GAYMARD in BLAINVILLE 1830 (type species of *Marginopora*).

*Archiacina verworni* RHUMBLER 1911.

To this list may be added "*Orbitolites*" *carpenteri* new name for *Orbitolites marginalis* CARPENTER 1883; not *Orbulites marginalis* LAMARCK 1816.

*Sorites dominicensis* EHRENBERG 1840 and ? *S. edentulus* EHRENBERG 1840 possibly belong to "*Orbitolites*" but are nomina dubia that cannot be placed with certainty.

Genus *Amphisorus* EHRENBERG 1840. (Type species *Amphisorus hemprichii* EHRENBERG 1840, by monotypy).

As *A. hemprichii*, *Orbulites marginalis* LAMARCK 1816 and *Nautilus orbiculus* FORSKÅL 1775 are very closely similar and probably represent variants of one species, EHRENBERG's distinction (1840) between *Sorites* and *Amphisorus* cannot be maintained. "*O.*" *hemprichii* was described as having two layers of chambers; in fact it has one layer with the subepidermal cellules inflated, leaving a marginal sulcus in which the apertural pores lie. "*O.*" *marginalis* and "*O.*" *orbiculus* have the same structure without as much inflation between the sutures, causing them to look single-layered. Some authors, e.g., HENSON (1950) have stated that these species have cycles of small chambers. This is a deceptive appearance due to the partitions and the inflation of the chamber walls between them; the chambers are essentially annular with subepidermal partitions randomly inserted on the two sides of the chamber and partially fused across the central zone of the chamber.

As *Sorites* is apparently based on an indeterminable species and was proposed at the same time as *Amphisorus*, it is best regarded as a potential synonym and as effectively junior to *Amphisorus*.

Genus *Bradyella* MUNIER-CHALMAS 1902. (Type species *Orbitolites duplex* CARPENTER 1883, original designation).

In the type species, the structure seems to agree with that of "*O.*" *carpenteri* in the earlier chambers (*Sorites* of DOUVILLÉ, 1902), but in later chambers the subepidermal partitions are distinct and only partly fused with partitions that are complete across the central zone, a hole being left at their junctions with the subepidermal partitions. In later chambers of some specimens where there are more than two rows of apertures, the partitions of the central zone are reticulate, each aperture corresponding to a cellule.

This genus has never been popular, but has more claim to being distinct than several others. *Marginopora* has a similar structure, except that the central zone is occupied by interseptal buttresses.

Genus *Dohaia* HENSON 1948. (Type species *Dohaia planata* HENSON 1948, original designation, monotypic).

The chamber structure is closely similar to that of *Amphisorus* and *Praesorites*, the subepidermal partitions leaving a small, empty, central zone of the chamber. They are, however, not shortened distally and the nepiont appears to be symmetrical.

*Qataria* differs from *Dohaia* in having the partitions alternating in successive chambers instead of being aligned. In other respects the similarity is so close that it is suspected that both are random arrangements in reality.

Genus *Qataria* HENSON 1948. (Type species *Qataria dukhani* HENSON 1948, original designation, monotypic). See *Dohaia*.

Genus *Marginopora* QUOY and GAYMARD 1830. (Type species *Marginopora vertebralis* QUOY and GAYMARD in BLAINVILLE 1830, monotypic).

The subepidermal zone with partitions is distinct from the central zone of the chamber with interseptal buttresses. These are often so crowded that they could be described as partitions with holes, but sometimes appear as discrete, slim, pillars.

Apart from "*Orbitolites*" s.l., this seems to be the only reasonable generic name for *Taberina daviesi* HENSON 1950, if one believes that the cyclical species should not be classified in the same genera as spiral species with a uniserial termination.

Genus *Praesorites* DOUVILLÉ 1902. (Type species *Praesorites moureti* DOUVILLÉ 1902, by monotypy).

This genus differs from all others of the Orbitolitidae in having a slightly skew nepiont, if the description by MARIE (1958) is correct. The subepidermal partitions are normal and complete, but their distal extensions into the central zone are not so well developed as the proximal ones, which usually fuse in pairs. The apertures are in one or two rows.

The chamber structure is very like that described by DOUVILLÉ for *Sorites* (based on "*O.*" *carpenteri*) or *Amphisorus* as described here. In *O. carpenteri* the partitions even show the same distal shortening in the central zone. Provisionally, the genus is kept distinct as the nepiont shows slight asymmetry. The latter character however has probably been overemphasised in importance, as peneroplids often show irregular asymmetry without structural differentiation.

Genus *Opertorbitolites* NUTTALL 1925. (Type species *Opertorbitolites douvillei* NUTTALL 1925).

*O. douvillei* is an Eocene species with considerable resemblance to *Orbitolites complanata*, but with thick lateral layers of shell material.

Genus *Somalina* SILVESTRI 1939 (1937 nomen nudum). (Type species *Somalina stefaninii* SILVESTRI 1939).

*S. stefaninii* is an Eocene species which is closely related to *Opertorbitolites*, differing in the presence of cavities between the lateral layers of shell material.

Generic names that should not be used at present are:

*Broeckina* MUNIER-CHALMAS 1882, nomen dubium. (Type species *Cyclolina dufrenoyi* D'ARCHIAC 1854, nomen dubium, original designation).

The type species cannot be identified with certainty with any known specimens. MARIE (1958) has reported that he failed to find authentic specimens known to have been seen by D'ARCHIAC. *Praesorites moureti* DOUVILLÉ 1902 has characters sufficiently

close to *C. dufrenoyi* to make it probable that the two are in fact synonymous. However, there is no proof of this. *C. dufrenoyi* is best suppressed to protect the well-known name *P. moureti*. *Broeckina* therefore has the status of nomen dubium and should be suppressed to protect *Praesorites*.

*Sorites* EHRENBURG 1840, nomen dubium. (Type species *Sorites dominicensis* EHRENBURG 1840 nomen dubium, designated by CUSHMAN, 1927).

Two species of the original list of species were available for designation as the type of *Sorites*; *S. dominicensis* and *Nautilus orbiculus* FORSKÅL 1775. CUSHMAN unfortunately designated *S. dominicensis*. This species cannot be recognised at present. EHRENBURG's collections are believed to be preserved in East Berlin and an authentic specimen might be found there. However, this is not certain, for the publication will give little help in the identification of the specimen unless it is adequately labelled. Subsequent attempts to use the name have not been impressive. Only RENZ (1948) has explicitly determined a specimen as *S. dominicensis*. His specimen came from Venezuela, not San Domingo, and he wrote no explanation of his grounds for identification. His description and figures are not adequate for reliable identification. They might apply to "*O.*" *orbiculus* but could be of "*O.*" *carpenteri* or some other species. DOUVILLÉ (1902) found a specimen from San Domingo in the DESHAYES collection but concluded that it was unlikely to be *S. dominicensis*. Lacking an explicit type locality or even an assurance that the specimen was either fossil or recent, identification seems impossible without a paratypic specimen as a guide.

Objection to the use of *Sorites* is based on further considerations. DOUVILLÉ emended *Sorites*, mentioning "*Orbitolites marginalis* et *Hemprichi* (*duplex*, CARPENTER)", but not designating a type. The text figure seems to represent "*O.*" *carpenteri*, which was almost certainly the species meant by "*O. marginalis*", following CARPENTER (1883). On DOUVILLÉ's descriptions, the distinction between *Praesorites* and *Sorites* seems quite inadequate; the annular stolon formed by the distal shortening of the partitions in the central zone is present in both and the difference of size has been exaggerated, to judge by direct comparison of *P. moureti* with "*O.*" *carpenteri*. If *Sorites* were to be conserved, DOUVILLÉ's description would need amendment if it were to be of any distinctive value. By "*O. Hemprichi*" there is little doubt that DOUVILLÉ meant "*O.*" *duplex*. This species seems to be very closely related to "*O.*" *carpenteri*, perhaps some cline between the two exists. Nevertheless, "*O.*" *duplex* has a complexity of the partitions of the central zone that contrasts with the simplicity of "*O.*" *carpenteri*, "*O.*" *orbiculus* and *P. moureti*. The figure given by DOUVILLÉ for "*Marginopora*" is a crude representation of the condition in "*O.*" *duplex*. The difference between the megalospheric nucleocoenoch of "*O.*" *carpenteri*, which is followed by a spiral nepiont, and "*O.*" *duplex*, which is not, is not at present fully understood. It may be a generic distinction, but is more probably a varietal character and is likely to be associated with trimorphic differences between successive generations, possibly differing in detail in different geographical races.

*Amphisorus hemprichii*, *Orbulites marginalis* and *Nautilus orbiculus* are shown in the

appendix to be exceedingly closely related, to the point of doubt that specific distinction can be maintained. EHRENBURG (1840) assumed that these were Bryozoa and his generic distinction between *Amphisorus* and *Sorites* was based on being two-layered or one. In fact, the distinction is quite spurious; being based only on the degree of inflation of the chamber walls at the margin, between the sutures of the partitions. "*O.*"*orbiculus* resembles "*O.*"*carpenteri* in many ways, the main differences being in proportions and in the shift of the hole in the fused partitions to a lower level, so that the partitions fuse distally as well as proximally around it. EHRENBURG strongly emphasised the similarity between *A.hemprichii* and *S.orbiculus* (sic!) in his descriptions and figures.

If *Sorites* is to be used as a genus at present, *Nautilus orbiculus* FORSKÅL 1775 must be taken as the effective type species; in this case it unquestionably would be a synonym of *Amphisorus*. Since *Amphisorus* is a valid genus at present, whatever opinion one may hold about its synonymy, and it was proposed in the same work as *Sorites* and therefore has the same seniority, it is obvious that only a plenary decision bluntly contrary to the *Règles internationales de la Nomenclature zoologique* (1953) could validate it, in any meaning yet proposed. It has been shown that the facts of morphology give no support to the idea that this might be desirable. Should *S.dominicensis* be identified and found to be congeneric with "*O.*"*orbiculus*, this would merely mean that *Sorites* would be established as an effectively junior synonym of *Amphisorus*. Should it be found to be generically distinct, it is likely that it would be conspecific with some subsequently named species and liable to upset the nomenclature of some other established genus. Both these effects would be highly undesirable.

*Taramellina* MUNIER-CHALMAS 1902, nomen nudum.

No named species have ever been attached to this genus. MUNIER-CHALMAS stated that the type was based on specimens like the simple type of *Orbitolites* described by CARPENTER (1853) but he did not state that they were identical.

Family Meandropsinidae HENSON 1948 (obsolete).

The type species of the family Meandropsinidae, *Meandropsina vidali* SCHLUMBERGER 1898, was placed in the Peneroplidae by HENSON (1950) and he therefore could not continue the use of the name Meandropsinidae. Although very different views on the genus *Meandropsina* SCHLUMBERGER 1898 are taken here from those of HENSON (1950) it is maintained that the genus is correctly assigned to the family Peneroplidae. The genera of the Meandropsinidae are now distributed between the families Peneroplidae, Alveolinidae, Cyclamminidae and Lituolidae. LOEBLICH and TAPPAN (1961) advocate that the Meandropsinidae should be reduced to the rank of subfamily but retained in the family Soritidae. Retaining HENSON's diagnosis, the Meandropsinidae would comprise all peneroplid genera with endoskeleton in the chambers. The diagnosis given by LOEBLICH and TAPPAN is invalid as it would not admit the type genus *Meandropsina*. *Meandropsina vidali* is found in Upper Cretaceous strata. It has a lenticular, involute, spiral test with very recurved septa and strongly vorticiform alar

prolongations that reach the poles accurately except in the latest stage of growth of the microspheric form, where the median chamber layer is cyclical and there are meandriiform lateral chambers. REICHEL (1952) stated that in *M. vidali* the partitions are mainly arranged in alignment from chamber to chamber and extend through the thickness of the chamber, leaving a continuous space at the distal end of the chamber that could be regarded as homologous with the preseptal canal of an alveoline. However, re-examination leads the writer to the belief that the organisation is more like the peneroplid than the alveolinid condition. The subepidermal partitions of *M. vidali* seem really to be arranged randomly from chamber to chamber, the natural consequence being that they quite often appear in alignment. The apertures all seem to lie in the central part of the chamber and not to be aligned with the spaces between the partitions, as is typical of those alveolinid species that show "continuous" chamberlets most clearly. The occasional terminal development of cyclical chambers is a character paralleled in the Peneroplidae but not in the Alveolinidae. These features are all shown in SCHLUMBERGER's type figures. For these reasons the genus *Meandropsina* is classified in the family Peneroplidae, although there is a remote possibility that its features may indicate a phyletic link between the Peneroplidae and the Alveolinidae in the Cretaceous.

A number of Upper Cretaceous species are congeneric with *Meandropsina vidali*: *Fallotia jacquoti* DOUVILLÉ 1902; *Fascispira colomi* SILVESTRI 1940, both the type species of their respective genera; probably also *M. larrazeti* SCHLUMBERGER 1898. SCHLUMBERGER suspected *Orbitolites chartacea* DES MOULINS 1864 of being conspecific with *M. vidali*, but this species remains a nomen dubium. ?*M. ruttleri* PALMER 1934 is not well enough described or figured to be assigned firmly to any genus. The Tertiary species *Meandropsina anahensis* HENSON 1950 and *M. iranica* HENSON 1950 agree more in structure with species described in the genus "*Orbitolites*" s.l. The assignment to families of the species of other genera that HENSON (1948) placed in the Meandropsinidae will be found in the discussions on these families.

Family Miliolidae EHRENBURG 1840.

The family Miliolidae is characterised by the streptospiral mode of coiling. There are two chambers per whorl, occasionally with an uncoiled uniserial termination. The degree of involution is variable; often it is slight but in some species, such as *Periloculina zitteli* MUNIER-CHALMAS and SCHLUMBERGER 1885 a progression from evolute to involute chambers progresses past the normal 180°, embracing to the hyper-involute condition where each chamber completely surrounds the previous test. *Lacazina* spp. (MUNIER-CHALMAS, 1882a) show most chambers in this hyperinvolute condition, the apertures alternating from pole to pole and therefore indicating that there are two chambers per whorl (not one as stated by REICHEL, 1937, p. 17). *Fabularia discolithes* DEFANCE 1820 is remarkable in having normally involute adult chambers. The genera mentioned all have endoskeleton in the chambers. This is mainly on the chamber floor with ridges rising towards the outer wall in *Periloculina*. In *Lacazina* the ridges form incomplete partitions which are otherwise of alveolinid type and in *Fabularia* they are



complete and form tubular chamberlets of alveolinid type and only the two-chambers-per-whorl distinguishes the genus from the Alveolinidae. *Raadshoovenia* VAN DEN BOLD 1946 seems to have the structure of *Fabularia*, but with a terminal uniserial stage. *Borelis cardenasensis* BARKER and GRIMSDALE 1937 was stated by REICHEL (1937) to have a uniserial termination and is therefore here regarded provisionally as a species of *Raadshoovenia* although the only description and figures show only a five-to six-chambered final planispiral whorl following a milioline stage. In all these genera with endoskeleton, the aperture is cribrate and opens in an anterior undivided part of the chamber that can be regarded as homologous to the preseptal canal of an alveoline. It is probable that the Alveolinidae are polyphyletically derived from the Miliolidae.

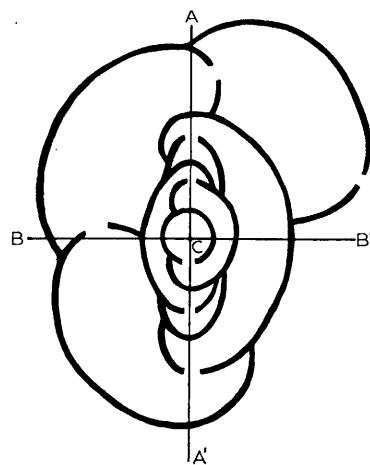


Fig. 4. Equatorial section; the megalosphere, "canal flexostyle", three milioline and three planispiral chambers are shown. Note how there are two milioline chambers per whorl, their apertures lying along one axis, alternately at each pole; while the planispiral chambers are typically more than two per whorl.

#### Family Ophthalmitidae CUSHMAN 1927.

The Ophthalmitidae are planispiral but otherwise resemble the Miliolidae. The chambers are typically long but there are usually rather more than two per whorl and a few species develop numerous chambers in the last whorl. *Discospirina italica* = *Pavonina italica* COSTA 1853 = *Orbitolites tenuissima* CARPENTER 1883, is classified in this family because the nepiont is obviously ophthalmitid but the later chambers are of peneroplid type with partitions that do not reach the distal septum. The Peneroplidae typically have many chambers per whorl when spiral, even in the microspheric nepiont, but they often have a deuteroconch in the megalospheric generation that occupies a half to a whole whorl. It is therefore possible that the Peneroplidae are derived from the Ophthalmitidae, but this is not proven.

#### Superfamily Lituolidea GLAESSNER 1945.

Most of the species of the superfamily Lituolidea have shell material mainly formed of agglutinated grains, with a microgranular matrix. A considerable number of species lack obvious agglutinated grains but, when fresh, the texture of their shell material is

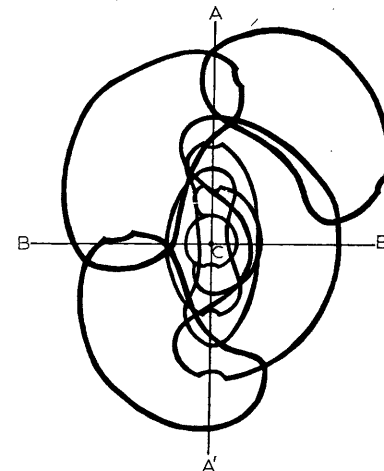


Fig. 5. Evolute test corresponding to Fig. 4, viewed as if transparent.

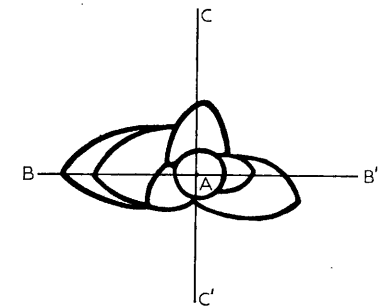


Fig. 6. Axial section of an evolute test of miliolid type.

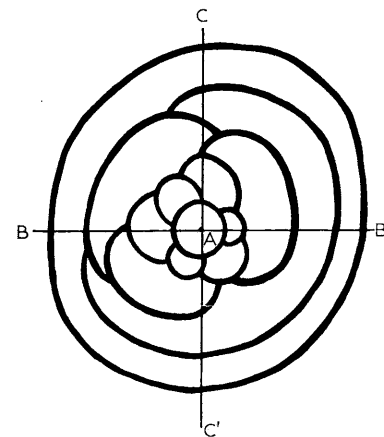


Fig. 7. Axial section of a test that is initially evolute but terminally hyperinvolute, after the manner of *Periloculina* and *Lacazina*.

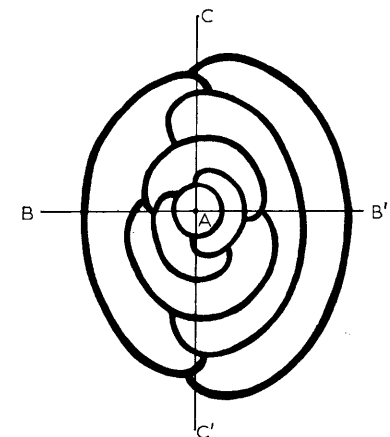


Fig. 8. Axial section of a precisely involute test, as is typical of the Alveolinidae.

Fig. 4-8. Diagrams to show the relationship of the milioline coiling to the equatorial plane, and the effect of variation in the degree of involution of the chambers in a streptospiral test.

obviously different from that of Foraminifera with porcellaneous test. Unfortunately the distinction between these types of shell material cannot be made in practice for many species of fossil Foraminifera, for minor diagenetic alteration produces the same final appearance in both, were there no agglutinated grains. In such cases, distinction between fossil porcellaneous genera and some of the Cyclamminidae becomes a matter of comparative anatomy and the nature of the shell material is deduced from this. The Lituolidea characteristically have the apertures in the central part of the chamber, as in the Peneroplidae and this feature serves to distinguish them from the Alveolinidae.

They commonly have subepidermal partitions; primary ones running in the direction of growth and secondary ones parallel and transverse to the septa, cutting the subepidermal region into roughly square cellules. When the partitions are exceptionally thick, the cavities of the cellules become tubular and are described as alveoles. When partitions parallel to the septa are present, the species cannot belong to the porcellaneous families. However, there are species of the Lituolidae that have primary subepidermal partitions only and distinction of such fossil species from the Peneroplidae, or sometimes even the Alveolinidae, can present difficulty.

Genera belonging to the superfamily Lituolidea that have been wrongly included in porcellaneous families are:

*Saudia* HENSON 1948; Meandropsinidae HENSON (1948), Peneroplidae HENSON (1950) and GRIMSDALE (1952).

*S. discoidea* HENSON 1948 (type species).

*S. labyrinthica* GRIMSDALE 1952.

*Pseudorbitolina* DOUVILLÉ 1910; Meandropsinidae HENSON (1948), Peneroplidae HENSON (1950).

*P. marthae* DOUVILLÉ 1910 (type species).

*Broeckinella* HENSON 1948; Meandropsinidae HENSON (1948), Peneroplidae HENSON (1950).

*B. arabica* HENSON 1948 (type species).

All the species listed have subepidermal cellules of lituolid type, formed by subepidermal partitions that are parallel to the septa as well as interseptal partitions.

The genera *Mangashtia* HENSON 1948, *Zekritia* HENSON 1948, *Cyclolina* D'ORBIGNY 1826 and *Cyclopsinella* GALLOWAY 1933 are insufficiently described for reliable classification. They all lack subepidermal partitions and the interpretation of their structure is therefore difficult. None of them seem to have any close relationship to the family Alveolinidae.

Family Alveolinidae (EHRENBERG 1840, pro fam. Alveolinea) nomen corr., STEINMANN 1881.

#### (1) Nomenclature.

Alveolinidae is the first name for this family to be correctly formed from a generic name and therefore stands. American authors have advocated the use of Alveolinellidae e.g., CUSHMAN (1928), GALLOWAY (1933), LOEBLICH and TAPPAN (1961) on the grounds that *Alveolina* is a junior synonym of *Borelis*, and therefore cannot serve as the type of the family. However, these authors do not remove *Alveolina* from this family and Clause 54 (1) (a) of the *Additions to and modifications of the Règles internationales de la Nomenclature zoologique* (1953), states that a junior synonym may serve as the type of a family and that its use as such is not subject to amendment when its status is discovered. "Alveolinidae" has been accepted throughout the European literature, e.g., by REICHEL (1937), GLAESSNER (1945), SIGAL in PIVETEAU, (1952), POKORNÝ (1958) and RAUZER-CHERNOUSOVA and FURSENKO (1959). Owing to difficulties with their type species, both *Alveolina* and *Borelis* are properly regarded as

nomina dubia. However, *Alveolina* is in general use with a precise definition stated by REICHEL (1936) and must be regarded as a nomen conservandum.

#### (2) Diagnosis.

The shell material is imperforate calcite of porcellaneous texture, without agglutinated material. The major part of the test consists of involute chambers, planispirally arranged, more than two and usually six or more per whorl, each with its independent wall which is never extended to cover other chambers. The chambers are always infilled with endoskeleton, in which there are chamberlets running in the direction of growth, all opening into a preseptal canal (open space below the apertural face). Minor complexities of the chamber/cavity such as postseptal canals and bullae occur in some genera. The apertures are related to the chamberlets, often aligned with them or regularly alternating with them. In species where there is a subepidermal layer of serried chamberlets, there are corresponding apertures in alignment with them, making the chamberlets appear continuous from chamber to chamber when seen in tangential sections. The shape of the test is not diagnostic; it is usually fusiform or globular but may be lenticular or discoidal. Cyclical species are unknown and species with a uniserial termination are excluded. The microspheric nepiont usually shows milioline coiling. This is sometimes present in the megalospheric tests also, but more usually, the globular proloculus is succeeded by a "canal flexostyle" of about one half whorl, lying in the equatorial plane and succeeded directly by chambers of ephebic type.

#### (3) Discussion.

The precise structure of the milioline nepiont is very difficult to reconstruct. If it is truly milioline, the apertures of the chambers should lie on an approximately straight line in the equatorial plane, there being two per whorl and their centre lines being at progressively different angles to the equatorial plane. REICHEL (1937, fig. 13, 22) illustrates nepionts in which the coiling seems even more complex, but the difficulties of drawing and interpretation are so great that these figures may contain some errors. Until someone examines a series of juvenile specimens, presumably of a living species, accurate description will not be possible.

The regularity of the involution of the ephebic chambers of Alveolinidae is remarkable. They usually overlap the poles regularly and only to the extent necessary to avoid the formation of umbilical depressions. Chambers with short alar prolongations, leading to ontogenetic change to the evolute condition, are never found. When a terminal flange is formed to the spire, the chambers become very recurved and the alar prolongations very vorticiform, sometimes with meandrine kinks in them, but they still reach to the poles regularly. The flange can be pseudevolute, but the extreme vorticity of the alar prolongations causes the chambers, even of part of the last whorl, to be partly covered. For the appreciation of the pseudevolute condition, we are indebted to HENSON (1950). Where an involute test suffers a sudden increase in whorl height of the terminal flange, the later chambers have a very large part of their height above the margin of the previous whorl. The central part of the test, which alone receives the alar prolongations of the chambers and so appears involute, is then a very small part of the total, which appears to be evolute. The family Peneroplidae has a number of spe-

cies that show the formation of a terminal flange with strongly recurved chambers, terminating in cyclical chambers. In those cases where the spiral chambers are all involute, the cyclical chambers are all evolute nevertheless. There may be no equivalent structures to the alar prolongations but in rare cases there are lateral chambers arranged in a meandrine manner. If, as seems likely, the Alveolinidae invariably have involute chambers, it follows that the cyclical habit is impossible for them.

Practical distinction between the Alveolinidae and the Peneroplidae is usually obvious on the external shape of the test but this is not reliable, for *Fusarchaias* REICHEL 1952 is a fusiform peneroplid, while complanate species of alveolines exist. Peneroplids with heavily developed subepidermal partitons can have some resemblance to alveolinids with unusually large lumina of the chamberlets. The apertures of the Peneroplidae avoid the subepidermal zone of the chamber, while the apertures of those Alveolinidae which are most likely to be confused with them lie in alignment with the cortical layer of chamberlets, as well as in the more central part of the apertural face. The central part of the chamber of an alveolinid, particularly in the later whorls, may contain massive endoskeleton (the "couche basale") in which supplementary chamberlets are less regularly arranged than in the primary chamberlet layer, but there is never an open space or a zone with reticulate partitions or interseptal pillars, as often occurs in the Peneroplidae.

There is no known case of a species without endoskeleton in the chambers that in other respects resembles the Alveolinidae.

REICHEL (1931, 1936–1937) makes much use of the distinction between the "continuous" mode of chamberlet arrangement and the "alternating" mode. Some genera show these modes very clearly and the "continuous" mode is very conspicuous in the cases where the primary chamberlets form a serried subepidermal layer and the pre-septal canal lies internal to them, so that the chamberlets open into it by pores at their distal ends and it does not intervene between them and the septum. In such a case, the continuous alignment of the chamberlets from one chamber to the next is reinforced by the alignment of apertures putting the chamberlets into communication with those of the next chamber. In such cases, a tangential section through the cortical chamber layer may appear to show completely continuous chamberlets with no visible septa. One must remember that the necessity for the increase in the number of chamberlets in successive chambers causes irregularities in either mode of alignment and in some species this causes the alignment of chamberlets from chamber to chamber to be effectively random. It is usual to find that the apertures of one chamber are the origin of the chamberlets of the next.

REICHEL (1936–1937) produced the first clear account of the family Alveolinidae and adequate diagnoses of genera. Obviously, there is considerable value in conserving his generic nomenclature, which has come into wide use. Dissent from REICHEL's nomenclature is mainly from American authors, who have relatively few species represented by sparse records. Disturbance of American usage would be trivial compared to the large number of records from the Old World which have been given according to REICHEL's scheme.

The following genera have not been the subject of confusion and require no further comment:

*Alveolinella* DOUVILLÉ 1907 (type species *Alveolina quoyi* D'ORBIGNY 1826); Miocene – Recent.

*Bullalveolina* REICHEL 1936 (type species *Alveolina bulloides* D'ORBIGNY 1826); Oligocene.

*Cisalveolina* REICHEL 1941 (type species *Cisalveolina fallax* REICHEL 1941); Cenomanian.

*Flosculinella* RUTTEN 1914 (SCHUBERT in RICHARZ 1910, nomen nudum; type species *Alveolinella bontangensis* RUTTEN 1913); Oligocene and Miocene.

*Multispirina* REICHEL 1947 (type species *Multispirina iranensis* REICHEL 1947); Cenomanian.

*Ovalveolina* REICHEL 1936 (type species *Alveolina ovum* D'ORBIGNY 1826); Cenomanian and Turonian.

*Praealveolina* REICHEL 1933 (type species *Praealveolina tenuis* REICHEL 1933); Cenomanian – Senonian.

*Pseudedomia* HENSON 1948 (type species *Pseudedomia multistriata* HENSON 1948); Campanian and Maastrichtian. This genus was recognised by EAMES and SMOUT (1955) as belonging to the family Alveolinidae and an emended description is given below.

The remaining generic names, from which names for two major genera need to be taken, are the subject of serious nomenclatural difficulties. It is possible here only to state the difficulties and to indicate the designations which, if adopted by plenary decision, would establish the widely accepted usage based on REICHEL (1936–1937).

Genus *Alveolina* D'ORBIGNY 1826 (type species *Oryzaria boscii* DEFRANCE in BRONN 1825; designation of doubtful validity); Paleocene and Eocene.

There is no possibility of maintaining *Alveolina* as a valid name under the *Règles*, except by plenary decision. This is obviously essential, as *Alveolina*, as defined by REICHEL (1936), is in wide use with a precise meaning. American authors from CUSHMAN (1928) to LOEBLICH and TAPPAN (1961) have advocated its suppression, but the weight of usage in the Old World is so great that suppression would be quite impossible in practice. The American viewpoint has not been accepted in Europe because it offered no clear generic descriptions for the alternative names recommended in place of those used by REICHEL and because the reasons given for the suppression of *Alveolina* as a junior synonym were not entirely convincing. ELLES and MESSINA stated that PARKER and JONES (1860) have designated *Nautilus melo* FICHTEL and MOLL 1798 as the type of *Alveolina*. In fact, they stated that all specimens of *Alveolina* could be attributed to one species with several varieties and that "... for nomenclatorial purposes the first established specific appellation accompanied by varieties will serve well; ... *Alveolina melo* vars. *sabulosa*, *elongata*, etc.". This cannot be taken as a valid designation of type. The statement that PARKER and JONES (1865) designated *Milolites sabulosus* MONTFORT 1808 as the type of *Alveolina* is open to doubt; the writer has

not succeeded in finding the reference, but this species is believed to be synonymous with *Oryzaria boscii* DEFRANCE in BRONN 1825 which was designated as the type of *Alveolina* by DOUVILLÉ (1907). Unlike *M. sabulosus*, *O. boscii* is a species of the original list of *Alveolina*.

*Alveolina* has the following senior subjective synonyms;

*Miliolites* MONTFORT 1808 (type species *Miliolites sabulosus* MONTFORT 1808). This name is a junior homonym of *Miliolites* LAMARCK 1804 and is therefore invalid.

*Fasciolites* PARKINSON 1811 (type species *Alveolina schwageri* CHECCHIA-RISPOLI 1905). No species were named in the original description and in the first revision by YABE and HANZAWA (1929), *A. schwageri* was designated as type. GALLOWAY (1933) determined PARKINSON's figures as of *Alveolina oblonga* D'ORBIGNY 1826 and claimed, wrongly, that this species is the type. REICHEL (1936) placed *Fasciolites* as a subgenus of *Alveolina*; however, the nomenclature is doubly wrong for *Fasciolites* is (a) the senior name and must be applied to the whole genus if it is used at all, and (b) REICHEL left no species in *Alveolina* sensu stricto. The action that would restore legality with the least disturbance of REICHEL's nomenclature, would be the suppression of *Fasciolites*, having the effect of assigning to *Alveolina* s.str. those species which REICHEL assigned to *Fasciolites*, which include *A. boscii*, and leaving *Alveolina* as the senior name for the genus.

Junior names subjectively synonymous with part of *Alveolina* s.l. are:

*Flosculina* STACHE 1880 (type species *Flosculina decipiens* SCHWAGER 1883). *F. decipiens* was the first species to be attributed to this genus and was formally designated by GALLOWAY (1933) as the type. *Flosculina* was regarded by REICHEL (1936) as a synonym of *Alveolina* s.l. because in his opinion the presence of flosculinised whorls is a variable character of infra-specific value.

*Eoalveolinella* SILVESTRI 1928 (type species *Alveolina violae* CHECCHIA-RISPOLI 1905).

This name was proposed as a subgenus of *Alveolina* and REICHEL (1936) perpetuated this.

*Glomalveolina* REICHEL 1936 (type species *Alveolina ovulum* STACHE in SCHWAGER 1883). This name was proposed as a subgenus of *Alveolina*.

Genus *Neoalveolina* SILVESTRI 1928 emended by REICHEL, 1937 (type species *Alveolina bradyi* SILVESTRI 1927, designated by BAKX, 1932 = *Nautilus melo* var.  $\beta$  FICHTEL and MOLL 1798 = *Nautilus melo* s.str. as emended by neotype, proposed p. 265). Miocene to Recent.

The identity of *Nautilus melo* is discussed in the Appendix on selected species. There are three prior objective synonyms of *Neoalveolina*: *Borelis* MONTFORT 1808, p. 170, *Clausulus* MONTFORT 1808, p. 178 and *Melonia* LAMARCK in DEFRANCE 1822. *Neoalveolina* therefore cannot be used unless these names are suppressed by the Commission on Zoological Nomenclature, using its plenary powers.

*Clausulus* and *Melonia* have never come into general use and their suppression is unlikely to arouse any dissent. *Borelis* has been widely used. REICHEL (1937) advocated its suppression to protect *Neoalveolina* and the same arguments apply today. Its type species being *Nautilus melo* var.  $\beta$  FICHTEL and MOLL 1798, it is in fact the senior

synonym of *Neoalveolina* and it might seem a simple matter to substitute the name. Unfortunately, American authors have maintained that *Borelis* is a synonym of *Alveolina*. We have seen above that this is a misinterpretation of the nomenclatural situation. In view of the inadequate generic diagnoses given in American textbooks and the resulting confusion in naming species by those who attempt to follow them, it seems that the existing references would be more easily understood if *Neoalveolina* were used in preference to *Borelis* in future, forcing the reader to consider the correct generic meaning of each record of *Borelis*.

#### (4) Phylogeny.

The stratigraphical record of the family Alveolinidae begins low in the Cenomanian with small, globular species of *Praealveolina*. No contemporary or earlier species are known that look as if they might be ancestral to *Praealveolina*. At higher horizons, larger and more fusiform species of *Praealveolina* appear and three genera, *Cisalveolina*, *Ovalveolina* and *Multispirina* are found which may have been evolved from *Praealveolina*. *Praealveolina* alone is found in the Turonian and its only known successor, *Subalveolina*, is the sole Santonian-Lower Campanian representative of the Alveolinidae.

Complex Peneroplidae, such as *Edomia reicheli* and *Taberina bingistani*, occur in the Cenomanian. They are very unlike the Cenomanian Alveolinidae, being of typical peneroplid shapes and having the much more open type of endoskeleton. Their microspheric nepionts are planispiral rather than milioline and one would naturally look for an ancestral form among lenticular or ophthalmiid species rather than globular miliolid ones. A common origin of the Peneroplidae and the Alveolinidae seems unlikely.

*Pseudedomia* first occurs in the Campanian, possibly at a higher horizon than the last *Subalveolina*. It has no resemblance to that genus in detail but has the general praealveolinid organisation of "continuous" chamberlets and supplementary chamberlets in the "couche basale". The lenticular shape is merely a matter of proportions; the relationship of a globular form to it is the same in principle as to a fusiform test, the relationship being in the opposite sense, with the equatorial diameter increased relatively to the axial length.

Miliolidae that have tests suggestive of being ancestral to the Alveolinidae are not known certainly before the Lower Senonian. *Periloculina* MUNIER-CHALMAS and SCHLUMBERGER 1885, has endoskeleton that divided the chamber cavity incompletely into longitudinal chamberlets, leaving an open space below the cribrate aperture that can be compared to the preseptal canal of alveolines. However, *Periloculina* has milioline coiling and the chambers become increasingly involute, leading to *Lacazina* MUNIER-CHALMAS 1882, but not to genera of the Alveolinidae. *Fabularia* DEFRANCE 1820, has the same general type of endoskeleton but in the type species there are two chambers per whorl that are strictly involute, not hyperinvolute. In other species, possibly better placed in *Raadshoovenia* VAN DEN BOLD 1946, the test passes through a planispiral stage into a uniserial development. In spite of the close parallel in organi-

sation, it seems most unlikely that the Cretaceous Alveolinidae can have evolved from these miliolids.

No direct link has been found between the Alveolinidae of the Cretaceous and the Tertiary. *Alveolina* is the only genus known from the Paleocene to the Middle Eocene. It parallels *Praealveolina* by starting with small, globular, species and developing larger, fusiform ones but it contrasts in having a strongly developed postseptal canal and alternating chamberlets. It has no resemblance to *Pseudedomia* and is most likely to have arisen independently of the Cretaceous Alveolinidae; possibly from *Raadshovenia*. *Alveolina* became extinct early in the Auversian and Alveolinidae are absent from most of the Upper Eocene. *Borelis* has been recorded in the Upper Eocene, but very rarely and because the beds may involve severe reworking, there is a possibility of stratigraphical revision of the occurrence. *Borelis* occurs abundantly in the lower Miocene and probably arose from some miliolid rather than from *Alveolina*, because both the microspheric and megalospheric generations have a milioline nepiont. The other Alveolinidae have a planispiral megalospheric stage although the microspheric nepiont is milioline (except perhaps in *Pseudedomia*). *Bullalveolina*, known only from the Oligocene, is of unknown origin. It has the primitive globular shape but the details of its apertural complexities are not suggestive of its being a link between *Alveolina* and *Borelis*. *Borelis* survives to the present day and *Flosculinella* (Miocene) and *Alveolinella* (Miocene to Recent) are obviously derived from it, showing more complex chambers and being more fusiform.

It seems probable that the family Alveolinidae represents one particular mode of specialisation of the family Miliolidae that has been followed by several lineages independently.

#### THE GENUS PSEUDEDOMIA HENSON 1948, EMENDED.

Type species *Pseudedomia multistriata* HENSON 1948, original designation.

#### (1) Diagnosis.

HENSON's original description was based on inadequate material and, as he foresaw, it has needed amendment although the genus was sufficiently well described to be easily recognisable. EAMES and SMOUT (1955) gave the following amended description: "Test porcellaneous, imperforate, lenticular (probably to globular), becoming discoidal in the microspheric form, planispiral, involute, spire simple, chambers subdivided as in *Praealveolina*, with the addition of buttresses in the preseptal canal. Microspheric form with a terminal flange of strongly recurved chambers which may attain a final cyclical arrangement; alar prolongations becoming vorticiform and sometimes meandriform. Dimorphism pronounced." To this must be added: The earliest clearly visible whorls, even in the microspheric test, are planispiral, but the first one or two have not been clearly seen and may prove to be streptospirally coiled. Cyclical median chambers have not been observed, although the extreme recurvature of the later chambers approaches

the cyclical condition. The alar prolongations of the later chambers of the microspheric form may be strongly vorticiform, with meandriform flexures, but in all cases where they are clearly visible, they run continuously from the median layer to the poles and there are no meandrine lateral chambers, such as are sometimes seen in *Meandropsina*. The buttresses in the preseptal canal are typically confined to a region near the equatorial plane; the earlier chambers have only one per chamber and these are then inconspicuous and easily overlooked. The primary chamberlets form a serried cortical layer with "continuous" arrangement. Less regularly arranged supplementary chambers are found in the "couche basale" of the later chambers only. Apertural pores correspond strictly to the chamberlets, except for irregularities caused by intercalation as the chambers become successively larger. No complexities associated with the apertures have been seen.

#### (2) Remarks.

The radical changes from HENSON's description of this genus are fully justified by the redescription of the type species, below. *P. multistriata* HENSON 1948 and *P. complanata* EAMES and SMOUT 1955, are very closely similar, differing in minor characters of size and proportions only. A third species is added here, again differing in proportions only. The generic differentiation from all previously named genera of the Alveolinidae is based on the presence of the complanate flange of the microspheric form. *Borelis cardenasensis* shows characters which seem to differentiate it from the species of *Pseudedomia*, and additional characters have been cited to provide a differential diagnosis from such species.

HENSON (1950) placed *Pseudedomia* in the synonymy of *Taberina* KEIJZER 1945, of the family Peneroplidae. *Taberina cubana* KEIJZER 1945, the type species, is a typical Tertiary peneroplid with a mainly spiral test that is terminally uniserial and has subepidermal partitions and interseptal pillars. The distinction of *Taberina* from *Pseudedomia* now made is not unexpected for HENSON (1950) remarked: "There is difficulty in accepting any direct linear relationship between the complex Cretaceous members of the Peneroplineae and those of Tertiary and Recent times that have similar structure".

#### (3) Occurrence.

*Pseudedomia* has so far been recorded only from the Campanian and Maastrichtian of Arabia and Iraq. It occurs mostly in shallow water limestones of lagoonal type.

#### (4) Key to species.

Test initially globular: . . . . . *P. globularis*

Test initially lenticular:

Form B over 5 mm diameter; form A with

numerous supplementary chamberlets: . . . . . *P. complanata*

Form B under 5 mm diameter; form A with

very rare supplementary chamberlets: . . . . . *P. multistriata*

*Pseudedomia multistriata* HENSON 1948

See Plate I, 1–6.  
Specimens: Holotype, British Museum (Natural History) P. 35961–2.  
Topotypes, P. 42638, 42641.  
Other specimens, P. 42639–40.

*Redescription of the microspheric form*

The holotype is still the only specimen known and it at present exists as two thin sections, one approximately equatorial, but varying because the test was thin and wavy. The second section is tangential – vertical and it is possible to see on the first section where the piece for the second was cut off. HENSON (1948) stated: “Test flabelliform; early stages planispiral, evolute, with whorls opening rapidly; later chambers serial, arcuate, tending to become cyclical; . . .”. This description is not supported by drawings or photographs and it is not compatible with what is now known about comparative morphology. The chambers were probably pseudevolute rather than evolute, the last whorl being so much larger than the earlier ones that the involute central part went unnoticed. There seems to have been no polar swelling. “Serial” seems to imply that the later chambers formed an aduncate termination to the spire. The present appearance of the section suggests this, but a reconstruction could also be made showing persistence of the spiral habit. The later chambers are strongly arcuate and subtend a considerable part of the margin of the test, but there is no proof that cyclical chambers were present and it is more probable that the spiral habit held throughout, as in all other alveolines.

The internal structure revealed by the equatorial section shows the chambers occupied with massive endoskeleton. There is a narrow preseptal canal, traversed by numerous pillars. Where the section is deep within the chamber, the endoskeleton is traversed by thin, widely spaced, chamberlets. Where the section is superficial, the chamberlets are much more closely spaced and they are continuous from one chamber to the next, the apertures through the septa being of exactly the same diameter as the chamberlets, so that the septa are not distinguishable. The preseptal canals lie too deep in the chamber to be seen in this part of the section. The early whorls are not seen clearly but it seems that they were planispiral and had fairly widely spaced, nearly straight septa, with the usual infilling of endoskeleton. Comparison with the better-known species *P. complanata* EAMES and SMOUT 1955 and *P. globularis* nov. sp. leaves no doubt that there is identity of structure, the differences being only in size and proportions.

The vertical section was prepared from a portion cut from the outer part of the flange. It is very obscure and it is doubtful if any features described from it are trustworthy, but a drawing of its possible features is given (Plate I, 6). It shows a rounded margin with chamberlets or more probably the preseptal canals of three chambers on the right-hand side. Five large, black, spots in the central part of the section were thought by HENSON (1948) to be interseptal buttresses, but they are too large; more probably they are post-mortem damage to the test. Faint pattern on

each side of this section may indicate alar prolongations of the last two or three chambers, although, because the section is confined to the last five chambers, it would indicate very extreme vorticity, and is more probably a false indication.

*Description of the megalospheric form*

The test is lenticular with a subacute margin and flat poles. The exterior is smooth and the septal sutures flush. There is no umbilical depression. Decorticated specimens show about six chambers per whorl with narrow preseptal canals and serried “continuous” chamberlets, their walls being slightly narrower than their cavities. The megalosphere is small and spherical. The margin is more acute in the early whorls than in the later ones. Occasional supplementary chamberlets occur in the “couche basale” of the chambers of the last two whorls, near the equatorial plane. No buttresses have been seen in the preseptal canal; one per chamber, near the equatorial plane would be expected but only an exceptionally well-orientated section would intersect one.

*Dimensions of microspheric form:*

Maximum observed equatorial diameter . . . . .	3.5 mm
Thickness at periphery . . . . .	0.26 mm
Primary chamberlets, diameter . . . . .	0.007 mm
spacing . . . . .	30 per mm
Subsidiary chamberlets, diameter . . . . .	0.009 mm
spacing . . . . .	17 per mm
Height of preseptal canal . . . . .	0.01 mm
Diameter of buttress . . . . .	0.04 mm

About three whorls are visible, with sixteen visible chambers in the last whorl. It is estimated that there were at least six whorls with about six chambers in the third to fifth whorls and over twenty in the last whorl.

*Dimensions of megalospheric form:*

Maximum observed diameter . . . . .	2.3 mm
Thickness at axis . . . . .	0.8 mm
Primary chamberlets, diameter . . . . .	0.007 mm
spacing . . . . .	30 per mm
Diameter of proloculus . . . . .	0.15 mm

There are about seven whorls with six to seven chambers in the last whorl.

*Remarks*

After describing *Pseudedomia complanata* EAMES and SMOUT 1955, it was evident that the megalospheric form of *P. multistriata* HENSON 1948 should be lenticular, probably rather compressed, and about 2 mm in diameter. Its primary chamber layer would have the same characteristics as that of the holotype and there should be about 6 chambers in the last whorl. Examination of material of similar age to the type locality, and at the type locality itself, yielded a few specimens that conformed to



expectations. They are nowhere abundant, mostly occurring in hard limestone, and only a single specimen showing the test in the round was found. It is only the knowledge gained from the more abundant material of *P. complanata* that has enabled *P. multistriata* to be described reliably.

Occurrence

Maastrichtian limestones of shallow water facies, in association with *Omphalocyclus macropora* (LAMARCK 1816); *Siderolites calcitrapoides* LAMARCK 1801, *Rotalia trochidiformis* (LAMARCK 1801); *Fissoelphidium operculiferum* SMOUT 1955; *Elphidiella multiscissurata* SMOUT 1955; *Orbitoides apiculata* SCHLUMBERGER 1901 and *Loftusia* spp.

Localities: Deep Boreholes at Jebel Dukhan, Qatar Peninsula of Arabia; Ratawi, Southern Iraq; other possible occurrences have been noted but poor preservation makes their recording undesirable.

*Pseudedomia globularis* nov. sp.

See Plate II, 1–18.

Specimens: Holotype, British Museum (Natural History) P. 42643.  
Paratypes, P. 42642, 42644–6.

Description

Dimorphism is slight, the external appearance of the test being much the same in both generations and there being no known difference of size. The immature test is globular with about eight chambers per whorl, after which it becomes lenticular and

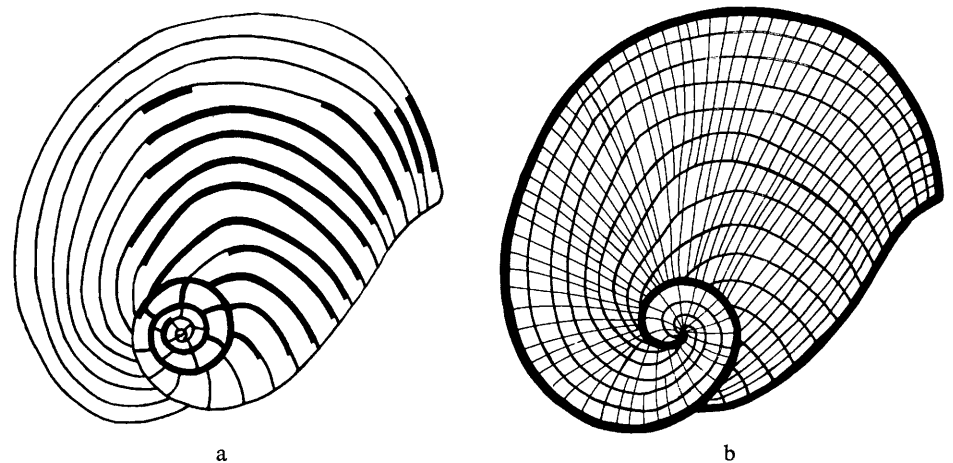


Fig. 9. *Pseudedomia multistriata* HENSON 1948. a. Reconstruction of the equatorial section of the holotype, lines actually seen bold, endoskeleton omitted; b. Reconstruction of the external appearance of the holotype, viewed from the side.

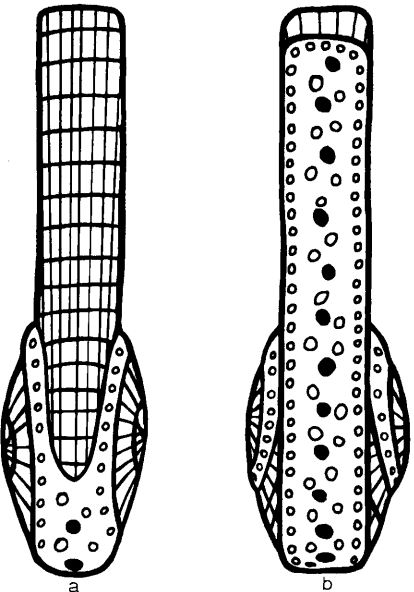


Fig 10. *Pseudedomia multistriata* HENSON 1948. Reconstructions of the external appearance of the holotype, viewed from the edge.

finally develops a large, narrow, pseudevolute flange with strongly recurved chambers. The alar prolongations of the final chambers have not been observed, which suggests that they are probably almost radially directed. There is a serried subepidermal layer of primary chamberlets of “continuous” type. Numerous supplementary chamberlets lie in the “couche basale”. They are larger than the primary chamberlets and spaced more widely. They are very irregularly arranged. In the early chambers they disturb the regularity of the primary chamberlet layer and in the very early chambers only primary chamberlets are present. The preseptal canal is abundantly provided with buttresses of irregular shape. The megalosphere is succeeded by a “canal flexostyle” in the equatorial plane of about a quarter of the whorl length. The microspheric nepiont has been seen only obscurely but it is probable that it is milioline.

Dimensions

Estimated equatorial diameter of a large specimen . . . . .	3.20 mm
Diameter of globular part of the test in the equatorial plane, approx. . . . .	2.0 mm
Thickness at axis of coiling . . . . .	1.6 – 2.0 mm
Thickness of flange at periphery . . . . .	0.6 – 0.8 mm
Primary chamberlets, diameter . . . . .	0.003 – 0.007 mm
spacing. . . . .	11 – 25 per mm
Supplementary chamberlets, diameter . . . . .	0.005 – 0.008 mm
Height of preseptal canal. . . . .	0.01 mm
Diameter of megalosphere . . . . .	0.2 – 0.3 mm
Maximum chamber height in flange . . . . .	1.1 mm

### Occurrence

Known only from the Bekhme Limestone formation of Campanian age at Bekhme Gorge, Northeastern Iraq. The occurrence is in limestone of shallow water facies.

### Remarks

This species is known only from very hard limestone and therefore has been seen only in random sections. The globular shape of the immature test and the strongly pseudovolute nature of the terminal flange distinguish it from the other species of the genus.

This species was referred to by Dunnington *et al.* (1960, p. 61) as *Cosinella* nov. sp. REICHEL M.S.

### APPENDIX

Notes on selected species of taxonomic interest, mainly of "*Orbitolites*" s.l.

The locality of a number of type specimens is quoted as "Challenger station no. 172". BRADY (1884) stated that this material was collected on July 22, 1874 off Nukualofa, Tongatabu, Friendly Islands, from a coral bottom at 18 fathoms.

#### *Orbitolites complanata* LAMARCK 1801

Selected synonyms:

*Orbitolites complanata* LAMARCK, 1801 [LAMARCK (1801), 376].

*Orbitolites complanata* LAMARCK; CARPENTER [(1856), 226/tabula 6, fig. 9].

*Orbitolites complanata* LAMARCK; DOUVILLÉ [(1902), 296–297/textfig. 5, 6].

Non *Orbitolites complanata* LAMARCK; CARPENTER (1883).

Non *Orbitolites complanata* LAMARCK; BRADY (1884).

This is a very well known and widespread species which has an authentic type deposited in the Musée d'Histoire naturelle, Paris. There is no other species with which it could easily be confused at the type locality and it is readily distinguished from all other species of the Orbitolitinae. CARPENTER (1883) and BRADY (1884) wrongly determined specimens of *Marginopora vertebralis* as this species, as was pointed out by DOUVILLÉ (1902).

In this species the subepidermal zone is very thin, almost vestigial, and the apertural pores are almost randomly scattered in a wide band that occupies almost the whole of the margin. The apertures are roughly aligned in transverse rows. Partitions run from side to side of the chamber, occasionally anastomosing with each other but mostly distinct. The partitions are strongly fluted with an aperture at the end of each groove. There are no holes through the partitions to put the cellules of the same chamber in direct communication with each other. The equatorial section and any sections parallel to it have a deceptive appearance of cycles of small arcuate chambers. This is caused by the twisted partitions, but it will be noted that superficial sections parallel to the axis show the partitions very clearly, and they can be observed readily on broken specimens.

#### "*Orbitolites*" *orbiculus* (FORSKÅL 1775)

See Plate IV, 3, 4.

*Nautilus orbiculus* FORSKÅL, 1775 [FORSKÅL (1775), 125].

*Sorites orbiculus* FORSKÅL; EHRENBERG [(1840), 144–145/tabula 1, tabula 2, fig. 2 a–d].

Neotype: British Museum (Nat. Hist.) specimen no. 1961.11.10.10.

Origin: Recent; Gulf of Aqaba, Red Sea, collected by Dr. F. R. S. HENSON.

The test is discoidal; outline sometimes irregular; margin only slightly thicker than the centre; sutures depressed. The chambers are annular, with subepidermal partitions that are randomly inserted on either side but fuse in pairs across the central zone in many cases, always leaving a central hole if not a gap. The cellules so formed are inflated marginally, giving the appearance of arcuate chambers disposed in cycles. The apertures lie in a slight central sulcus, roughly in a single to double row, roughly aligned with the partitions. The megalospheric (or very large microspheric?) proloculus is followed by an undivided deuteroconch, succeeded by about four spiral chambers with partitions and four or more reniform chambers. The spiral and reniform chambers are involute, their alar prolongations forming a small central star on the exterior. Maximum diameter of the test about 3 mm.

FORSKÅL's description is inadequate to differentiate this species from other *Orbitolites* and it is only by inference that the species is placed as originating in the Red Sea. EHRENBERG (1840) published a redescription and figures that have been widely accepted as characteristic of this species and the Neotype specimen has been chosen from specimens from the Red Sea which agree very closely with EHRENBERG's figures. There can be little doubt that the species described as *Sorites orbiculus* by LACROIX (1959) is the same species, but he did not figure external views.

*Orbulites marginalis* LAMARCK 1816 and *Amphisorus hemprichii* (EHRENBERG 1840) are only varietal forms of this species. "*O.*" *marginalis* is small with a larger, bicellular, nucleconch and reduced involute, spiral stage. "*O.*" *hemprichii* is thicker with more inflated cellules and the apertures more definitely arranged in a double row; it should not be confused with "*O.*" *duplex*.

#### "*Orbitolites*" *marginalis* (LAMARCK 1816)

See Plate IV, 5, 6.

*Orbulites marginalis* LAMARCK 1816 [LAMARCK (1816), 196].

Neotype: British Museum (Nat. Hist.) specimen no. 1961.11.10.9.

Origin: Recent, shore near Priola, Sicily, Mediterranean Sea, collected by Dr. F. E. EAMES.

The test is discoidal; outline and chambering sometimes irregular; margin only slightly thicker than the centre; sutures depressed. The chambers are annular, with subepidermal partitions that are randomly inserted on either side but fuse in pairs across the central zone in many cases, always leaving a central hole if not a gap. The

cellules so formed are inflated marginally, giving the appearance of arcuate chambers disposed in cycles. The apertures lie in a slight central sulcus, roughly in a single to double row, roughly aligned with the partitions. The nucleoconch is megalospheric, consisting of a deuteroconch enclosing the proloculus, followed by one undivided chamber and a few evolute spiral chambers that are divided by partitions, passing through a reniform stage of a few chambers before the annular ephebic type of chamber is produced. Maximum diameter of the test about 2 mm.

LAMARCK's description indicated a discoidal species of about 2 mm diameter with a porous margin found in the Mediterranean Sea. The specimen selected as a Neotype satisfies this in all details. MARIE (1940) stated that he had searched for LAMARCK's specimens and failed to find them, so the present erection of a new type is necessary. MARIE noted that DESHAYES and EDWARDS (1836) in their re-editing of LAMARCK's work stated that this species has two layers of chambers. This persistent error of description affects a number of species of the Orbitolitinae and need not be taken seriously. When the cellules of an annular chamber are marginally inflated, the test appears superficially to be two-layered. Specimens of this type are strictly regarded as "*O. hemprichii*" but are thought to be conspecific with this species, which typically shows only slight marginal inflation of the cellules and has the apertures almost in a single row. "*O. orbiculus*" seems to be a senior synonym. It typically differs in the nepiont; "*O. marginalis*" may be the  $A_1$  form of "*O. orbiculus*", which is itself probably B, or  $A_2$ .

CARPENTER (1883) applied the name *O. marginalis* LAMARCK to the species here named "*O. carpenteri*". This is a much larger Pacific species not reliably recorded from the Mediterranean Sea, in which the chambers are obviously annular and the apertures are transverse slits arranged in a single row. Many authors have erroneously followed CARPENTER's use of the name, but LACROIX (1955) has correctly placed it in the synonymy of "*O. orbiculus*". His opinion carries great weight since he made a special study of Red Sea and Mediterranean Sea species.

"*Orbitolites*" *hemprichii* (EHRENBERG 1840).

*Amphisorus Hemprichii* EHRENBERG 1840 [EHRENBERG (1840), 130/tabula 3, fig. 3].

Neotype: British Museum (Nat. Hist.) specimen no. 1962. 6. 26.1.

Origin: Recent, Gulf of Aqaba, Red Sea, collected by Dr. F. R. S. HENSON.

The test is discoidal; outline sometimes irregular; margin thicker than the centre, sutures strongly depressed. The chambers are annular, with subepidermal partitions that are randomly inserted on either side but fuse in pairs across the central zone in many cases, always leaving a central hole if not a gap. The cellules so formed are strongly inflated marginally, giving the appearance of arcuate chambers disposed in cycles. The apertures lie in a well-developed central sulcus in slightly offset pairs, rarely in threes in later chambers. The apertures thus form two rows. The type specimen is probably microspheric or  $A_2$  megalospheric but the species is probably

trimorphic. The microspheric test has the proloculus followed by two undivided chambers, succeeded by about four spiral chambers and a few reniform chambers. The nepionic chambers are involute, their alar prolongations forming a central star as in "*O. orbiculus*". Maximum diameter of the test about 3 mm.

The selection of a Neotype which is not from EHRENBERG's collection requires justification. It is understood from Dr. K. DIEBEL, who has generously offered any help in his power, that the EHRENBERG collection is preserved in East Berlin; most of the specimens being in spreads of canada balsam on glass. The identification of specimens as syntypes is likely to be subjective and there is no guarantee of even this limited success.

The specimen from Akaba in the British Museum (Nat. Hist.) agrees well with EHRENBERG's description and figure and there is no reason to doubt that it represents the species that EHRENBERG intended. A further consideration in making an immediate designation of type is the convenience in having the types of *A. hemprichii*, *Nautilus orbiculus* and *Orbitolites marginalis* in the same depository, where direct comparison is possible. It is also a matter of urgency because of the theoretical implications on the description of the subfamily Orbitolitinae and its genera.

EHRENBERG's description and figure leave no doubt that this species has the general appearance of "*O. orbiculus*", probably even to being the same size. The Neotype specimen has been chosen from specimens from the Red Sea that meet these requirements. No specimens are known in which two layers of chambers are actually present, but specimens such as that chosen have a high degree of inflation of the cellules marginally, which gives an appearance like two layers of chambers arranged in cycles.

CARPENTER (1883) identified specimens of "*O. duplex*" or a species closely allied to it from the Red Sea as *A. hemprichii* and many subsequent authors have followed his synonymy. It seems unlikely that Ehrenberg would have omitted to mention the notable differences of this species from "*O. orbiculus*", if it were the species that he had in mind. In describing *A. hemprichii* as generically distinct from *S. orbiculus* (sic!), the distinction between one and two layers weighed very heavily with EHRENBERG, for he thought that he was describing Bryozoa.

*A. hemprichii* is merely a varietal form of "*O. orbiculus*" and there seems to be complete gradation between them in some populations. They differ only in the degree of inflation of the cellules and a slight difference in the apertural pattern. Microspheric specimens are likely to show the *hemprichii* characters more often than megalospheric ones.

"*Orbitolites*" *carpenteri* nomen novum

*Orbitolites marginalis* LAMARCK; CARPENTER [(1883), 20-25/tabula 3, fig. 1-7; tabula 4, fig. 1-5] non LAMARCK 1816.

Holotype: British Museum (Nat. Hist.) specimen no. 1961.11.10.7.

Origin: Recent, Fiji reef; Challenger station no. 172.

The test is discoidal, rarely fluted or flanged; margin only slightly thicker than the centre. The subepidermal partitions are spaced at about the chamber height and are

strongly developed, leaving a hole in the central zone of the chamber. The apertural pores are transversely elongate and form a single row; each is aligned over the hole in the fused part of the subepidermal partition. The megalospheric nucleococonch consists of three chambers but the third is small and in obvious spiral succession; there are about four spiral chambers and about four reniform chambers before the annular habit is assumed. Maximum diameter of the test is about 6 mm. This species is trimorphic with some variation in the size of the test.

The specimens described by CARPENTER (1883) as "*O.*" *marginalis* are most unlikely to be conspecific with the specimens given the name by LAMARCK; they were from the Pacific Ocean, not the Mediterranean Sea, and many specimens attain a size two or three times the 2 mm cited by LAMARCK. These specimens have a strong resemblance to "*O.*" *duplex*, but differ in the structure of the megalospheric nucleococonch and in the possession of only a singly row of apertures. It is highly desirable that this form should receive a distinct name. It is the species described by DOUVILLÉ (1902) as typical of *Sorites*.

The specimen selected as Holotype may have been the original of the drawing by CARPENTER [(1883), tabula 3, fig. 1].

"*Orbitolites*" *duplex* CARPENTER 1883

*Orbitolites duplex* CARPENTER 1883 [CARPENTER (1883), 25–29/tabula 3, fig. 8–14; tabula 4, fig. 6–10; tabula 5, fig. 1–10].

Lectotype: British Museum (Nat. Hist.) specimen no. 1961.11.10.1.

Origin: Recent, Fiji reef; Challenger station no. 172.

The test is discoidal, sometimes with accessory flanges that are more or less radial, rarely slightly fluted; margin moderately thicker than the centre; sutures almost flush. The subepidermal partitions are spaced at about the chamber height and are strongly developed, leaving a small empty central zone which is sometimes crossed by buttresses. The apertural pores are transversely elongate and form two rows, the arrangement in each row being random with respect to the other. The megalospheric nucleococonch has three chambers and is directly succeeded by annular chambers. This species is trimorphic. Maximum diameter of the test about 8 mm.

The specimen here designated as lectotype is possibly the specimen used in drawing pl. 3, fig. 8 of CARPENTER (1883), selected from the syntypes of CARPENTER's collection; its authenticity is beyond doubt.

ELLIS and MESSINA state that this is a new name. If so, it would have to be considered a junior synonym of *Amphisorus hemprichii* EHRENBERG 1840, for this is the oldest species named in CARPENTER's synonymy. However, CARPENTER did not state that *duplex* was a new name formally; in his text he said "... these (specimens) I could pretty certainly identify with the forms on which Professor EHRENBERG had founded his genus *Amphisorus*...". This is a qualified identification and refers to specimens from the Red Sea, whereas the description of "*O.*" *duplex* was explicitly founded on specimens from the Fiji reefs in the Pacific. The identity of *A. hemprichii* has been the subject of some discrepancies in the literature and therefore a Neotype has been

proposed here which agrees in all respects with EHRENBERG's description and figure. It is a specimen closely resembling "*O.*" *orbiculus*. "*O. duplex*" occurs in the same sample and is specifically quite distinct.

"*Orbitolites*" *vertebralis* (QUOY and GAYMARD in BLAINVILLE, 1830)

*Marginopora vertebralis* QUOY and GAYMARD in BLAINVILLE, 1830 [BLAINVILLE (1830), 377 (Vol. 60)].

*Orbitolites complanatus* LAMARCK; CARPENTER [(1883) 29–43/tabula 5, fig. 11–18; tabula 6–7], non LAMARCK, 1801.

Neotype: British Museum (Nat. Hist.) specimen no. 1961.11.10.8.

Origin: Recent, Fiji reef; BRADY collection, probably Challenger Station no. 172.

The test is discoidal, occasionally irregularly fluted; margin considerably thicker than the centre; sutures almost flush. The subepidermal partitions are spaced at less than the chamber height and the subepidermal zone is narrow. The central zone is traversed by irregular and incomplete partitions. The apertures are small, circular pores arranged randomly in a broad band. The megalospheric nucleococonch has three chambers, followed directly by annular chambers with partitions. This species is probably dimorphic. Maximum diameter of test 20 mm.

It is a reasonable inference from the mention of QUOY that this species is from the Pacific Ocean and the original description fits the specimen now designated as the Neotype. No indication has been found in the literature of the location of the specimens available to BLAINVILLE (1830).

This species is highly distinctive; the closeness of the subepidermal partitions and the small, numerous apertural pores scattered in a wide median band round the margin, are not paralleled by any other living species of the Orbitolitinae. It is sharply distinct from "*O.*" *duplex*, and has little resemblance to the Eocene species *O. complanatus*. The latter species has transverse rows of apertural pores associated with fluted partitions. CARPENTER figures a protracted development of complex annular chambers with numerous pores and complex buttresses between them from simple chambers with subepidermal partitions only. In most megalospheric specimens the ephelic type of chamber is established by the fourth or fifth chamber.

"*Orbitolites*" *vertebralis* var. *plicata* (DANA 1848).

*Marginopora vertebralis* QUOY and GAYMARD in BLAINVILLE (1830), var. *plicata* DANA 1848 [DANA (1848), 706/tabula 60, fig. 9, 9a, 9b].

*Orbitolites laciniatus* BRADY 1881 [BRADY (1881), 47].

*Orbitolites complanata* var. *laciniata* BRADY (sic!); CARPENTER [(1883), tabula 7].

*Orbitolites complanata* var. *laciniata* BRADY 1884 [BRADY (1884), 220–221/tabula 14, fig. 8–11].

Lectotype: British Museum (Nat. Hist.) specimen no. 1959.5.5.772, figured by BRADY [(1884), tabula 16, fig. 10a, b].

Origin: Recent, Fiji Reef; Challenger station no. 172.

The test is discoidal but very highly fluted, the margin being doubled or trebled in most specimens. The margin is considerably thicker than the centre. The subepidermal partitions are spaces more closely than the chamber height and the subepidermal zone is very narrow. The central zone is filled in the earlier chambers by partitions with holes in them, but in later chambers the central zone is occupied by slender pillars. The apertures are small and circular and arranged in a broad band. The megalospheric nucleocoenoch is thought to be three-chambered and is probably not significantly different from that of *M. vertebralis*. Maximum diameter of test about 25 mm.

This form was described as a variety of *Marginopora vertebralis*, and this is probably correct. It should however be noted that it is a very distinct variety and that the very frank development of pillaring is not comparable in *M. vertebralis* s.str., being much more crowded into dubious partitions in that form. The majority of specimens fall into one of two groups, those with a more or less simple disc and those with the lacinate habit.

*Orbitolites* "mouretti" (DOUVILLÉ 1902)

*Praesorites mouretti* DOUVILLÉ 1902, [DOUVILLÉ (1902), 291–293/tabula 9, fig. 1–4].

*Praesorites mouretti* DOUVILLÉ; HENSON [(1950), 54–55/tabula 10, fig. 1].

*Praesorites mouretti* DOUVILLÉ; MARIE [(1958), 130/tabula 1, fig. 9–11].

Lectotype: the specimen figured by DOUVILLÉ [(1902), tabula 9, fig. 1]; collection of the École des Mines, Paris; collected by M. ARNAUD; Lower Campanian P. I., Saint-André, Charentes, France.

This specimen has been seen by myself and has been redescribed by HENSON (1950) and MARIE (1958).

MARIE (1958) stated that the megalospheric nepiont of this species is slightly twisted to one side of the median plane. He figured partitions in a reniform deuteroconch; a very unusual feature in the Orbitolitinae, for most species have no endoskeleton until the third or some later chamber. MARIE's figures are conventionalised drawings. The figure by HENSON (1950, pl. 10, fig. 1), a topotype specimen, shows that the subepidermal partitions are completely inter-septal but that their extensions into the otherwise empty central zone of the chamber penetrate more deeply proximally than distally. DOUVILLÉ's figures show a double row of apertures (although not on topotype specimens), but MARIE reports a single row of apertures. DOUVILLÉ is more probably correct.

"*Orbitolites*" *dufrenoyi* (D'ARCHIAC 1854)

*Cyclolina dufrenoyi* D'ARCHIAC 1854 [D'ARCHIAC (1854), 203/tabula 2, fig. 1 a–d].

*Broeckina dufrenoyi* (D'ARCHIAC); MUNIER-CHALMAS [(1882), 470–471 partim].

*Praesorites dufrenoyi* (D'ARCHIAC); MARIE [(1958), 125–139].

MARIE has recorded that specimens seen by D'ARCHIAC cannot be found. He redescribed the species from D'ARCHIAC's description and figure but found no specimens

from the type locality or elsewhere to fit the description. This species is very like *Praesorites mouretti* DOUVILLÉ 1902 and there is naturally a grave suspicion that they are really synonymous. *B. dufrenoyi* is therefore at present a nomen dubium and it would be better to obtain a ruling against its use rather than risk the substitution of *dufrenoyi* for *mouretti* and *Broeckina* for *Praesorites* at some future date.

*Sorites dominicensis* EHRENBERG 1840, nomen dubium

*Sorites dominicensis* EHRENBERG, 1840 [EHRENBERG (1840), 134].

The brief latin description is inadequate for recognition of this species and there was no figure. Until the specimens of EHRENBERG's collection in Berlin are examined, it is uncertain whether authentic specimens can be established. Unless they are labelled adequately, the species will remain a nomen dubium. There seems to be a very strong case for the suppression of this name because it is highly probable that the species has received a name, probably of later date, by which it is now known.

Recognition of this species has been claimed by only one author, RENZ (1948) and he obtained his specimens from Venezuela and failed to give any justification for the application of this name to them. DOUVILLÉ (1902) mentioned a specimen in the DESHAYES collection from San Domingo that might be this species, but he did not describe or figure it. CUSHMAN and PONTON (1932) described a species from the Lower Miocene Chipola Marl of Florida that they thought might be *S. dominicensis*. There is therefore no established usage for this name.

*Nautilus melo* FICHTEL and MOLL 1798

The following synonyms have been proposed:

*Nautilus melo* var.  $\alpha$  FICHTEL and MOLL 1798:

*Clausulus indicator* MONTFORT 1808, 178–180 (type of *Clausulus* MONTFORT 1808); new name.

*Melonites sphaerica* LAMARCK 1816 (type of *Melonites* LAMARCK 1816); new name.

*Alveolina haueri* D'ORBIGNY 1846; subjective synonym.

*Nautilus melo* var.  $\beta$  FICHTEL and MOLL 1798:

*Borelis melonoides* MONTFORT 1808, 170–172 (type of *Borelis* MONTFORT 1808); new name.

Neotype: SCHLUMBERGER Collection, Sorbonne, Paris, specimen 2405 (3), figured by REICHEL [(1937), tabula 10, fig. 8].

The original description and figures indicate a globose alveoline with "continuous" arrangement of chamberlets. D'ORBIGNY (1852) included under this name specimens which would now probably be determined as the Eocene species *Alveolina globosa* (LEYMERIE 1846) but REICHEL (1937) gave an exceedingly careful account in which he concluded that *N. melo* var.  $\alpha$  is synonymous with *Neoalveolina haueri* (D'ORBIGNY 1846) and *N. melo* var.  $\beta$  is synonymous with *Neoalveolina bradyi* (SILVESTRI 1927).

Application will be made to the Commission of Zoological Nomenclature for the suppression of *C. indicator*, *M. sphaerica* and *B. melonoides*.

The neotype has been deliberately selected to conform to *Nautilus melo* var.  $\beta$ , to maintain the usage of REICHEL (1937). One would normally select var. *a* as the type of *N. melo* but this form is commonly known as *Neolaeolina haueri* (D'ORBIGNY 1846). The suppressions recommended not only remove unfamiliar names but have the effect that *N. haueri* is the first accepted new name and applies to *N. melo* var. *a*, leaving var.  $\beta$  as *N. melo* s.str.

## NOTE

A major work on *Orbitolites* has appeared while this paper was in press: LEHMANN R., 1961. Strukturanalyse einiger Gattungen der Subfamilie Orbitolitinae. *Eclogae Geol. Helv.*, 54 : 597–667. This gives an excellent account of the morphology of several of the species described here. LEHMANN has been uncritical in his adoption of names, except in the unfortunate case where his recognition of the similarity of chamber arrangement in *Orbitolites*, *Opertorbitolites* and *Somalina* has led him to place them in mutual synonymy, ignoring the perfectly usable diagnostic characters of the lateral layers on which the original differential diagnoses rest. He has ignored the difficulties surrounding the type of *Sorites*, assuming that *Orbitolites carpenteri* can be regarded as the type. The discussion and designation of types in this paper enables a synonymy to be given for LEHMANN's species:

Correct name:	LEHMANN's name:
<i>Orbitolites complanata</i>	<i>Orbitolites complanata</i>
<i>Opertorbitolites douvillei</i>	<i>Orbitolites douvillei</i>
<i>Orbitolites (Amphisorus) orbiculus</i>	<i>Sorites orbiculus</i>
<i>Orbitolites carpenteri</i>	<i>Sorites marginalis</i>
<i>Orbitolites orbitolitoides</i>	<i>Sorites orbitolitoides</i>
<i>Orbitolites (Marginopora) vertebralis</i>	<i>Marginopora vertebralis</i>
<i>Orbitolites duplex</i> (?juvenile)	<i>Amphisorus hemprichi</i>
<i>Somalina stephanii</i>	<i>Orbitolites stephanii</i>

The introduction of three new species closely resembling *Orbitolites complanata* raises problems for the practical palaeontologist who may have to determine poor specimens. This can easily be overcome by regarding *armoricensis*, *cotentinensis* and *reicheli* as subspecies of *O. complanata*, preserving the whole of LEHMANN's work but permitting laxer determination where necessary.

The subfamily definition of the Orbitolitinae proposed here would necessitate removal of *Yaberinella* to the subfamily Peneroplinae.

The discrepancies in the nomenclature have been emphasised here as it is evident that the paper by LEHMANN will deserve the position of a standard work and provides a most valuable source of information that has not hitherto been readily available.

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## SUMMARY

The taxonomy and phylogeny of the family Alveolinidae is discussed, directed to the understanding of the genus *Pseudedomia* HENSON 1948. The characters and relationships of many known species of large, complex Foraminifera, particularly those from the Middle East, are reviewed to establish their distinctive characters and assess their possible phyletic relationships to *Pseudedomia*. The genera concerned are mostly porcellaneous forms of the superfamily Miliolidea but some are crypto-agglutinating forms of the superfamily Lituolidea. Taxonomic notes are given where necessary for the families Peneroplidae and Alveolinidae; type designations and redescrptions being given where necessary. A formal emendation of *Pseudedomia* is based on a redescription of the type species *P. multistriata* HENSON 1948, the megalospheric form being described for the first time. A new species, *P. globularis*, is described.

## REFERENCES

- BAKK, L. A. J., 1932. De genera *Fasciolites* en *Neolaeolina* in het Indo-Pacifische gebied. *Verhandel. Ned. Geol. Mijnbouw. Genoot. Ned. en Koloniën*, 9: 205–266.
- BARKER, R. W. and GRIMSDALE, T. F., 1937. Studies of Mexican fossil Foraminifera. *Ann. Mag. Nat. Hist., London, Ser. 10*, 19: 161–178.
- BERMÚDEZ, P. J., 1935. Foraminiferos de la Costa Norte de Cuba. *Mem. Soc. Cubana Hist. Nat.*, 9: 129–224.
- BRADY, H. B., 1881. Notes on some of the reticularian Rhizopoda of the Challenger Expedition, pt. 3. *Quart. J. Microscop. Sci., N. Ser.*, 21: 31–71.
- BRADY, H. B., 1884. Report on the Foraminifera dredged by H.M.S. "Challenger" during the years 1873–1876. *Report on the sci. research of the Voyage of H.M.S. Challenger, Zoology*, 9: 210–212.
- CARPENTER, W. B., 1850. On the microscopic structure of *Nummulina*, *Orbitolites* and *Orbitoides*. *Quart. J. Geol. Soc. London*, 6: 21–38.
- CARPENTER, W. B., 1856. Researches on the Foraminifera. 1st. series; On *Orbitolites*. *Phil. Trans. Roy. Soc. London*, 146: 181–236.
- CARPENTER, W. B., 1883a. Report on the specimens of the Genus *Orbitolites* collected by H. M. S. CHALLENGER during the years 1873–1876. *Report on the sci. research of the Voyage of H. M. S. Challenger, Zoology*, 7: 1–47.
- CARPENTER, W. B., 1883b. Researches on the Foraminifera. Supplemental memoir: On an abyssal type of the genus *Orbitolites*; a study in the theory of descent. *Proc. Roy. Soc. London*, 35: 276–279.
- CARTER, H. J., 1853. Description of *Orbitolites Malabarica* (H. J. C.) illustrative of the spiral and not concentric arrangement of chambers in D'ORBIGNY's order Cyclostegues. *Ann. Mag. Nat. Hist., London, Ser. 2*, 11: 425–427.
- CHECCHIA-RISPOLI, G., 1905. Sopra alcune Alveoline eoceniche della Sicilia. *Palaeontografica ital.*, 11: 147–167.
- COLOM, C. G., 1935. Las especies de la familia Peneroplidae actuales y fósiles de las Baleares. *Bol. Soc. Española Hist. Nat.*, 35: 83–102.
- COSTA O. G., 1856. Paleontologia del regno di Napoli, parte II, *Accad. Pontaniana, Atti*, 7: 113–378.



- CUSHMAN, J. A., 1918. The smaller fossil Foraminifera of the Panama Canal Zone. *Bull. U.S. Natl. Museum*, 103: 45–87.
- CUSHMAN, J. A., 1927a. An outline of a re-classification of the Foraminifera. *Contrib. Cushman Lab. Foraminiferal Research*, 3: 1–105.
- CUSHMAN, J. A., 1927b. The designation of some genotypes in the Foraminifera. *Contrib. Cushman Lab. Foraminiferal Research*, 3: 188–190.
- CUSHMAN, J. A., 1928. Foraminifera. Their classification and economic use. *Cushman Lab. Foraminiferal Research, Spec. Publ.*, 1: 1–401.
- CUSHMAN, J. A., 1955. *Foraminifera. Their Classification and economic Use*. 4th. Ed. Harvard Univ. Press, Cambridge, Mass., 478 pp.
- CUSHMAN, J. A. and PONTON, G., 1932. The Foraminifera of the Upper, Middle and part of the Lower Miocene of Florida. *Bull. Florida Geol. Surv.*, 9: 7–147.
- DANA, J. D., 1846. Zoophytes. U.S. Exploring Expedition during the years 1838–1842 under the command of Charles Wilkes. *U.S. Navy*, 10: 1–740.
- DEFrance, M. J. L., 1820. Minéralogie et Géologie. In: F. G. LEVRAULT *Dictionnaire des Sciences Naturelles*. Paris, 16: 1–567.
- D'ARCHIAC, A. and HAIME, J., 1854. Coupe géologique des environs de Bains de Rennes (Aude) suivie de la description de quelques fossiles de cette localité. *Bull. Soc. géol. France, 2e sér.*, 11: 205–206.
- DE GREGORIO, A., 1894. Description des faunes Tertiaires de la Vénétie; Monographie des fossiles éocéniques (Étage Parisien) de Mont Postale. *Ann. géol. Palermo*, 14: 1–55.
- DES MOULINS, C., 1864. Le bassin hydrographique du Couzeau dans ses rapports avec la vallée de la Dordogne, le question diluviale et les silex ouvrés. *Soc. Linn. Bordeaux, Actes*, 25, 3e Sér., 5: 67–242.
- D'ORBIGNY, A., 1826. Tableau méthodique de la classe des Céphalopodes. *Ann. Sci. Nat., Paris, 1e sér.*, 7: 96–314.
- D'ORBIGNY, A., 1839. Foraminifères. In: DE LA SAGRE, R., *Histoire physique, politique et naturelle de l'Île de Cuba*. A. Bertrand, Paris. 224 pp.
- D'ORBIGNY, A., 1846. *Foraminifères fossiles du Bassin tertiaire de Vienne Autriche*. Gide et Comp., Paris. 303 pp.
- DOUVILLÉ, H., 1902a. Essai d'une révision des *Orbitolites*. *Bull. Soc. géol. France, 4e sér.*, 2: 289–306.
- DOUVILLÉ, H., 1902b. Distribution des *Orbitolites* et des *Orbitoides* dans la Craie du sud-ouest. *Bull. Soc. géol. France, 4e sér.*, 2: 307–313.
- DOUVILLÉ, H., 1907 a (for 1906). Les Calcaires à Fusulines de l'Indo-Chine. *Bull. Soc. géol. France, 4e sér.*, 6: 576–587.
- DOUVILLÉ, H., 1907b (for 1906). Evolution et enchaînements des Foraminifères. *Bull. Soc. géol. France, 4e sér.*, 6: 588–602.
- DOUVILLÉ, H., 1910. La Craie et le Tertiaire des environs de Royan. *Bull. Soc. géol. France, 4e sér.*, 10: 51–61.
- DOUVILLÉ, H., 1919. Les Cyclostègues de D'ORBIGNY. *Compt. rend. Acad. Sci.*, 169: 1130–1135.
- DOUVILLÉ, H., 1924 (for 1923). Les *Orbitoides* et leur évolution en Amérique. *Bull. Soc. géol. France, 4e sér.*, 23: 369–376.
- DUNNINGTON, H. V., WETZEL, R. and MORTON, D. M., 1960. *Lexique Stratigraphique International* Vol. III: Asie; fasc. 10a: *Iraq, Mesozoic and Palaeozoic*. Centre Nat. Recherche Sci., Paris, 333 pp.
- EAMES, F. E. and SMOUT, A. H., 1955. Complanate Alveolinids and associated Foraminifera from the Upper Cretaceous of the Middle East. *Ann. Mag. Nat. Hist.*, 12e sér., 8: 505–512.
- EHRENBERG, C. G., 1840 (for 1838). Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. *K. Akad. Wiss., Berlin, Physik. Abhandl.*, 1838: 59–147.
- ELLIS, B. F. and MESSINA, A. *Catalogue of Foraminifera*. Loose-leaf publication.
- FLINT, J. M., 1899 (for 1897). Recent Foraminifera. A descriptive catalogue of specimens dredged by the U.S. Fish Commission Steamer Albatross. *U.S. Natl. Museum Ann. Rept.*, 1: 249–349.
- FORSKÅL, P., 1775. *Descriptiones animalium. Hauniae* Carsten Niebuhr, Copenhagen, 164 pp.
- GALLOWAY, J. J., 1933. *A Manual of Foraminifera*. Bloomington, Indiana, 450 pp.
- GEINITZ, H. B., 1846. *Grundriss der Versteinerungskunde*. Arnold, Dresden – Leipzig, 26 pp.
- GLAESSNER, M. F., 1945. *Principles of Micropaleontology*. Melbourne Univ. Press, Melbourne, 296 pp.
- GRIMSDALE, T. F., 1952. Cretaceous and Tertiary Foraminifera from the Middle East. *Bull. Brit. Museum, Geol.*, 1: 223–247.
- HEMMING, F., 1953. *Copenhagen Decisions on Zoological Nomenclature*. International Trust for Zoological Nomenclature, London, 135 pp.
- HENSON, F. R. S., 1948. *Larger imperforate Foraminifera of South-Western Asia*. Brit. Museum, London, monography, 127 pp.
- HENSON, F. R. S., 1950. *Middle Eastern Tertiary Peneroplidae (Foraminifera), with Remarks on the Phylogeny and Taxonomy of the Family*. West Yorkshire Press Co., Wakefield, 70 pp.
- HOFKER, J., 1930. *The Foraminifera of the Siboga Expedition*, pt. 2; Siboga Exped. Leiden, pt. 4a; 79–170.
- HOFKER, J., 1950. Recent Peneroplidae, Pt. 1, *J. Roy. Microscop. Soc., London*, 70: 388–396.
- HOFKER, J., 1951a. Recent Peneroplidae. Pt. 1 (continued). *J. Roy. Microscop. Soc., London*, 71: 223–239.
- HOFKER, J., 1951b. Recent Peneroplidae. Pt. 2. *J. Roy. Microscop. Soc., London*, 71: 342–356.
- HOFKER, J., 1952a. Recent Peneroplidae. Pt. 3. *J. Roy. Microscop. Soc., London*, 71: 450–463.
- HOFKER, J., 1952b. Recent Peneroplidae. Pt. 4. *J. Roy. Microscop. Soc., London*, 102–122.
- HOFKER, J., 1953. Recent Peneroplidae. Pt. 5. *J. Roy. Microscop. Soc., London*, 73: 40–46.
- KEIJZER, F. G., 1945. *Outline of the Geology of the eastern Part of the Province of Oriente, Cuba (E. of 76° WL) with notes on the Geology of other Parts of the island*. Thesis Univ. Utrecht, 238 pp.
- LACROIX, E., 1940. Les *Orbitolites* de la Baie de Cauda. *Bull. Inst. Océanographie, Monaco*, 787: 1–16.
- LACROIX, E., 1941. Les *Orbitolites* du Golfe d'Akaba. *Bull. Inst. Océanographie, Monaco*, 794: 1–38.
- LACROIX, E., 1959. Les *Orbitolites* du Golfe d'Akaba. In: Mission Robert Ph. Dollfus en Égypte. Pt. 3, 23, Foraminifera I: 7–34. *Centre Natl. Recherche Scientifique, Paris*.
- LAMARCK, J. B., 1801. *Système des Animaux sans Vertèbres*, Paris. 432 pp.
- LAMARCK, J. B., 1804. Suite des mémoires sur les fossiles des environs de Paris. Paris. *Musée Natl. Hist. Nat., Ann., Paris*, 5: 349–357.
- LAMARCK, J. B., 1816. *Tableau encyclopédique et méthodique des trois Regnes de la Nature; Pt. 23; Mollusques et Polypes divers*. Paris, 3: 1–16.
- LAMARCK, J. B., 1845. *Histoire naturelle des Animaux sans Vertèbres*. Revue et augmentée par G. P. DESHAYES et H. MILNE EDWARDS. 2e Ed., Paris, 11: 665 pp.
- LEYMERIE, A., 1851. Mémoire sur un nouveau type pyrénéen. *Mém. Soc. géol. France, 2e sér.*, 4: 177–202.
- LOEBLICH, A. L. and TAPPAN, H., 1961. Suprageneric classification of the Rhizopodea. *J. Paleontol.*, 35: 245–330.
- MARIE, P., 1940. A propos des foraminifères d'un sable de plage provenant de Tahiti. *Bull. du Musée 2e sér.*, 12, 6.
- MARIE, P., 1958. Peneroplidae du Crétacé supérieur à faciès récifal. 1. A propos des genres *Broeckina* et *Praesorites* et sur le nouveau genre *Vandenbroeckina*. *Rev. Micropaleontol.*, 1: 125–139.
- MIOHELIN, H., 1846. *Iconographie zoophytologique*. P. Bertrand, Paris, 21–26: 222–230.
- MONTFORT, D., 1808. *Conchyliologie systématique et Classification méthodique des Coquilles*; etc. F. Schoell, Paris, 410 pp.
- MUNIER-CHALMAS, E., 1882a (for 1881–1882). Des genres *Renulites*, *Broeckina*, *Archiacina*. *Bull. Soc. géol. France, 3e sér.*, 10: 470–471.
- MUNIER-CHALMAS, E., 1882b (for 1881–1882). Du genre *Lacazina*. *Bull. Soc. géol. France, 3e sér.*, 10: 471–472.
- MUNIER-CHALMAS, E., 1902. Sur les Foraminifères rapportés au groupe des *Orbitolites*. *Bull. Soc. géol. France, 4e sér.*, 2: 351–354.
- MUNIER-CHALMAS, E. and SCHLUMBERGER, C., 1885 (for 1884–1885). Note sur les Miliolidées trematophorées. *Bull. Soc. géol. France, 3e sér.*, 13: 273–323.
- NUTTALL, W. L. F., 1925. The stratigraphy of the Laki Series (Lower Eocene) of parts of Sind and Baluchistan (India); with a description of the larger Foraminifera contained in those beds. *Quart. J. Geol. Soc. London*, 81: 417–453.
- PALMER, D. K., 1934. Some large fossil foraminifera from Cuba. *Mem. Soc. Cubana Hist. Nat.*, 8: 235–264.
- PARKER, W. K. and JONES, T. R., 1861. On the nomenclature of the Foraminifera. Pt. VI. *Alveolina*. *Ann. Mag. Nat. Hist., London, Ser. 3*, 8: 161–168.
- PARKER, W. K. and JONES, T. R., 1865. *Ann. Mag. Nat. Hist., London, Ser. 3*, 16: 35.
- PARKINSON, J., 1811. *Organic Remains of a former World*. 3, Sherwood, Neely and Jones, London, 455 pp.
- POKORNY, V., 1958. *Grundzüge der zoologischen Mikropaläontologie*, 1, VEB Deutscher Verlag der Wissenschaften, Berlin, 582 pp.

- QUOY, J. R. C. and GAYMARD, J. T. Mollusques, vers et zoophytes. In: DE BLAINVILLE, H. M. D., 1830. *Dictionnaire des Sciences Naturelles*, Paris, 60: 377.
- RAUZER-CHERNOUSOVA, D. M. and FURSENKO, A. V., 1959. *Osnovy palaeontologii*. pt. 1. *General part and Protozoa*. Akad. Nauk. S.S.S.R., Moscow. 482 pp.
- REICHEL, M., 1933. Sur une Alvéoline cénomanienne du bassin de Beausset. *Eclogae Geol. Helv.*, 26: 269–280.
- REICHEL, M., 1936–1937. Étude sur les Alvéolines. *Mém. Soc. paléontol. Suisse*, 57–59: 1–147.
- REICHEL, M., 1941. Sur un nouveau genre d'Alvéolines du Crétacé supérieur. *Eclogae Geol. Helv.*, 34: 254–260.
- REICHEL, M., 1947. *Multispirina iranensis* nov. gen., nov. sp. *Mém. Soc. paléontol. Suisse*, 65: 1–13.
- REICHEL, M., 1952 (for 1951). *Fusarchaias bermudezi* nov. gen., nov. sp., pénéroplidé alvéoliniforme de l'Oligo-Miocène de Cuba. *Eclogae Geol. Helv.*, 44: 458–464.
- RENTZ, H. H., 1948. Stratigraphy and fauna of the Agua Salada group, State of Falcón, Venezuela. *Mem. Geol. Soc. Am.*, 32: 219 pp.
- REUSS, A. E., 1860. Ueber die Foraminiferen aus der Familie der Peneropliden. *K.Böhm. Ges. Wiss., Prag, Math. Naturwiss. Cl. Sitzberichte Prag*: 68–74.
- RHUMBLER, L., 1911. Die Foraminiferen (Thalamophoren) der Plankton-Expedition; Erster Teil: Die allgemeinen Organisationsverhältnisse der Foraminiferen. *Plankton-Exped. Humboldt-Stiftung, Ergeb., Kiel und Leipzig*, 3: 1–331.
- RICHARZ, P. S., 1909. Der geologische Bau von Kaiser Wilhelms-Land nach dem heutigen Stand unseres Wissens. In: Geologische Mitteilungen aus dem Indo-Australischen Archipel. *Neues Jahrb. Min. Geol. Palaeontol.*, 29: 406–536.
- RUTTEN, L., 1913. Studien über Foraminiferen aus Ost-Asien: 2. Eine neue *Alveolinella* von Ost-Borneo. *Samml. Geol. Reichsmuseums, Leiden, Ser. 1*, 9: 219–224.
- SACCO, F., 1922. Sul gigantismo di alcune forme eoceniche dell'Istria. *Rev. accad. Sci., Torino*, 57: 351–357.
- SCHLUMBERGER, C., 1898. Note sur le genre *Meandropsina* MUN.-CHALM., nov. gen. *Bull. Soc. géol. France, 3e sér.*, 26: 336–339.
- SIGAL, J., 1952. Ordre des Foraminifera. In: PIVETEAU, J. *Traité de Paléontologie*. Masson et Cie, Paris, I: 133–301.
- SILVESTRI, A., 1920. Fossili rari o nuovi in formazioni del Paleogene. *Boll. soc. geol. ital.*, 39: 57–80.
- SILVESTRI, A., 1928. Intorno all' *Alveolina melo* D'ORBIGNY (1846). *Riv. ital. paleontol.*, 34: 17–37.
- SILVESTRI, A., 1937. Foramini feridell' Oligocene e del Miocene della Somalia. *Paleontologia della Somalia: V. Fossili dell' Oligocene e del Miocene. Palaeontografica ital.*, 32 (suppl. 2): 45–264.
- SILVESTRI, A., 1939. Foraminiferi dell' Eocene della Somalia. Parte II. *Paleontologia della Somalia: IV. Fossili del' Eocene. Palaeontografica ital.*, 32 (suppl. 4): 1–102.
- SILVESTRI, A., 1940 (for 1939). Illustrazione di specie caratteristica del Cretaceo superiore. *Boll. soc. geol. ital.*, 58: 225–234.
- SMOUT, A. H. and EAMES, F. E., 1958. The genus *Archaias* (Foraminifera) and its stratigraphical distribution. *Palaeontology*, 1: 207–225.
- STACHE, G., 1880. Die Liburnische Stufe. *Abhandl. Geol. Reichsanstalt*, 1880: 195–209.
- STACHE, G., 1889. Die Liburnische Stufe und deren Grenz-Horizonte, eine studie über die Schichtenfolgen der Cretacisch-Eocänen oder Protocänen Landbildungsperioden im Bereiche der Küstländer von Oesterreich-Ungarn. *Abhandl. Geol. Reichsanstalt*, 13: 1–170.
- STACHE, G., 1912. Ueber *Rhipidionina* ST. und *Rhapydionina* ST. *Jahrb., Geol. Reichsanstalt*, 62: 659–680.
- STEINMANN, G., 1880. Mikroskopische Thierreste aus dem deutschen Kohlenkalk (Foraminiferen und Spongien). *Z. Deut. Geol. Ges.*, 32: 394–400.
- THALMANN, H. E., 1932. Nomenclator (Um- und Neubenennungen) zu den Tafeln 1 bis 115 in H. B. BRADY's Werk über die Foraminiferen der Challenger-Expedition, London, 1884. *Eclogae Geol. Helv.*, 25: 293–312.
- VAN DEN BOLD, W. A., 1946. *Contribution to the Study of Ostracoda, with special Reference to the Tertiary and Cretaceous Microfauna of the Caribbean Region*. Thesis Univ. Utrecht, 167 pp.
- VAN WESSEM, A., 1943. *Geology and Paleontology of central Camagüey, Cuba*. Thesis Univ. Utrecht, 91 pp.
- VERBEEK, R. D. M. and FENNEMA, R., 1896. *Description géologique de Java et Madoura*. J. G. Stemler Cz. Amsterdam, 2: 925–1183.

- VON FICHEL, L. and MOLL, J. P. C., 1798 (1803 reprint). *Testacea microscopica aliaque minuta ex generibus Argonauta et Nautilus ad naturam delineata et descripta*. Camesina Wien, 124 pp.
- WEAVER, T., 1841. On the composition of chalk rocks and chalk marl by invisible organic bodies: from the observations of Dr. EHRENBURG. *Ann. Mag. Nat. Hist., London*, 7: 296–315, 374–398.
- WILLIAMSON, W. C., 1851. On the minute structure of the calcareous shells of some recent species of Foraminifera. *Trans. Microscop. Soc.*, 3: 105–128.
- YABE, H. and HANZAWA, S., 1929. Tertiary foraminiferous rocks of the Philippines. *Sci. Repts. Tôhoku Imp. Univ., Ser. 2 (Geol.)*, XI: 137–190.
- ZITTEL, K. A., 1876. *Grundzüge der Paläontologie*. R. Oldenbourg, München – Leipzig, I: 765 pp.

## PLATE I

*Pseudedomia multistriata* HENSON 1948.

1. Holotype: form B;  $\times 41$ ; nearly equatorial section (after HENSON, 1948); specimen P. 35961. Maastrichtian, Jebel Dukhan, Qatar. Reproduced by permission of the British Museum (Natural History).

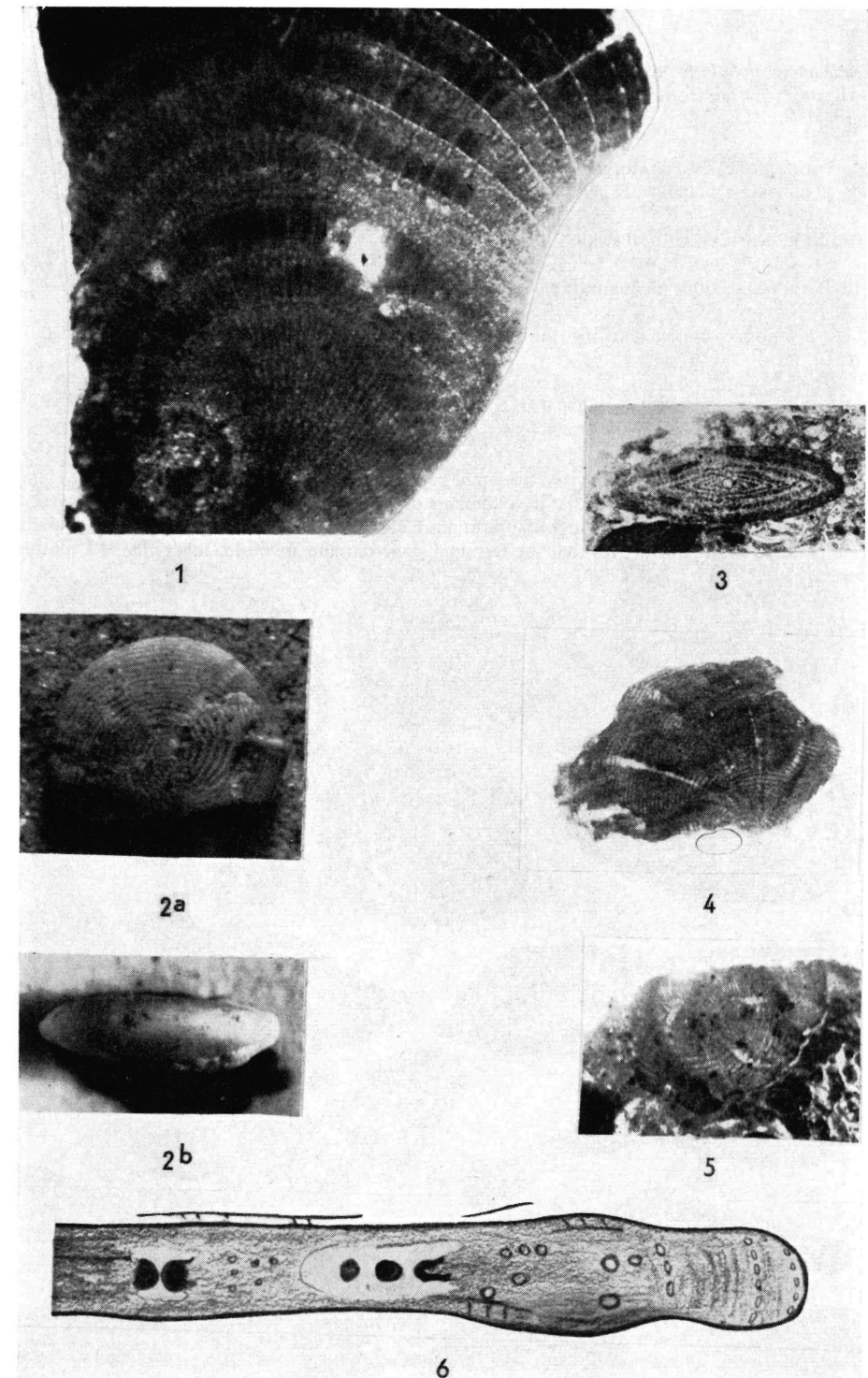
2. Topotype: form A;  $\times 20$ ; a. lateral; b. edge view; specimen P. 42638.

3. Form A;  $\times 20$ ; axial section; specimen P. 42640; Maastrichtian, Ratawi, South Iraq.

4. Topotype: form A;  $\times 20$ ; specimen P. 42641; oblique section.

5. Form A;  $\times 20$ ; oblique section; specimen P. 42639; Maastrichtian, Ratawi, South Iraq.

6. Reconstruction of the appearance of the tangential section through the top edge of the holotype (cf. HENSON, 1948, pl. XI, fig. 2). Little reliance can be placed on this drawing for the original section is very obscure.



## PLATE II

*Pseudedomia globularis* nov.sp.

All specimens are from the Bekhme Limestone, of Campanian age, near Shiranish Nasara, North Iraq.

1-6. Form A, nearly equatorial sections. No. 4 and 5 show an increase of whorl height that is very marked in the last whorl;  $\times 15$ . No. 5 holotype; specimen P. 42643.

7. Form B, nearly equatorial section;  $\times 15$ .

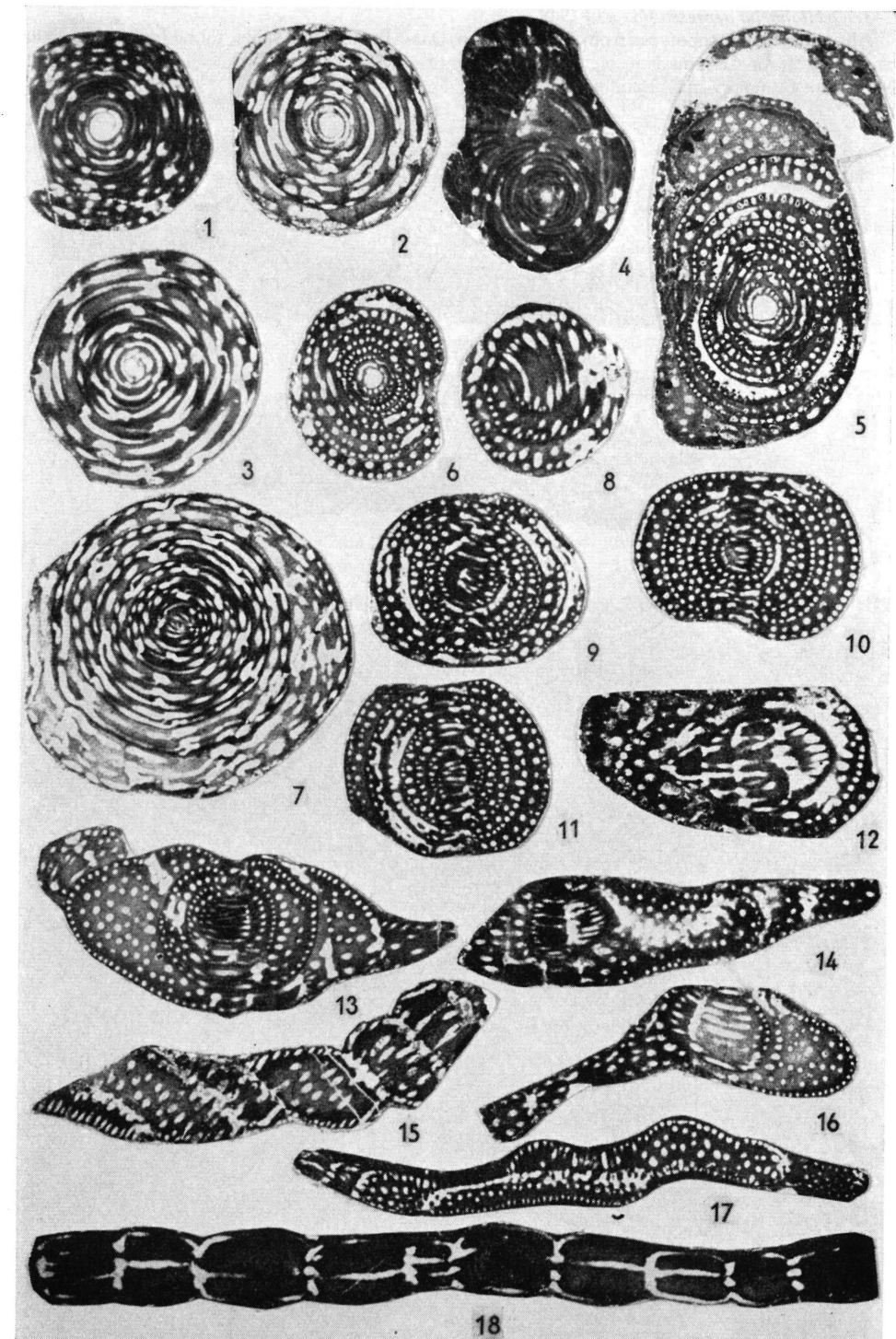
8-12. Random sections through the globular early part of the test;  $\times 15$ .

13-15. Random sections showing the transition from the globular stage to the terminal flange,  $\times 15$ .

16-18. Specimens in rock sections; British Random sections through the terminal flange;  $\times 10$ . Museum (Nat. Hist.) specimens P. 42642-6.

Note that most specimens show the preseptal canal clearly and the buttresses can be seen in No. 5, 9, 11, 12, 16, 18. No. 17 shows that the chambers of the terminal flange are high and recurved. No. 18 is an almost axial section through the terminal flange, the direction of growth being to the left. None of these specimens proves that the terminal stage remains involute; this remains a matter of inference.

## PLATE II



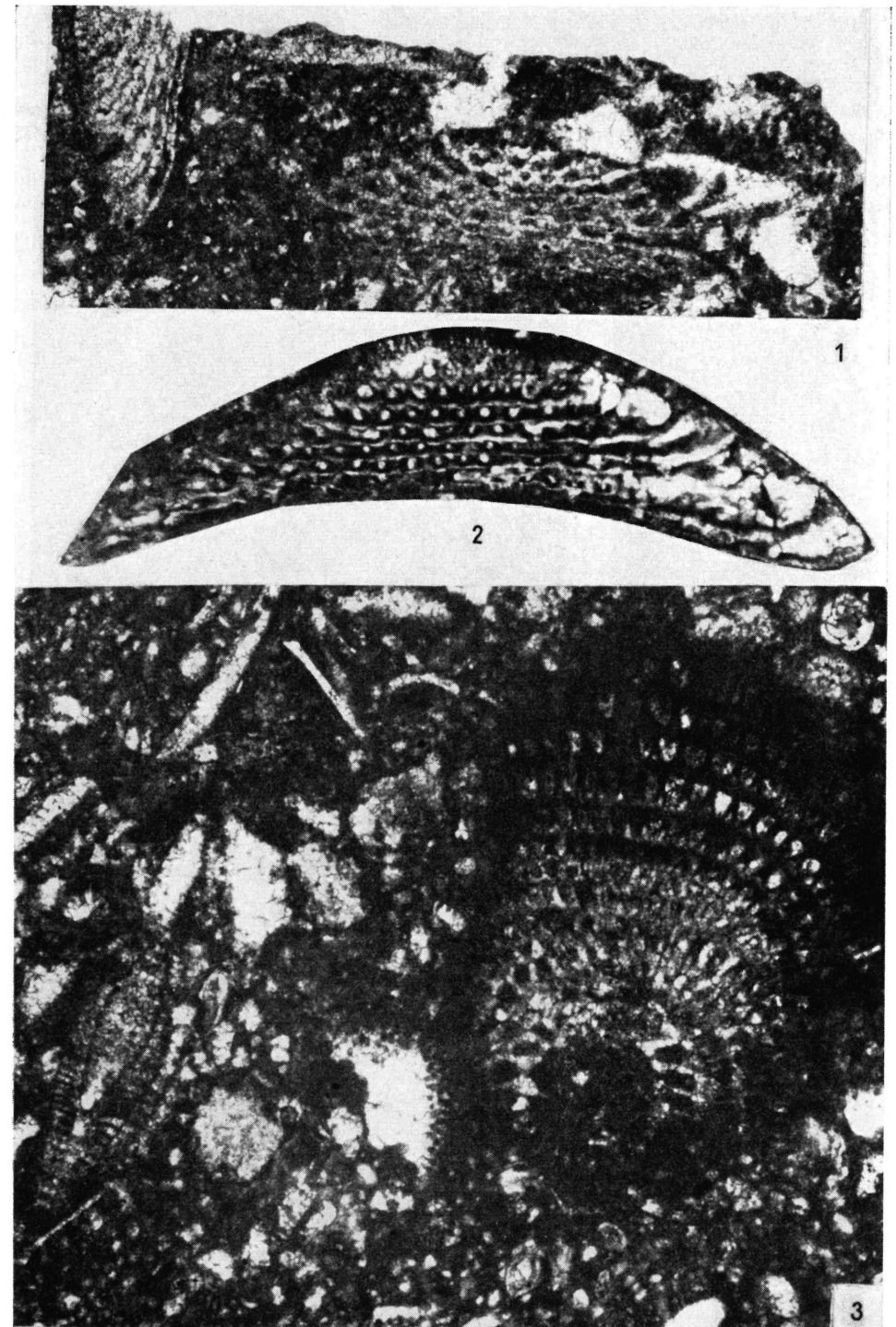


## PLATE III

1-3. *Orbitolinella depressa* HENSON 1948.

All specimens are topotypes from Jebel Dukhan, Qatar Peninsula, Arabia; found in limestones that are probably of Cenomanian age;  $\times 50$ . Specimens are deposited in the collections of the Iraq Petroleum Company Ltd., London.

## PLATE III



## PLATE IV

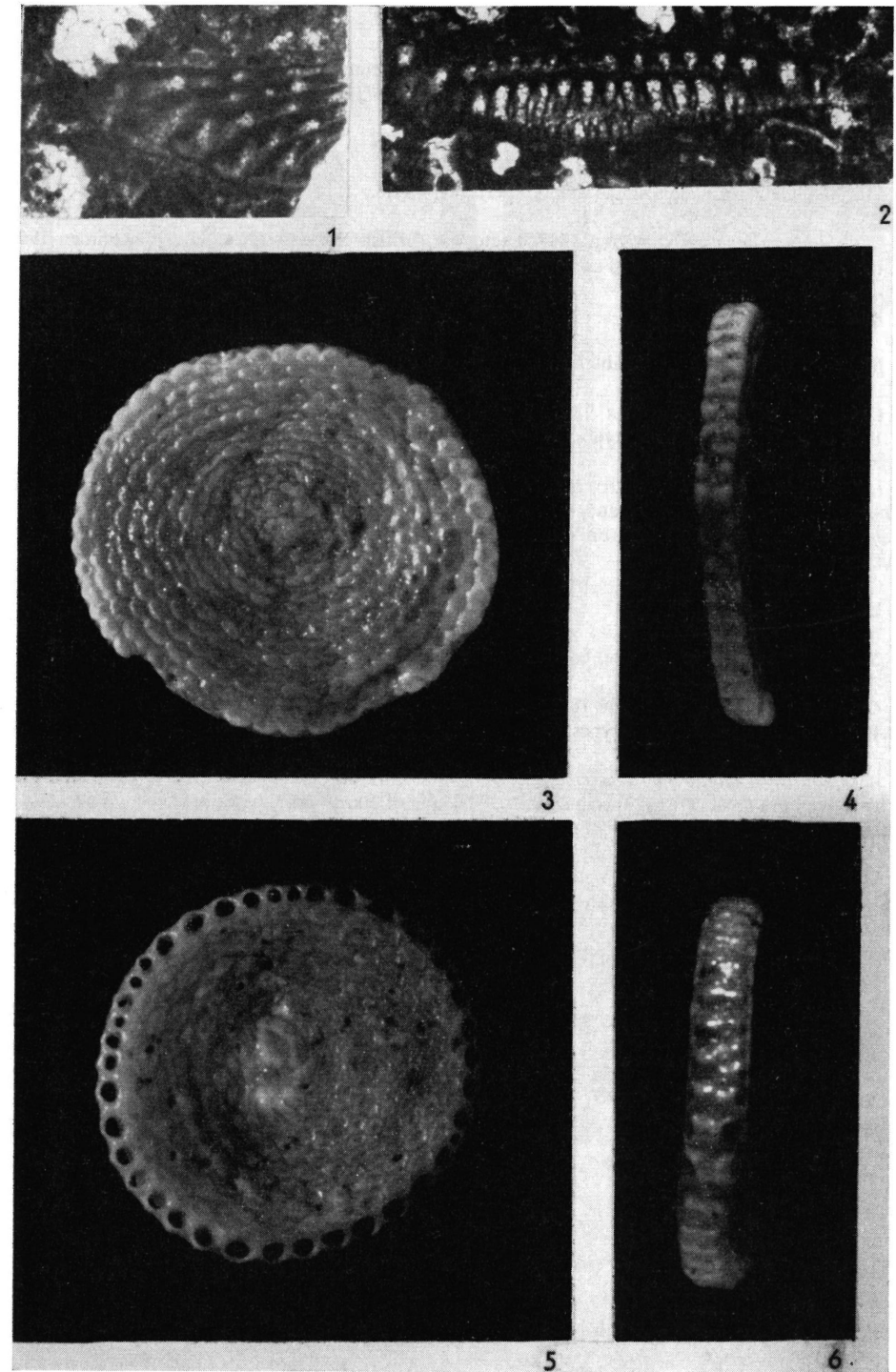
1, 2. *Orbitolinella depressa* HENSON 1948.

Further random sections of topotypes from Jebel Dukhan, Qatar Peninsula, Arabia; probably Cenomanian;  $\times 50$ .

3, 4. "*Orbitolites*" *orbiculus* (FORSKÅL 1775). Lateral and edge views; Gulf of Aqaba, Red Sea; Recent;  $\times 35$ . British Museum Specimen 1961.11.10.10; Neotype of *Nautilus orbiculus* Forskål, 1775.

5, 6. "*Orbitolites*" *marginalis* (LAMARCK 1816). Lateral and edge views; shore near Priola, Sicily; Recent;  $\times 50$ . British Museum Specimen 1961.11.10.9; Neotype of *Orbulites marginalis* LAMARCK 1816.

## PLATE IV





## PLATE IV

1, 2. *Orbitolites carpenteri* nov. sp. Holotype, British Museum (Nat. Hist.); specimen 1961.11.10.7, selected from specimens determined as "*Orbitolites marginalis* LAMARCK" by CARPENTER (1883).

1. Lateral view; x 6.4.

2. Marginal view, showing a single row of apertures; x 12.8.

3, 4. *Orbitolites duplex* CARPENTER 1883. Lectotype, British Museum (Nat. Hist.); specimen 1961.11.10.1, selected from CARPENTER's syntypes.

3. Lateral view; x 4.5.

4. Marginal view, showing a double row of apertures; x 10.

5. *Orbitolites duplex* CARPENTER 1883. Paratype, British Museum (Nat. Hist.); specimen 1961.11.10.3; one of CARPENTER's syntypes. Equatorial section of the megalospheric nucleoconch; x 96.

6, 7. "*Orbitolites* (*Marginopora*) *vertebralis* (QUOY and GAYMARD in BLAINVILLE 1830). Neotype of *Marginopora vertebralis* QUOY and GAYMARD in BLAINVILLE 1830. British Museum (Nat. Hist.); specimen 1961.11.10.8, selected from specimens determined as "*Orbitolites complanata* LAMARCK" by CARPENTER (1883).

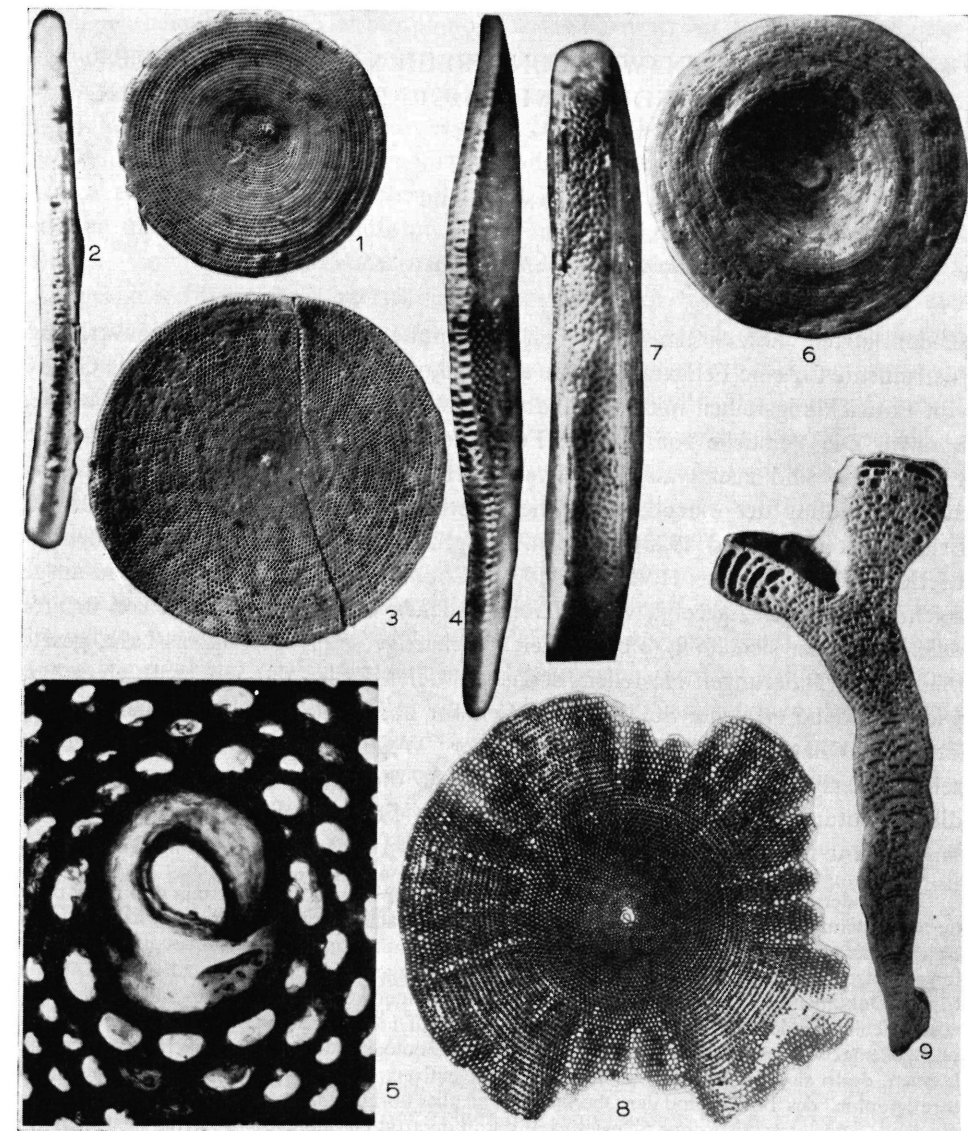
6. Lateral view; x 6.4.

7. Marginal view showing a broad band of randomly arranged apertures; x 12.8.

8. *Orbitolites duplex* CARPENTER 1883. Paratype, British Museum (Nat. Hist.); specimen 1961.11.10.2, one of CARPENTER's syntypes. Equatorial section; x 4.5.

9. "*Orbitolites*" (*Marginopora*) *vertebralis* QUOY and GAYMARD var. *plicata* DANA 1848. Paratype, British Museum (Nat. Hist.); specimen ZF. 2038, one of BRADY's syntypes of *Orbitolites laciniatus* BRADY 1881. Vertical section showing doubling of the margin; x 4.5.

All the figures on this plate are published by permission of the British Museum (Natural History) and are taken from photographs made by the staff of specimens in the W. B. CARPENTER and H. B. BRADY Collections. All specimens were found in Challenger samples at Station no. 172 and were probably living at the time of collection.



## PLATE V

# EVOLUTIONARY TRENDS IN FORAMINIFERA

A COLLECTION OF PAPERS DEDICATED TO

I. M. VAN DER VLERK

ON THE OCCASION OF HIS 70TH BIRTHDAY

edited by

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