

THE TROCHAMMINACEOUS TEST AND THE TAXONOMIC CRITERIA USED IN THE CLASSIFICATION OF THE SUPERFAMILY TROCHAMMINACEA.

by

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With 3 plates

ZUSAMMENFASSUNG

Organisation und Terminologie eines allgemeinen *Trochammina*-Gehäuses stehen im Mittelpunkt der vorliegenden Arbeit. Auf Grund der gegenwärtigen Kenntnisse wird der Beschaffenheit des Agglutinanten wenig taxonomische Bedeutung zugeordnet, ganz im Gegensatz zum Aufbau der Gehäusewand, der taxonomische Bedeutung auf höherer Ebene zukommt. Die Wandstrukturen von *Trochammina inflata* (MONTAGU) und von *Asarotammina asarotum* BRÖNNIMANN werden im einzelnen beschrieben und auf besondere Gehäuse mit „spicular“- und Barium-Agglutinant hingewiesen.

Die Hierarchie der Merkmale für die Unterscheidung und Gruppierung der Trochamminen wird dargestellt. Für Definitionen von Spezies und Subspezies werden Einzelheiten des trochospiralen Gehäuses (Zahl der Kammern, Zahl der Umgänge, etc.) und dessen Dimensionen verwendet. Die Kriterien für Definitionen von Genus und Subgenus liegen in den Einzelheiten der Apertur und der Form des erwachsenen Gehäuses. Die Subfamilien werden durch das allgemeine System der Apertur bestimmt. Für die Definitionen der Familien und höheren Taxa werden die Art und Weise der Aufrollung, innere Strukturen, und die Beziehung zwischen umbilikalem Durchmesser und der Höhe der Aufrollungsachse verwendet.

Die von BRÖNNIMANN, ZANINETTI & WHITTAKER 1983 eingeführte Klassifikation der Trochamminen basiert hauptsächlich auf rezenten Formen, doch kann sie ohne weiteres auch auf guterhaltene fossile Trochamminen ausgedehnt werden.

Es werden 3 Superfamilien mit agglutinierten, trochospiralen Gehäusen angenommen: Trochamminacea SCHWAGER 1877, Remaneicacea LOEBLICH & TAPPAN 1964 und Dictyopsellacea BRÖNNIMANN, ZANINETTI & WHITTAKER 1983. Das erste Kapitel der vorliegenden Studie beschäftigt sich mit allen 3 Superfamilien, die übrigen Kapitel betreffen ausschließlich die Trochamminacea.

ABSTRACT

This study deals with the organization of the trochamminaceous test. Its terminology is explained and the wall structure of two well-studied trochamminaceous species, *Trochammina inflata* (Montagu) and *Asarotammina asarotum* Brönnimann described; additional remarks on some interesting species with spicular and baryte tests are also given. The nature of the agglutinant in the Trochamminacea is, on the basis of present knowledge, regarded as being of little taxonomic value. Potentially of higher taxonomic significance, on the other hand, is the detailed structure of the wall.

A logical hierarchy of taxonomic criteria for differentiating trochamminaceous foraminifera from superfamily down to subspecies level is outlined. The details of the trochospire and its dimensions are used for the definition of species and subspecies, while the details of the aperture and the type of adult growth form are used for generic and subgeneric differentiation. The overall apertural systems are used at

subfamily level, while the modes of enrolment, the internal structures, certain aspects of the wall, and the relationship between the height of the axis of enrolment and the umbilical diameter of the test are features used for family and superfamily definitions. The classification system introduced by Brönnimann *et al.* 1983, although based largely on Recent forms, can, it is argued, be also applied to fossil Trochamminacea.

The families Trochamminidae Schwager 1877, Remaneicidae Loeblich and Tappan 1964, and the subfamily Dictyopsellinae Brönnimann, Zaninetti and Whittaker 1983, are all now elevated to superfamily rank. The first chapter of this paper, on the organization of the trochamminaceous test, refers to all three superfamilies, the other chapters, on wall structure, taxonomic criteria, and fossil forms, only to the Trochamminacea.

THE ORGANIZATION OF THE TROCHAMMINACEOUS TEST.

Under the term, trochamminaceous [for the etymology of the term *trochamminaceous*, see Brönnimann and Whittaker 1984a: p. 311; and for the history of *Trochammina*, see Hedley *et al.* 1964: p. 418.] are included all agglutinated *Carterina* Brady, 1884, *Zaninetta* Brönnimann and Whittaker 1983a, and *Asarotamina* Brönnimann 1986a, are all regarded as having agglutinated tests.] multilocular foraminiferal tests (independent of internal structures) characterised by a trochospiral enrolment where the test height, expressed by the length of the coiling axis, is smaller than or equal to, the maximum umbilical diameter (see Brönnimann *et al.* 1983). Trochamminaceous tests belong to 3 superfamilies, as defined herein: the Trochamminacea Schwager 1877 (Carboniferous or older - Recent), devoid of inner structures, and the new superfamilies, the Remaneicacea Loeblich and Tappan 1964 (Recent only) and the Dictyopsellacea Brönnimann, Zaninetti and Whittaker 1983 (Cretaceous only), both with internal structures, though rather differently developed.

The term, *trochospiral*, which describes the mode of enrolment of a trochamminaceous foraminifer, is derived from the Greek words *trochos*, meaning anything round or circular such as a wheel or a ball, and *speira* (Latin, *spira*), meaning anything coiled or twisted (Brown 1954). In biological usage, the term trochospiral means a configuration in space as represented by a conical spiral or by the helicoid enrolment of the shell of a snail (Lehmann 1964). In our sense, trochospiral is used consistently to describe the arrangement of the chambers in space, or the mode of organization, of the multilocular trochamminaceous test. The first or initial chamber, or proloculus, usually the smallest chamber of the test, occupies its apex, and the final or last or ultimate chamber, usually the largest increment of the test, is situated at the end of the last or basal volution (whorl) of the trochospire.

The upper or spiral side of the trochospire is evolute, or almost so, in all species of the family

Trochamminidae and in the superfamilies Remaneicacea and Dictyopsellacea. The lower or umbilical side is involute or semi-involute in all species of the superfamilies Trochamminacea, Remaneicacea and Dictyopsellacea. The spiral side is, in the adult, involute in species of the family Adercotrymidae (see Brönnimann and Whittaker 1987a). The "umbilicus" or axial depression or cavity is closed when the enrolment is tight (e.g. in *Arenoparrella mexicana* (Kornfeld) 1931, or in *Pseudotrochammina atlantica* (Parker) 1952), or it can be open when the enrolment is loose. In forms with semi-involute umbilical sides, it may show not only the chambers of the final whorl, but also the axial portions of the chambers of the previous whorl (or whorls) inside the axial depression (e.g. species of the genus *Rotaliammina* Cushman 1924, or in many species of the genus *Asterotrochammina* Bermúdez and Seiglie 1963, or in some species of the genus *Paratrochammina* Brönnimann 1979). The character of the "umbilicus" or axial depression (open or closed), is therefore determined by the looseness or tightness of the enrolment.

The *adult growth form* of the trochamminaceous test is governed by three factors: first, by the mode of enrolment (coiling); secondly, by the inflation of the chambers; and, thirdly, by the height of the axis of enrolment. Where the axis of enrolment is short and the adult chambers axially compressed, the adult growth form is termed *lepidoid* (from the Greek, *lepis*, *-idos*, a scale). Such a test is found in *Deuterammina* (*Lepidodeuterammina*) *ochracea* (Williamson) 1858, in *Paratrochammina* (*Lepidoparatrochammina*) *haynesi* (Atkinson) 1969, and in virtually all members of the superfamilies Remaneicacea and Dictyopsellacea; some examples are also shown in plate 1, figures 4,5; plate 2, figures 6-8. Where the axis of enrolment is high (but not greater than the umbilical test diameter) and the adult chambers are inflated and axially only slightly compressed, the adult growth form is termed *non-lepidoid*. Such a test is found in *Paratrochammina* (*Paratrochammina*) *simplissima* (Cushman and McCulloch) 1948, and in *Portatrochammina murrayi* Brönnimann and Zaninetti 1984; other examples are shown in plate 1, figures 1-3,6.

Lepidoid tests are well adapted for attachment and for a fixed mode of life. In the species of the lepidoid genus *Rotaliammina* Cushman (1924) a special adaptive feature is developed in the form of a very thin, narrow peripheral flange which is rich in organic matter and thus flexible under water (see Brönnimann *et al.* 1983, plate 1). This peripheral extension of the test allows a close and tight attachment to the substratum. It is nevertheless a fragile structure and often is destroyed during sample preparation. In *Rotaliammina*, the test may be completely covered by a secreted or agglutinated grayish-white finely granular calcareous substance called by Rhumbler (1938) the "toga". The primary function of the "toga" is here thought not to be for fixing the test to the substratum - though along the margin of the flange this may be the case - but rather for protection and perhaps for sealing off the test under adverse conditions of life. But there are also non-lepidoid tests which become well adapted for fixation (e.g. species of the genera *Tritaxis* Schubert 1920 and *Trochamminella* Cushman 1943); they develop a flattened umbilical side and, in some cases, a secreted or agglutinated substance by which they "glue" themselves to the substratum (see plate 1, figures 7,8). A probably secreted, light grayish substance may also occur in the axial depression, along the intercameral sutures and over the aperture, in some species, closing it completely (e.g. *Paratrochammina* (*Paratrochammina*) *simplissima* (Cushman and McCulloch) 1948). The function of this substance, in this case, is not to "glue" the specimen to the substratum as in *Tritaxis* and *Trochamminella* (for further comments and a revision of these genera, see Brönnimann and Whittaker 1984b), but to protect the cytoplasm under adverse conditions or in the course of the reproductive cycle (temporary cysts).

The trochospire itself is a completely asymmetric and polarised structure, and its morphological differentiation takes place in the course of ontogeny between the beginning (proloculus; apex of test) and end (ultimate chamber) of growth. This asymmetric, heteropolar trochospire is invariably developed by the test of trochamminaceous foraminifera, at least in early ontogeny, and is independent of the formation of internal elements. The characterization of such a complex structure and its distinction from similar structures requires a specialised terminology (see Brönnimann and Whittaker 1987b, in press). The final ontogenetic stages may deviate from the basic organization of the trochospire, for instance by involution of the spiral side of the trochospire or by uncoiling in the plane of the final volution or by a tendency to uncoil, but such a deviation does not change the original trochospire in any essential way (see revision of *Adercotryma* Loeblich and Tappan 1952, by Brönnimann and Whittaker 1987a).

In this connection it now seems useful to consider the relationship between the trochospiral, the irregular or streptospiral, and the planispiral types of enrolment. It is emphasized that any transitional configurations between these three basic modes of enrolment as encountered in the Trochamminacea Schwager (trochospiral), the Acupeinacea Brönnimann and Zaninetti (streptospiral) and the Lituolacea de Blainville (planispiral) simply do not exist. Either a form starts trochospirally, streptospirally or planispirally. It never starts both trochospirally or streptospirally, or trochospirally and planispirally, etc. However, in later ontogeny a certain type of initial enrolment may be completely replaced by another one. Possibly, these later or late ontogenetic modifications which occasionally may predominate, even mask the early type of enrolment, gave rise to reports in the literature of the occurrence of "transitional enrolments". In late ontogeny, a trochospire may gradually change into a planispire such as in a new genus from deep Antarctic waters (Brönnimann and Whittaker 1987b, in press) which has an almost planispiral adult coil. A streptospiral enrolment, moreover, may change into a planispiral one (e.g. *Glomospirella* Plummer 1945), or a test which is initially planispiral, may develop, in late ontogeny, irregularly arranged chambers (e.g. *Trochamminita* Cushman and Brönnimann 1948). Other examples could be added.

The important fact remains that the *early enrolment*, be it trochospiral, or streptospiral, or planispiral, is of crucial taxonomic significance. Independent of the final structure of the test, it determines, occasionally together with another feature, the superfamily to which a given form belongs (Maync 1952; Brönnimann 1986a). In the case of the trochamminaceous foraminifera, a second important feature, represented by the internal structures, will refer a particular taxon either to the Trochamminacea Schwager 1877 (where such structures are absent), or to one of the new superfamilies, the Remaneicacea Loeblich and Tappan 1964, and the Dictyopsellacea Brönnimann, Zaninetti and Whittaker 1983 (both characterized by inner structures, though different in their morphology; see Brönnimann *et al.* 1983 and Loeblich and Tappan 1985, for further details). As a taxonomic criterion, this second feature, however, is always subordinate to the early mode of enrolment.

For morphological and stratigraphical reasons it is inferred that the Carboniferous (or older) to Recent superfamily, the Trochamminacea is ancestral to both the Dictyopsellacea (Late Cretaceous only) and the Remaneicacea (Recent only). These last two superfamilies show that internal structures, though of a different nature, were developed by the

Trochamminacea at least twice in time. The Remaneicacea, therefore, are not directly related to the Dictyopsellacea and cannot be interpreted as their evolutionary descendants.

WALL STRUCTURE OF SOME TROCHAMMINACEA

The morphological features used in the definition of species and subspecies of trochamminaceous foraminifera are three in number: first, the *details of the trochospire* (outline of test in spiral/umbilical and side view, type of coiling (loose, tight), total number of chambers, number of chambers in final whorl, total number of volutions, outline and other features of the axial depression (open, closed, stellate, etc.), characters of spiral and intercameral sutures, changes of shape of chambers and sutures during ontogeny, shape (umbilical, spiral) and arrangement of chambers in final whorl, etc.); secondly, the *wall structure* and the *agglutinant*; and, thirdly, the *dimensions*. The nature of the agglutinant is not, as yet, used taxonomically by us above species level.

The wall of trochamminaceous foraminifera is agglutinated and therefore all belong to the Textulariina. As already mentioned in previous papers (Brönnimann and Whittaker 1983a; Brönnimann 1986a), we differ in this respect from Loeblich and Tappan (1955, 1964, 1981) who would separate off *Carterina spiculotesta* (Carter), 1877, as a distinct group; the suborder Carterinina is here rejected as premature and unnecessary.

In the present discussion of the trochamminaceous wall structure, we are restricting ourselves to observations on two Recent species of the Trochamminacea, namely *Trochammina inflata* (Montagu) 1808, and *Asarotamina asarotum* Brönnimann 1986a. These are chosen because their wall structure has been investigated in some detail. A few remarks are also added on *Carterina* Brady 1884, and *Zaninettia* Brönnimann and Whittaker 1983, two genera with spicular tests, and a curious, but as yet, undescribed trochamminaceous with barytic agglutinant (Brönnimann and Whittaker 1987b, in press).

Trochammina inflata (Montagu)

This is the type-species of the genus *Trochammina* Parker and Jones 1859, itself type-genus of the subfamily Trochammininae Schwager 1877; hence of taxonomic significance for the entire superfamily Trochamminacea. It has recently been revised by Brönnimann and Whittaker (1984a: pp. 311-315, figures 1-11) and a neotype chosen. This neotype is refigured in plate 1, figure 1, herein. In addition, the

wall structure of specimens from Trobay, Devon, S.W. England (the type locality) and West Williamson, Dyfed, S.W. Wales, was examined from broken tests. It consisted of 3 "layers": (1) a thin organic inner "layer", also called the *inner lining*, beneath (2) a relatively thick agglutinated and organic middle "layer", in short, the *agglutinated layer*; and (3), if the test is well preserved or was living at the time of collection, a very thin, veneer-like organic *outer "layer"* on the outside of the agglutinated layer. This outer "layer" produces the brilliant lustre seen in living specimens of *T. inflata*. Normally, this outer organic veneer has been removed by bacterial and/or algal activity or through post-mortem abrasion; the test then often appears dull. Possibly this organic outer veneer may be developed in other smooth-surface Trochamminacea but it is only rarely preserved. The somewhat thicker inner organic lining, on the other hand, is not only better protected but also more resistant and is, therefore, quite often partially or totally preserved after death. As shown by the broken fragments (Brönnimann and Whittaker 1984a; p. 314, figures 6-11), the thick agglutinated layer contains organic matter which serves to "glue" the individual foreign elements together. These are irregularly shaped sediment grains of variable size, but their nature has not been determined. They are arranged in such a way that they produce a rather tightly packed and closely-fitted texture, resistant enough to withstand a fairly strong pressure when prodded with a dissecting needle. Even more surprising than the detailed texture of the agglutinated layer is the fact that *T. inflata*, with this type of irregular-shaped and rather coarse, random sized material, produces a relatively smooth test surface (see plate 1, figure 1). It is slightly more granular on the umbilical side than on the spiral side, but shows a very high degree of order in the construction of the surface of the agglutinated layer. Although there are several grains (usually 3 or more) making up the thickness of the agglutinated layer. Although there are several grains (usually 3 or more), making up the thickness of the agglutinated layer, their arrangement does not suggest any layering. This type of undifferentiated agglutinated layer is here termed *single-layered*. It seems to be the normal type of structure of the agglutinated layer in at least the members of the Trochamminacea and the Remaneicacea that we have studied; that of the Dictyopsellacea has not been examined. In the agglutinated layer, furthermore, there are no indications of perforations or alveolae as found, for instance, in *Textularia agglutinans* d'Orbigny and in *Cyclamina cancellata* Brady, nor were there any signs of pores on the inner and outer organic surfaces. For these reasons, the wall of *T. inflata* has been termed *imperforate*, and from our experience it would seem that this is the case with all trochamminaceous tests.

As eventually only the agglutinated layer of the wall will be preserved after death and in fossils, the agglutinated layer is therefore termed the *wall*, and the sum of the foreign elements that constitute it, is termed the *agglutinant*.

Asarotamina asarotum Brönnimann.

The complete wall of this species consists of 2 layers: (1) a thick organic inner layer, much thicker than that of *T. inflata* of which it is the homologous formation; and outside it, (2) a relatively thin agglutinated and organic outer layer. The brilliant veneer-like surface layer, seen in *T. inflata*, does not occur. The surface of the agglutinated layer is not smooth but coarsely irregular (Brönnimann 1986a: p. 94, plate 3, figures 1-4). The agglutinant consists solely of magnesium-free crystals of calcium carbonate. The underlying thick organic layer is characterised by a high iron, sulphur and magnesium content, but is low in calcium. The crystals are of different size and shape. They form an agglutinated layer of 2 or 3 grains in thickness. The lowermost or inner grains are deeply embedded in the thick organic layer and organic substance separates them. They are arranged as an irregular mosaic. The outer grains are "glued" to the inner ones and to each other by organic matter. The agglutinated layer is not differentiated vertically into layers and has, therefore, to be termed single-layered. The wall is devoid of perforations or alveolae and is imperforate.

Significance of the wall structure.

A comparison of the wall of *Trochammina inflata* (Montagu) with that of *Asarotamina asarotum* Brönnimann, shows the presence in both species of inner organic lining, thin in the former, thick in the latter, and an agglutinated layer. The outer organic veneer occurs only in *T. inflata*. The agglutinated layer is, in both species, undifferentiated, single layered and imperforate. The agglutinated layer is a tightly constructed formation in *T. inflata*, with a smooth surface, quite different from that of *A. asarotum*, characterised by loosely added homogenous crystal grains and a rough and irregular surface.

The morphological analysis of the wall of *T. inflata* and of *A. asarotum* has shown that within the superfamily Trochamminacea the wall structure can differ considerably. However, it has also become evident that in these species, selected at random and quite different in their construction of the wall, the agglutinated layer (i.e. the wall proper) shows the same characteristics: it is single layered and imperforate.

These features concern the construction of the wall of the Trochamminacea, independent of the type of

agglutinant/organic matter used in keeping the wall together. They represent criteria which are of superfamily significance. They are quite different from the surface appearance of the test (granular, smooth, mosaic-like, rough, etc.), the nature and composition of the agglutinant (homogenous, heterogeneous), the colour of the surface, etc., features which can only be employed at low taxonomic levels (for species, subspecies, ecophenotypic variants).

The chemistry of the organic phase of the agglutinated wall is not well enough known to enable this criterion to be used in the classification. The work undertaken by Hedley (1963), Towe (1967), Murray (1973) and Lipps (1973) showed that the organic cement of certain agglutinated foraminifera contained varying amounts of iron and calcium. Some progress has been made in this field using electron microprobe analysis. Commeau et al. (1985) have particularly studied the agglutinant and concluded that its composition varies with: (1) the nature of the local substrate characteristics; (2) the physiochemical properties of the water column; and (3) the species dependent selectivity of test components. Bevan (in Brönnimann, 1986a), in addition to analysing the agglutinant, found in *A. asarotum*, calcium, iron, sulphur and magnesium in the organic cement. In order to use this type of data taxonomically, the organic cement of many more species of agglutinating foraminifera would have to be analysed before certain stable characteristics could be found.

Selection and order in the agglutinant.

Brönnimann (1986a) already discussed the taxonomic implications of the type of agglutination and tentatively concluded that the elements and their arrangement were only taxonomically significant when a high degree of selection/order in their disposition were shown. In fact, in the agglutinated foraminifera, the taxonomic significance of the agglutinant and the disposition of the elements is in direct proportion to the degree of selection and the degree of order exhibited. In *Asarotamina asarotum*, the agglutinant is of a homogenous nature, that is, the degree of selection is high. On the other hand, the agglutinated layer is irregular and does not form a smooth surface, and therefore the degree of order in its construction is low. In *Trochammina inflata*, the degree of order in the formation of the agglutinated layer is high. Nothing can be said about the degree of selection because the composition of the agglutinant has not been examined by us.

Normally, there is no particular selective action recognisable and consequently the taxonomic standing of the agglutinant can be regarded as low.

Similarly, there is normally no special order in the arrangement of the elements and thus the taxonomic standing of the disposition of the elements is also low. Indeed, both criteria can be neglected in classification; in such cases, the agglutinant is taxonomically only of ecophenotypic significance. It simply reflects the availability/random uptake of building material at a certain locality (see also Brönnimann and Whittaker 1983 on *Zaninettia* and *Carterina*; Brönnimann (1986a,b) on *Asarotamina* and *Toretamina*, respectively).

The agglutinant, including that of *Carterina*, *Zaninettia*, *Asarotamina* and various species of *Paratrochammina* and *Deuterammina* (see plate 3 for some examples), is not used by us as a criterion for specific or generic, let alone suprageneric classification. These forms, with their particular and selective agglutinants, are placed in our classificatory framework as outlined by Brönnimann et al. (1983), using other features (e.g. internal structures, apertures) of higher taxonomic weight.

Remarks on the wall structure of *Carterina* and *Zaninettia*-spicular tests.

The origin of the spicules in *Carterina spiculostesta* (Carter), 1877, has long been a contentious issue (see Brönnimann and Whittaker, 1983a, for a review). Whereas Loeblich and Tappan (1981) would consider the spicules to have been formed by the foraminifer and constitute the placement of the single species in a separate suborder, the Carterinina, Brönnimann and Whittaker (op. cit.) would consider it to be an agglutinating foraminifer within the Trochamminacea. Only work on laboratory cultured individuals will solve the problem of the origin of the spicules.

If nothing else, our paper did show clearly that there were in fact two distinct types of spicular foraminifera, a situation hinted at previously by Keij, (1976). First, there is *Carterina* Brady, 1884 (without internal chamber partitions), and *Zaninettia* Brönnimann and Whittaker, 1983, with secondary septa. A specimen of *Carterina* together with several other foraminifera with specialised agglutinant, is shown in plate 3. If we consider these spicular forms to be agglutinating foraminifera, in the absence of definitive evidence to the contrary, and even though the selective nature of the agglutinant is remarkable, this criterion is of much lower taxonomic weight than the apertural features which separate *Carterina* from all other known members of the Trochamminacea and the internal structures which would place *Zaninettia* into a separate superfamily, the Remaneicacea.

Remarks on other specialized wall structures - baryte tests.

Brönnimann and Whittaker (1983a:19,20) list a series of examples of agglutinating foraminifera which select, some exclusively, particular elements from which they make their test. These include sponge-spicules and coccoliths, the use of the latter being also discussed and illustrated by Murray et al. (1983). A striking example of a test composed entirely of coccoliths is shown in plate 3, figures 1,2. At least, the nature of coccoliths is known and so one cannot suspect the foraminifer of having made them!

Recently, a new, rather curious example of specialised agglutinant has come to light. In the course of our revision (Brönnimann and Whittaker 1987b in press) of the trochamminaceous foraminifera of the Antarctic and South Atlantic, originally described by Heron-Allen and Earland (1932-1936) in the Discovery Reports, the tests of several species belonging to 3 distinct genera, were found to possess very small agglutinated ovoid bodies, the like of which we had not seen before. Generally less than 5 microns in maximum diameter, they vary in their distribution from very sparse (to other agglutinated mineral grains), by gradation through to specimens where the test is apparently made up completely of these bodies (see Plate 3, figures 4-7). Electron microprobe analyses have shown that the mineral content of these bodies is at least 90% baryte (barium sulphate); up to 3% TiO₂ is present and other elements are likely to occur in very small amounts. The bodies have a remarkably constant composition from locality to locality, from specimen to specimen, from species to species.

The enigmatic bodies could either be from an inorganically produced mineral deposit, or they could be organic in origin coming from another organism (xenophyophores are a possibility, see Gooday & Nott, 1982). It is not thought that the foraminifer made them itself as some tests have very few baryte bodies compared to mineral grains and organic baryte is supposed to contain strontium (Church, 1970), which is absent here. The ovoid bodies have a rounded smooth surface. Baryte commonly forms well-shaped orthorhombic crystals, and when occurring as globular aggregates of radiating crystals some indication of structure can be seen. The generally uniform size of the bodies is more consistent with an organism population than growths of inorganic origin, which would tend to vary greatly in size according to the supply of material and order of nucleation. The bodies are not pure baryte. Natural baryte is known to contain Pb, Sr, with or without Ca, but Ti is not known as a substituting element.

Baryte deposited out of solution occurs as a pure substance rather than an admixed one, and is crystalline; amorphous baryte has not been recorded. Examination of the baryte with the Scanning Electron Microscope (Plate 3, figures 5-7) did not reveal a great deal of detail, as the whole of the test was covered with what could possibly be a very thin outer organic veneer (c.f. *Trochammina inflata*, p.). Ion beam etching was used to remove this layer and the wall re-examined under the SEM. Now a smooth surface on the baryte bodies was revealed with a number of small holes, together with an indication of lines which could be crystal boundaries. For the moment these bodies must remain something of an enigma.

THE CLASSIFICATION OF THE TROCHAMMINACEA

After the presence or absence of internal structures, which are used to distinguish the superfamily Trochamminacea (without internal structures) from the Remaneicacea and Dictyopsellacea (both with internal structures), and after the family criterion represented by the mode of enrolment (Brönnimann & Whittaker, 1987a; Brönnimann et al., in preparation), the criteria used for the definition of subfamilies are the overall apertural features. The genera and subgenera are differentiated on the basis of the details of the apertural features and on the adult growth forms. In the superfamilies Remaneicacea and the Dictyopsellacea, which will not be considered further in the present paper, other features, mainly the nature of the internal subdivisions, are used for differentiating the subfamilies and genera.

Brönnimann et al.'s (1983) classification proposed 5 subfamilies within the Trochamminidae Schwager, 1877 and 21 genera. This framework is again followed but the family characters used previously are now raised to superfamily rank. Two families, the Trochamminidae Schwager, 1877 and the Adercotrymidae Brönnimann and Whittaker, (1987a) are included. Suitably emended suprageneric definitions are now given based on the criteria listed above. To the genera here within the Trochamminidae is added *Portatrochammina* Echols, 1971, making 22 in total. New taxa introduced since 1983, however, will be dealt with in a forthcoming full revision of our classification (Brönnimann et al., in preparation).

Superfamily: TROCHAMMINACEA Schwager, 1877, emend.

Emended definition: Test free or attached; wall agglutinated, imperforate; trochospiral, length of axis of enrolment shorter than or equal to maximum umbilical diameter; trochospire may become

modified by involution of spiral side or by tendency to uncoil in plane of final whorl; aperture interiomarginal or areal, single or multiple; devoid or infoldings of umbilical chamber walls and inner structures.

Families 1. TROCHAMMINIDAE Schwager, 1877, emend.

Emended definition: Test free or attached; wall agglutinated, imperforate; trochospiral; adult spiral side evolute; enrolment may show tendency to uncoil in plane of final whorl; aperture interiomarginal or areal, single or multiple; devoid of infoldings of umbilical chamber walls and inner structures.

2. ADERCOTRYMIDAE Brönnimann and Whittaker, 1987a.

Definition: Test free wall agglutinated, imperforate, trochospiral; adult spiral side involute; aperture interiomarginal; devoid of infoldings of umbilical chamber walls and inner structures.

Family TROCHAMMINIDAE Schwager, 1877.

Subfamilies: 1. TROCHAMMININAE Schwager, 1877

Definition: aperture interiomarginal, single.

Genera: TROCHAMMINA Parker and Jones, 1859

Definition: Aperture sitting completely on wall of first chamber of last volution, not in direct contact with axial cavity (umbilicus). (see Plate 1, figure 1).

ARENONIONELLA Marks, 1951

Definition: Aperture single, interiomarginal, equatorial, on first chamber of last volution.

PARATROCHAMMINA Brönnimann, 1979

Definition: Aperture extending from wall of penultimate to that of final chamber of last volution, in direct contact with axial cavity (umbilicus).

SUBGENERA: P. (PARATROCHAMMINA) Brönnimann, 1979

Definition: With inflated chambers (non-lepidoid growth form). (see Plate 1, figures 2, 3).

P. (LEPIDOPARATROCHAMMINA) Brönnimann and Whittaker, 1986

Definition: With lepidoid adult growth form. (see Plate 1, figures 4-5).

PORTATROCHAMMINA Echols, 1971

Definition: Aperture as in *Paratrochammina* but extension of chamber wall covers axial cavity. Development of lamellar structure in axial cavity. (see Plate 1, figure 6).

ROTALIAMMINA Cushman, 1924

Definition: Aperture at axial end of stem-like symmetric extension of chamber. Test with peripheral flange.

SIPHOTROCHAMMINA Saunders, 1957

Definition: Aperture at end of short tunnel-like asymmetric extension of chamber.

TIPHOTROCHA Saunders, 1957

Definition: Aperture at end of short tunnel-like symmetric extension of chamber. Test without peripheral flange.

TRITAXIS Schubert, 1920

Definition: Aperture of *Trochammina*-type. Test in adult typically with 3 chambers. Umbilically flat or almost so. (See Plate 1, figures 7-8).

TROCHAMMINOPSIS Brönnimann, 1976

Definition: Aperture of *Paratrochammina*-type resting on walls of penultimate and first chamber of final volution, symmetric in shape, axially positioned. (see Plate 2, figure 1).

VALVULAMMINA Cushman, 1933

(See *Discorinopsis*)

2. Subfamily TROCHAMMINELLINAE

Brönnimann, Zaninetti and Whittaker, 1983

Definition: Aperture areal, single or double.

Genera: *TROCHAMMINELLA* Cushman, 1943

Definition: Aperture areal, close to base of septal face. Test in adult typically with 3 chambers. Umbilically flat or almost so.

AMMOGLOBIGERINOIDES Frerichs, 1969

Definition: Aperture double, both areal: one on umbilical side, the other on spiral side of septum.

PSEUDOTROCHAMMINA Frerichs, 1969

Definition: Aperture single, areal, close to base of septum. (see Plate 2, figure 2).

SEPETIBABELLA Brönnimann and Dias Brito, 1982

Definition: Aperture single, terminal, areal.

3. POLYSTOMAMMININAE Brönnimann and Beurlen, 1977

Definition: Aperture double: primary aperture interiomarginal; secondary aperture at umbilical tip of chamber in sutural position, posteriorly or axially directed.

Genera: *POLYSTOMAMMINA* Seiglie, 1965

Definition: Aperture double: primary aperture interiomarginal, hook-like; secondary aperture at umbilical tip of chamber in sutural-axial position, posteriorly directed. (see Plate 2, figures 4-5).

DEUTERAMMINA Brönnimann, 1976

Definition: Aperture double: primary aperture of *Trochammina*-type; secondary aperture at umbilical tip of chamber in sutural-axial position, posteriorly or axially directed. (see Plate 2, figure 6; plate 3, figures 1-2).

SUBGENERA: *D.* (*DEUTERAMMINA*) Brönnimann, 1976

Definition: With inflated chambers (non-lepidoid growth form); posteriorly directed secondary apertures.

D. (*LEPIDODEUTERAMMINA*) Brönnimann and Whittaker, 1983b

Definition: Lepidoid growth form; posteriorly directed secondary apertures.

D. (*CENTRODEUTERAMMINA*) Brönnimann and Whittaker, 1983c

Definition: With axially directed secondary apertures.

4. Subfamily ARENOPARRELLINAE Saidova, 1981 (emend. Brönnimann et al., 1983)

Definition: Aperture double or multiple, interiomarginal or areal, or interiomarginal and areal.

Genera: *ARENOPARRELLA* Andersen, 1951

Definition: Aperture double or multiple: primary aperture an elongate slit, interiomarginal or areal; secondary aperture(s) areal, in peripheral position.

DISCORINOPSIS Cole, 1941

Brönnimann et al. (1983) removed the genera *Valvulammina* Cushman, 1933 and *Discorinopsis* Cole, 1941 from the Ataxophragmacea and placed them in the Trochamminacea on account of their low trochospiral coiling. Since the present paper went to press, new work undertaken by us on the wall structure of their respective type species has shown that neither genera can now be included in the Trochamminacea.

We have examined topotypes of *Discorinopsis gunteri* Cole, 1941 from the Middle Eocene of Florida, kindly loaned to us by the U.S. National Museum, Washington. First, it develops a large Perforate vulvular tooth, a feature unknown in the Trochamminacea. Secondly, the wall consists of much fine-grained "cement" into which are incorporated rather rare foreign elements. This cement is very dense and is thought more likely to be of a secreted nature. Axial thin-sections, moreover, show the wall to have fine perforations with blind distal endings arranged parallel to each other and perpendicular to the wall surface. Such features (cement and alveolar "pseudo-perforations") are equally unknown in trochamminacean morphology.

Specimens of *Valvulammina globularis* (d'Orbigny), 1826 from the Lutetian of Hauteville, France (ex d'Orbigny sample no. 139), were also examined using matrix-free and thin-sectioned material. Again we came to the same conclusion. The presence of a large valvular tooth and a wall structure identical to that of *Discorinopsis* both necessitate the removal of *Valvulammina* from the Trochamminacea.

ENTZIA Daday, 1883

Definition: Aperture multiple, symmetrically arranged areal pores.

JADAMMINA Bartenstein and Brand, 1938

Definition: Aperture multiple: primary aperture interiomarginal, equatorial; secondary apertures - areal pores. (see Plate 2, figure 3).

TROCHAMMINULA Shchedrina, 1955

Definition: Composite interiomarginal aperture: primary aperture umbilical-extraumbilical slit from which extends short perpendicular slit.

5. Subfamily CARTERININAE Loeblich and Tappan, 1955

Definition: Aperture in early stage, interiomarginal (of *Rotaliammina*-type); in adult, multiple.

Genus: *CARTERINA* Brady, 1884

Definition: As for subfamily.

Family ADERCOTRYMIDAE Brönnimann and Whittaker, 1987a

Subfamily: 1. ADERCOTRYMINAE Brönnimann and Whittaker, 1987a

Definition: aperture single, interiomarginal, umbilical, symmetric in shape.

Genus: *ADERCOTRYMA* Loeblich and Tappan, 1952

Definition: As for subfamily.

4. CLASSIFICATION OF FOSSIL TROCHAMMINACEA

The trochamminacean classification presented by Brönnimann et al., (1983), was established essentially with Recent species (see Chapter 3, above). Few fossil taxa were included in view of the many Recent species that first had to be understood both morphologically and taxonomically; previously, even these had been poorly known. The dictyopsellids, an extinct Late Cretaceous group, were originally included in the Trochamminacea by us (loc. cit., 1983: 206, 207) as a subfamily within the Remaneicidae Loeblich and Tappan, (1964), but following work by Loeblich and Tappan (1985) they are now much better known. Rather than place them in the planispiral Loftusiacea (Loeblich and Tappan, 1985: 177), however, we consider them worthy of distinct superfamily status. The prominent subepidermal network and radial beams found in the Dictyopsellacea are not now thought to be homologous with the infoldings of the chamber wall and secondary septa developed in the Recent remaneicids, which are here also raised to the level of superfamily.

Lately, one of us (P.B.) has begun to examine fossil Trochamminacea, in particular from the Paleocene-Early Eocene Lizard Springs Formation and from the Oligo-Miocene Karamat and Navet formations of central and southern Trinidad, West Indies. All these lithological units are characterized by flysch-type agglutinated foraminifera. A few trochamminacean species encountered in the Hobson Clay, Lizard Spring Formation, central Trinidad, show well preserved tests, where enrolment, aperture and adult growth form are all readily recognizable. One of the particularly common species from this clay has been referred to by authors as *Trochammina altiformis* Cushman and Renz, 1946. It has a subglobular test with 4 chambers in the final whorl and a single axially-located and relatively small, rounded,

interiomarginal aperture. We have encountered similar morphologies in deep Antarctic waters and these will be described in the forthcoming revision of the Trochamminacea of the Discovery Expeditions (Brönnimann and Whittaker, 1987b, in press). The other trochamminacean species of the Lizard Springs Formation are also generally well preserved and can easily be placed in our classificatory system. Others, from the Navet and Karamat formations (also deepwater) are more difficult to analyse because the tests are usually deformed - that is the individual chambers are compressed, probably not through penecontemporaneous collapse of the original subglobular to globular chamber walls, but diagenetically, through sediment pressure. Therefore, the nature of the deformation in fossil agglutinating foraminifera should not be considered as taxonomically significant (see Bartenstein and Bolli, 1986: 953, 954). Even in these secondarily modified morphologies, the enrolment, the original chamber form, the apertural features and the adult growth form can usually be determined and the species placed in our classification. We have, in fact, met with few morphological and taxonomic problems when dealing with fossil Trochamminacea and these usually concern the apertures. Poor preservation, recrystallization of the test or infilling of the umbilicus with sedimentary matrix may make it difficult to ascertain the apertural features. It may then be difficult, for instance, to assign a fossil species to *Paratrochammina* or *Trochammina*. In the case of *Conotrochammina* Finlay, 1940, based on a fossil type-species and said to have an areal aperture, it has proved impossible to be certain that there is a true aperture in that position. All except one of the types that we examined fail to show an areal aperture, the one remaining appears to have a hole in the middle of the final septum. It is, however, conceivable that an areal aperture could easily be blocked with sedimentary matrix or made difficult to see through diagenetic alteration. (For more information on this particular problem, see Brönnimann et al., 1983: 206). Now that the distinguishing features of Recent genera are better understood, only time will tell whether the criteria that we have outlined above can be readily used for fossil assemblages. We hope fellow workers will now look again carefully at their material in the light of these studies.

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PLATE 1

- Figure 1. *Trochammina inflata* (Montagu). Oblique-umbilical view. To show *Trochammina*-type aperture. Neotype, BMNH No. ZF 4267. From Devon, S.W. England. x145.
- Figure 2, 3. *Paratrochammina* (*Paratrochammina*) *tricamerata* (Earland). Oblique-umbilical and edge views. To show *Paratrochammina*-type aperture and subglobose test characteristic of sub-genus. Paralectotypes, BMNH no. ZF 4145 (from the South Shetland Islands) and ZF 4146 (between the Falkland Islands and South Georgia), respectively. x200 (figure 2), x275 (figure 3).
- Figure 4, 5. *Paratrochammina* (*Lepidoparatrochammina*) *lepida* (Brönniman and Whittaker). Oblique-umbilical and edge views. To show *Paratrochammina*-type aperture and lepidoid test characteristic of the subgenus. Paratypes, BMNH nos. ZF 4327 and ZF 4331, respectively. From the South Shetlands, Antarctica. x300 (4), x330 (5).
- Figure 6. *Portatrochammina bipolaris* Brönnimann and Whittaker. Umbilical view. To show extension of chamber wall covering axial cavity (apertural flap); preservation of previous apertural flaps give lamellar structure in axial cavity, typical of genus. BMNH no. ZF 3980. From the South Shetlands. x280.
- Figure 7, 8. *Tritaxis fusca* (Williamson). Oblique-umbilical view of free specimen (Neotype) showing *Trochammina*-type aperture, and spiral view of attached specimen respectively. BMNH nos. ZF 4209 and ZF 4203. From Skye, W.Scotland and New Zealand. x145 (7), x115 (8).

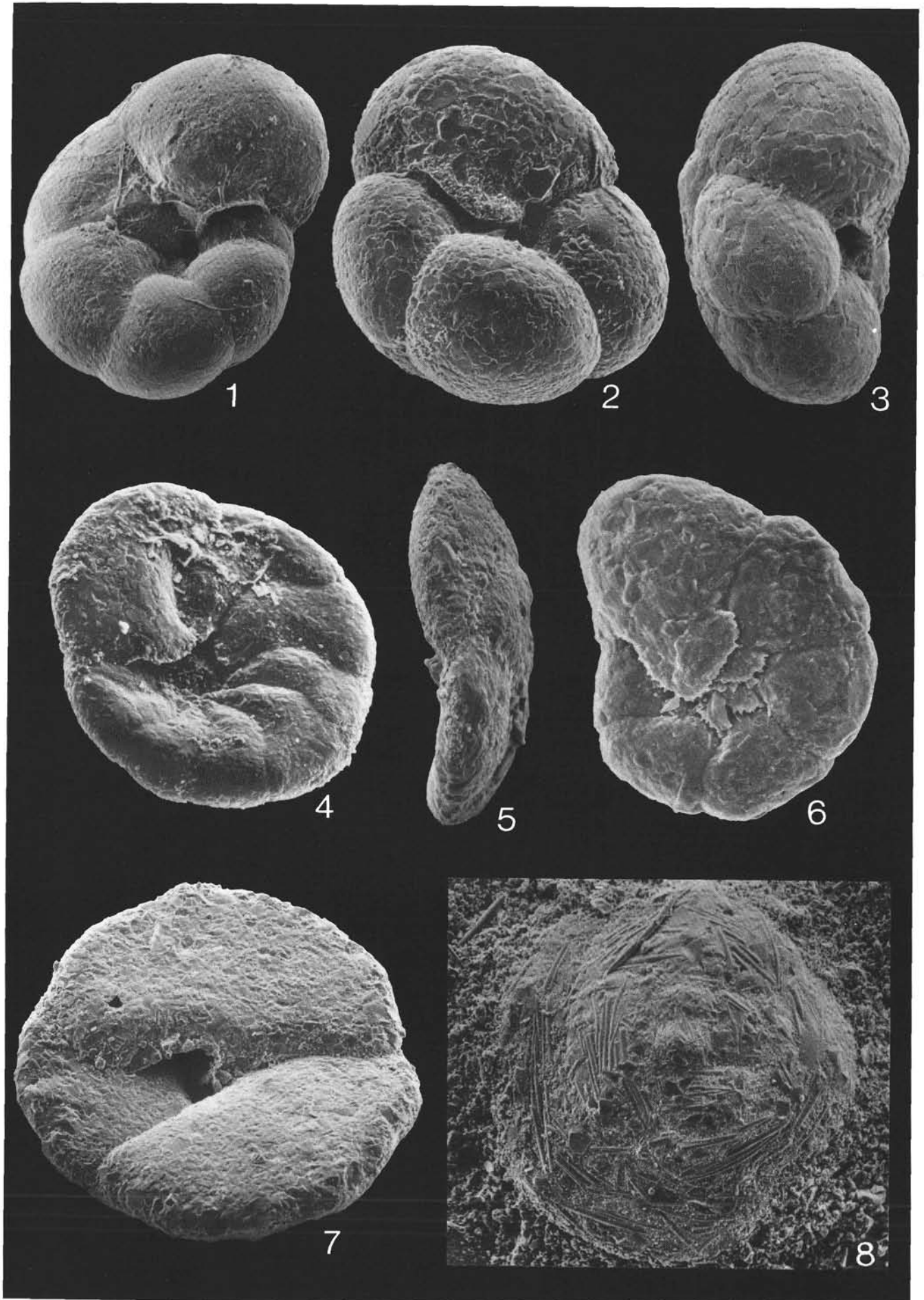


PLATE 2

- Figure 1 *Trochamminopsis globulosus* (Cushman). Umbilical view to show subglobose test and symmetric aperture in axial position. Topotype, BMNH no. ZF 4170. From the Gulf of Mexico. x65.
- Figure 2. *Pseudotrochammina arenacea* (Heron-Allen and Earland). Oblique-umbilical view showing areal aperture. Lectotype, BMNH no. ZF 4355. From off Oates Land, Antarctica. x195.
- Figure 3. *Jadammina macrescens* (Brady). Edge view to show interiomarginal primary aperture and secondary areal apertures. Paralectotype, BMNH no. ZF 4213. From Islay, W. Scotland. x175.
- Figures 4, 5. *Polystomammina* sp. Umbilical and edge views to show primary interio-marginal ("interio-areal") aperture and secondary apertures at umbilical tips of chambers, suturally situated and posteriorly-directed. BMNH nos. 4132 and 4131, respectively. From the Falkland Islands. x155.
- Figure 6. *Deuterammina* (*Lepidodeuterammina*) sp. Oblique-umbilical view to show primary interiomarginal opening and secondary apertures and the lepidoid test, generic and subgeneric characters, respectively. From off the Eddystone Lighthouse, S.W. England. x415.
- Figures 7, 8. *Remaneica plicata* (Terquem). Oblique-umbilical view to show infoldings of the umbilical chamber walls along the radial suture, one of the characters that differentiates the Remaneiceacea from the Trochamminacea. Note *Deuterammina*-type aperture, not previously seen (figure 8). From off the Eddystone Lighthouse, S.W. England. x175 (7), x620 (8).

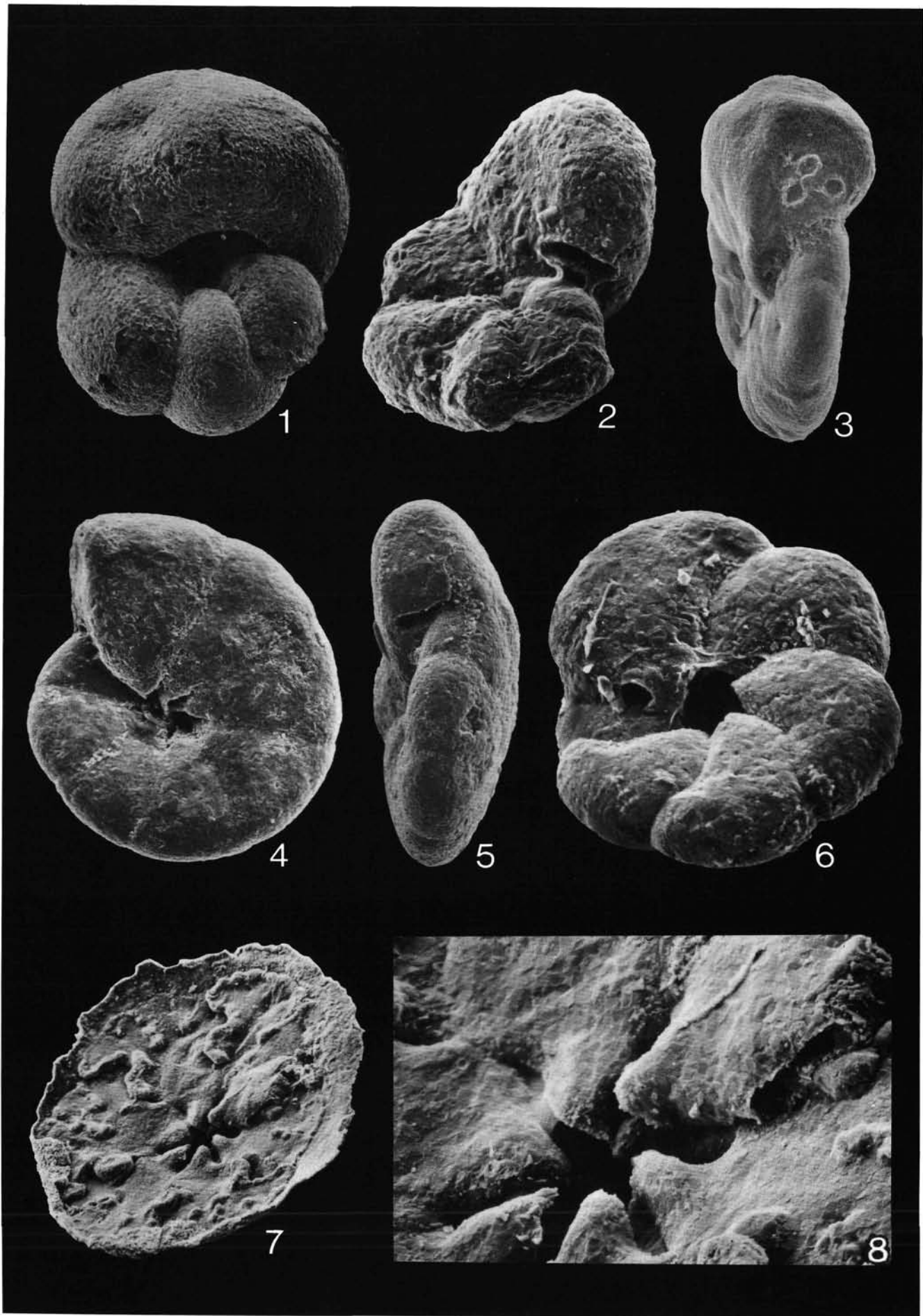


PLATE 3

- Figure 1, 2. *Deuterammina (Deuterammina)* sp. Umbilical side and oblique-umbilical close-up of axial cavity, respectively. The agglutinant consists entirely of plates of the coccolith, *Cyclococcolithus leptoporus*. Note primary and secondary apertures in figure 2. BMNH no. ZF 4341. From Gough Island, South Atlantic. x375 (1), x1,650 (2).
- Figure 3. *Carterina spiculotesta sensu* Brady. Umbilical view. Are the spicules made by the foraminifer itself or are they another example of particular selection and order of the agglutinant? BMNH no. 1959.5.5.245. From the Gulf of Suez. x55.
- Figure 4-7. *Deuterammina (Deuterammina)* sp. Spiral view (4), details of the peculiar agglutinant on the spiral side (5, 6) and section through the broken wall (7). Are the baryte bodies made by the foraminifer (cf. Xenophyophorida), or another example of particular selection and order of agglutinant? If the latter, where do these baryte bodies come from? BMNH no. ZF 4117. From the Bellingshausen Sea, Antarctica. x250(4), x1,300(5), x5,500 (6), x6,500 (7).

