

EARLY OCCURRENCES AND SOME PHYLOGENETIC IMPLICATIONS OF SPINY, HONEYCOMB TEXTURED PLANKTONIC FORAMINIFERA

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ABSTRACT

Cancellate walls of several fossil species are compared and homologized with the spiny, honeycombed wall of modern *Globigerinoides*. Spiny, honeycomb wall texture is primitive, dating back at least to late Oligocene and was much more widespread among

planktonic foraminifera in the past than it is today. Several modern types of walls appear to have been derived from this primitive texture. A new genus, *Paragloborotalia*, is proposed.

INTRODUCTION

As it becomes more apparent that most test features in planktonic foraminifera have developed iteratively and therefore the same morphologic expressions are often found in distinct lineages, increased emphasis is now placed on wall texture as a guide to inferring species relationships. A number of useful textural categories have been recognized for this purpose (Fleisher, 1974), based largely on a consideration of fossil species, but much remains to be done in relating fossil textures to the ones that now characterize the modern fauna.

In this paper several fossil species with cancellate walls are compared and homologized with the modern spiny, honeycomb walled *Globigerinoides*, using *G. trilobus* as the basis for comparison. While only a few species are considered here, they cover a wide morphotypic range that includes globigerine, turborotalid and orbuline forms. On the basis of textural comparisons and other considerations, a new genus, *Paragloborotalia*, is proposed with *Globorotalia opima opima* Bolli as type species.

BACKGROUND ON WALL TEXTURE

In the last decade SEM photographs have become the principal means of illustrating planktonic forami-

nifera and are now essential in the formulation of taxonomic concepts. The "Age of the SEM" may be said to have begun with Blow (1969) who illustrated a large number of species ranging in age from middle Eocene to Quaternary with SEM photographs. In the same year Hemleben (1969) produced an SEM analysis of the morphogenesis of wall texture in modern spinose species of planktonic foraminifera. Since that time, many more fossil species have been illustrated with the SEM, largely in the voluminous DSDP Reports; comparatively little has been done with modern, living species. The principal value of the SEM, other than its convenience as a means of illustration, is that it has helped elucidate textural features of the wall which were formerly obscure. With this added enlightenment, workers have followed the lead of Parker (1962) and Lipps (1966) who, working under the limitations of reflected and transmitted light, perceived the taxonomic and phylogenetic significance of wall texture. As a result, species relationships are now looked at somewhat differently than they were in the past.

In a study of Recent bottom sediments Parker (1962) separated the spinose and the nonspinose species into two families, the Globigerinidae and the Globorotaliidae. Lipps (1966) followed Parker and produced a classification of planktonic foraminifera, using wall

texture as a major defining character. He recognized three textural categories: smooth wall, spinose wall and pitted, nonspinose wall.

In a study of Oligocene and Neogene sediments of DSDP cores in the Arabian Sea, Fleisher (1974), aided by the SEM, took a critical look at the wall textures of the planktonic foraminifera. He noticed that species normally assigned to *Globigerina* included two groups with distinct kinds of wall texture. In one group the wall was hispid and spinose, corresponding to the modern *Globigerina*. In the other group the wall displayed a pitted or cancellate texture, with a network of ridges enclosing individual pores. Fleisher believed that the textural differences between these two groups indicated separate phylogenetic lineages, so he removed the cancellated species from *Globigerina* proper and informally designated them as "*Globigerina*." He found the same cancellate texture in turborotalid species. Fleisher recognized five textural categories but only three are of concern here: spinose, cancellate and finely perforate. The spinose texture is typified by the modern, spiny *Globigerina*. The cancellate texture is characterized by a reticulated ridge pattern surrounding individual pores (pore pits), as in *Turborotalia*. The finely perforate texture is smooth walled, with no pore pits or spines and is typified by *Globorotalia*.

Later, Steineck and Fleisher (1978) used the same textural scheme, except that cancellate spinose and cancellate nonspinose were listed as separate categories and *Globoquadrina* replaced *Turborotalia* as the generic example of cancellate nonspinose. The reason for the generic change was Fleisher's (1975) earlier recognition that *Turborotalia* is an inappropriate designation for post-Eocene turborotalids. A discussion of the *Turborotalia* problem will be given later.

The "gray area" in this scheme lies between cancellate spinose and cancellate nonspinose, since there can be a problem in determining whether a fossil specimen with a cancellated wall did or did not bear spines. On the other hand, anyone who has examined modern, living species cannot help but be impressed with the textural resemblance between the modern *Globigerinoides* and many fossil species with cancellated walls, after making allowance for differences in preservation. Indeed, in light of the descriptions and discussions to follow it could be argued, though perhaps not unequivocally, that the *Globoquadrina dehiscens* shown by Steineck and Fleisher (1975) is spinose.

In dealing with modern species it is customary to use the term honeycomb for a reticulate pattern of

ridges surrounding individual pores. Honeycomb appears to be fully equivalent to cancellate or pitted; terms used for fossil forms. In the textural comparisons between the modern *Globigerinoides trilobus* and the several fossil species that follow, the term honeycomb will be used.

SPINOSE HONEYCOMB TEXTURE IN MODERN *GLOBIGERINOIDES*

GENERAL REMARKS ON SPINOSE SPECIES

Most modern species of planktonic foraminifera show variability in wall thickness and textural development. The variability occurs not only among individuals within a population of a species, but also between chambers of a single individual. Importantly, the final, therefore most recently formed chamber is often thinner and texturally more simple than the preceding ones. It is this variability that allows for some interpretation of ontogenetic development of wall texture. Hemleben (1969) has described the morphogenesis of some spinose textures and additional descriptions have been given by Cifelli (in press).

In spinose species a newly formed chamber has a thin, smooth wall, usually with weakly developed pores. Some spine projections unsupported by bases (buttresses), may already be visible on the smooth wall. Later, the pores become fully developed as the chamber wall is reinforced and thickened by additional calcification. Thickening occurs both by secretion of sheetlike laminations that envelop the chamber, and by the accretion of discrete tiers of platy crystallites. These neatly arranged terraced structures originate, in most cases at least, as buttresses around the bases of the spines. Occasionally, they are restricted in development and remain isolated from each other. In such cases the wall surface has a hispid appearance. Much more often, the spine bases spread laterally, forming ridges composed of tiered platelets. The ridges may develop in an erratic fashion, independently of pore location. Where the ridges join, they almost always enclose two or more pores. This irregular kind of ridge development is typified by *Globigerina bulloides* and is shown by Scott (1974).

TEXTURAL DEVELOPMENT OF *GLOBIGERINOIDES*

In *Globigerinoides* the ridges develop in a notably regular fashion with respect to the pores. They grow laterally from spine bases and fuse with the ridges from neighboring spine bases to surround single pores, resulting in a honeycombed wall surface. When this

texture is well formed, each pore is totally enclosed in hexagonally or pentagonally shaped enclosures of ridges with spines, or spine bases, protruding from the corners of the enclosures. However, the purity of geometric form seen in siliceous organisms is seldom achieved, so that the ridge enclosures usually appear somewhat distorted or subrounded, or portions of the ridges may not be fully developed. Also, a full complement of spines may not be visible around individual pores, or there may be a doubling of spine bases at particular corners of an enclosure. Nevertheless, all modern species of *Globigerinoides* have a distinctive honeycomb appearance with at least nearly geometric enclosures composed of tiered platelets surrounding single pores and spine bases projecting from the corners of the enclosures.

The actual elongate spiny projections are often absent, since spines are delicate structures and easily destroyed. Even in live material brought up in plankton tows, species known to be spinose many times lack or contain few spines. On occasion, the spines become detached, leaving hollow openings in their bases. In the fossil record hollowed bases are probably the best evidence for original spinosity. Much more commonly, however, the spines are broken just above their buttressed bases, so that their remnants appear as short angular projections above the ridge surfaces, as in the specimen of *G. trilobus* shown in Pl. 1, Fig. 1a.

The specimen of *Globigerinoides trilobus* shown in Pl. 1, Figs. 1, 1a has a mature texture that is characteristic of modern representatives of *Globigerinoides*. Honeycomb structure is well developed with hexagonally or pentagonally shaped ridge enclosures around each of the pores and projecting angular spine bases. The tiers of platy crystallites composing the ridges are clearly visible. The pore areas bounded by the ridge enclosure areas are generally called pore funnels, but they are not always funnel shaped. A funnel shape results when the ridge platelets grow obliquely towards the rim of the pore. When there is little or no extension towards the pore rim, the shape appears cylindrical. Intermediate shapes are shown in Pl. 1, Fig. 1a.

As in other planktonic species, the texturally mature stage of *Globigerinoides* is followed by heavy calcification which tends to obscure earlier features. The textural form of this encrusting phase in *Globigerinoides* is shown by the specimen of *G. trilobus* figured in Pl. 1, Figs. 2, 2a. Coarse knobs cover the spine bases as the spines have been either discarded or resorbed, except in the apertural and sutural areas. The

knobs are rounded and have a platy structure; they have spread laterally to encroach on the pores. In the final chamber development of the knobs has just commenced, and the honeycomb patterned texture remains intact. However, in the earlier chambers the texture is largely obliterated by the coarse, rounded knobs.

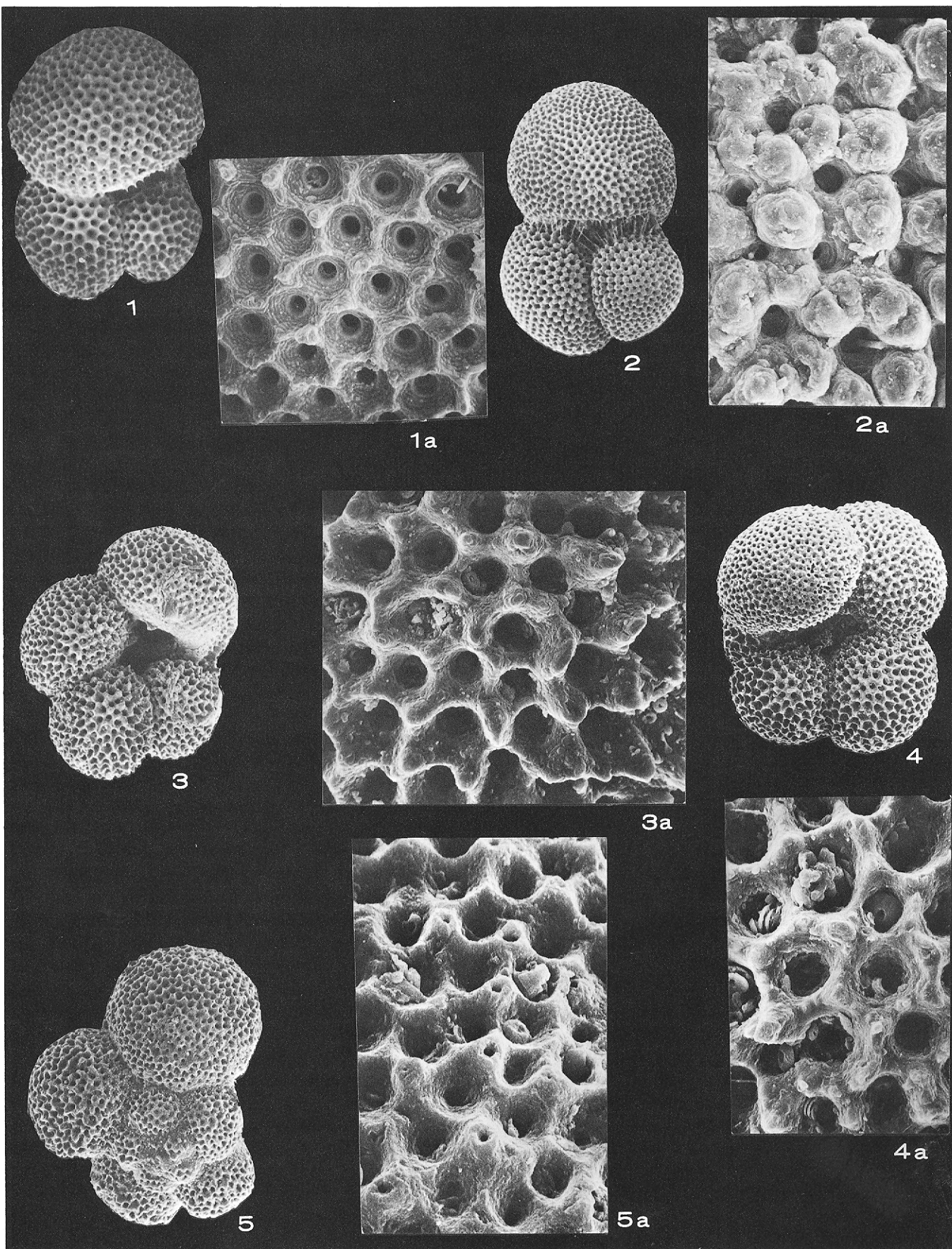
SPINOSE HONEYCOMB TEXTURE IN FOSSIL SPECIES

A major handicap in the textural study of species found in older sediments is the scarcity of material totally suitable for examination. Primary texture is revealed mostly by specimens with relatively thin walls, in early to mature stages of development. Such specimens occur less commonly than the thicker forms that have already become somewhat encrusted. Encrustation tends to eclipse the earlier formed textural features. Among the available thinner, totally unencrusted specimens, there are, in most cases, some signs of deterioration in structural detail of texture due to dissolution, abrasion, or other effects of post mortem burial. Especially subject to damage or deterioration are the spine bases and the terraced structure of the ridges surrounding the pores. The few examples shown here were selected from a large set of SEM photographs. Many other photographs show indications of honeycomb texture (numerous others could be cited from the literature) but for the most part they lack sufficient detail to make a good comparison with the modern *Globigerinoides*.

As additional well preserved material becomes available, it may well turn out that a wide variety of species, ranging from late Oligocene or earlier to near Recent, were characterized by a honeycomb texture. The principal problem at present is that the texture of incompletely preserved forms cannot be distinguished with surety from the texture of *Neogloboquadrina*, which is very similar to that of *Globigerinoides*. The question of *Neogloboquadrina* will be discussed later.

GLOBIGERINE FORMS

Examples of honeycomb texture in species that would normally be assigned to *Globigerina* (or "*Globigerina*" of Fleisher, 1974) are provided by *G. euapertura* Jenkins and *G. cf. G. gortanii* Borsetti. A late Oligocene specimen of *G. euapertura* is illustrated in Pl. 1, Figs. 3, 3a. The specimen comes from a DSDP core (Leg 9, Site 78) in the Equatorial Pacific at a horizon assigned to the *Chiloguembelina cubensis* Zone (Jenkins and Orr, 1972). It displays a typical glo-



bigerine form with four inflated chambers in the peripheral whorl and an open aperture that is largely confined to the umbilical area. A view of the whole specimen (Pl. 1, Fig. 3) shows a well-formed honeycomb pattern on all existing chambers (the final chamber obviously has been broken off). Each pore is individually enclosed by rather coarse ridges, giving the test a very rugose appearance. The ridge enclosures are roughly pentagonal or hexagonal in shape, and even at this relatively low magnification ($\times 200$) short spiny projections can be seen protruding from the ridge corners. Details of the honeycomb texture on the n-2 chamber are shown in Pl. 1, Fig. 3a, where the magnification has been increased to $\times 1000$. While the surface of the chamber has been subjected to some wear, the terraced platelet structure of the ridges, characteristic of the modern *Globigerinoides trilobus* (Pl. 1, Fig. 1a), is clearly visible. The pore areas tend to be more cylindrical than funnel shaped but show no actual disagreement in form from those of the modern *G. trilobus* (Pl. 1, Figs. 1, 1a). Also, while some of the spine bases of *G. euapertura* are blunted by wear, the ones visible at the bottom and center of Pl. 1, Fig. 3a are unusually well preserved. They have retained their angularity and compare very favorably with the spine bases of the modern *G. trilobus* shown in Pl. 1, Fig. 1a.

The other globigerine form included here, *Globigerina* cf. *G. gortanii*, comes from the *Globorotalia opima opima* Zone of Bolli (1957) in Trinidad. While identification of this form is tentative, it clearly belongs to a species that would be placed in *Globigerina* on general morphology. The chambers of *G. cf. G. gortanii* are even more inflated than in *G. euapertura* while the aperture is open, mostly umbilical, extending far short of the peripheral margin. Viewed as a whole, the specimen of *G. cf. G. gortanii* (Pl. 1, Fig. 4) shows a maturely developed honeycomb texture on all but the final chamber. Each pore is surrounded by mostly pentagonally shaped ridges, with short, angular projections extending from the ridge corners. While not as sharply defined, the pore ridges (Pl. 1, Fig. 4a) have

the same terraced platelet structure seen in *G. euapertura* and *Globigerinoides trilobus* with reasonably well preserved spine bases projecting from the ridge corners. Pore areas are cylindrical in shape. The final chamber is texturally less mature than the previous ones, with incompletely developed ridges and a pore network that is still partially open.

Without doubt the globigerine forms with a spiny honeycomb texture warrant a separate generic designation, as originally recommended by Fleisher (1974). A new genus can not be proposed here because the specimens of the species examined are not from the type localities. Also, it is possible that the globigerine Paleogene genus *Subbotina* could adequately accommodate these forms. Judgment is deferred here until a closer comparison of textural details is made.

TURBOROTALID FORMS

The species originally designated as *Globigerina angulosuturalis* Bolli and *Globorotalia opima opima* Bolli provide examples of spiny honeycomb texture in turborotalid forms. These species are placed in the new genus *Paragloborotalia* for reasons discussed later. Examined specimens of both species come from the type locality of the late Oligocene *Globorotalia opima opima* Zone of Bolli (1957) in Trinidad.

The specimen of *Paragloborotalia angulosuturalis* shown in Pl. 1, Fig. 5 has the characteristic turborotalid features, with a flattened spiral side and rounded to sublobulate chambers. All chambers have a well developed, mature honeycomb texture with the pores individually enclosed by rather coarse ridges; short spinelike projections protrude from the ridge corners. A magnified portion of the final chamber (Pl. 1, Fig. 5a) shows the terraced platelet structure of the ridge enclosures. The pore areas vary from funnelled to cylindrical in shape. Structural detail is somewhat blunted by some abrasion of the wall surface, but the spine bases protruding from the ridge corners are sufficiently distinct. Importantly, most of the spine bases have hollow openings, which provide the best possible evi-

PLATE 1

1. *Globigerinoides trilobus* (Reuss). $\times 230$. 1a. Detail of n-2 chamber; $\times 1000$. Recent plankton tow, tropical North Atlantic.
2. *Globigerinoides trilobus* (Reuss). $\times 1,000$. 1a. Detail of n-2 chamber; $\times 1,000$. Recent plankton tow, North Atlantic.
3. *Globigerina euapertura* Jenkins. $\times 200$. 1a. Detail of n-2 chamber; $\times 1,000$. DSDP leg 9, site 78, core 25, section 3; Upper Oligocene. *Chiloguembelina cubensis* zone.
4. *Globigerina* cf. *G. gortanii* Borsetti. $\times 200$. 4a. Detail n-2 chamber; $\times 1,500$. Trinidad; Late Oligocene, *Globorotalia opima* zone, type locality.
5. *Globigerina angulosuturalis* Bolli. $\times 300$. 5a. Detail of n chamber; $\times 1,500$. Trinidad; Late Oligocene, *Globorotalia opima* zone, type locality.

dence that the bases did, in fact, bear spines. Instances of spines becoming fully detached and discarded from their bases are relatively scarce in the fossil record. In those cases where spines do become fully detached the hollow openings of the spine bases may become closed or concealed by postmortem wear. Loss of openings is indicated in Pl. 1, Fig. 5a where only minute openings remain on occasional spine bases, while on others there is no evidence of holes. However, viewed as a whole, the total surface covered by Pl. 1, Fig. 5a shows a rather dense concentration of hollow spine bases, indicating that *P. angulosuturalis* was fully spinose in its living state.

Paragloborotalia opima opima is represented here by two specimens, both of which have been photographed from the umbilical side (Pl. 2, Figs. 1, 1a; 2, 2a). In this view they clearly show the extraumbilical extension of the aperture, an important feature of the turborotalid form which distinguishes it from the globigerine form and allies it with the globorotalids. Chambers are less inflated than in *P. angulosuturalis*, but are still distinctly rounded. Profiles, not shown in the illustrations here, are also distinctly rounded as is also the case in *P. angulosuturalis*. Both specimens of *P. opima opima* show well developed honeycombed patterns on all chambers, but there is a difference between the two specimens in stage of textural maturity.

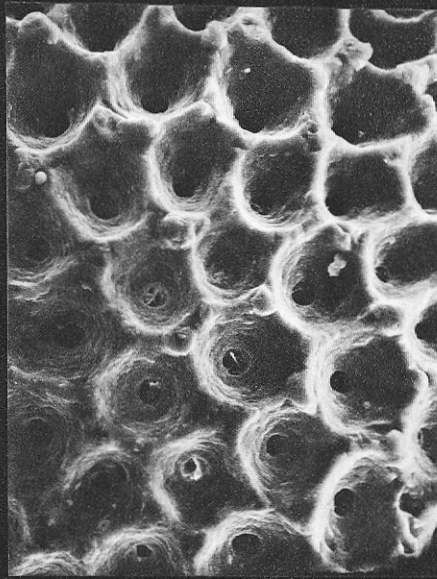
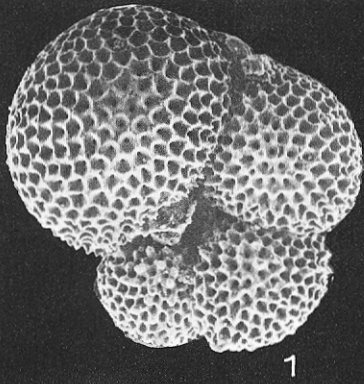
The specimen in Pl. 2, Figs. 1, 1a has a mature texture with fully formed, pentagonally or hexagonally shaped ridges enclosing each of the pores. Preservation of this specimen is unusually good and structural detail is sharp. The terraced structure of the enclosing ridges is well defined and the angular spine bases stand out in bold relief. One spine base near the top and right of Pl. 2, Fig. 1a is hollow. Pore areas are distinctly funnel shaped. There is a remarkably close comparison here with the wall texture of the modern *Globigerinoides trilobus* (Pl. 1, Fig. 1a) considering, especially, the ancient age of *P. opima opima*. This example is the best one available here to uphold the view of Steineck and Fleisher (1978) that wall texture

has tended to remain conservative and is therefore a good guide for tracing lineages of planktonic foraminifera. The specimen in Pl. 2, Figs. 2, 2a shows a later stage of development where some encrustation has begun. It should be compared with the modern form of *Globigerinoides trilobus* shown in Pl. 1, Figs. 2, 2a. Blunt, rounded knobs have overgrown the spine bases and have begun to fuse with each other. The knobs are not as large as those in Pl. 1, Fig. 2a, and they do not encroach on the pores, so that the honeycomb pattern is still visible on all chambers. Nevertheless, the textures appear essentially similar, except that in *P. opima opima* encrustation is less advanced.

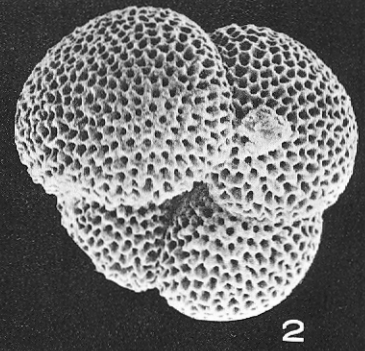
The occurrence of a coarse, honeycomb spiny texture in *Paragloborotalia opima opima* has interesting evolutionary implications, since the *P. opima* species group appears to be the most likely choice for a root stock of the Neogene globorotalid radiation. Most representatives of *Globorotalia* have elegantly smooth walls and an ancestry with a type of wall that is found today in *Globigerinoides* may at first seem unlikely. Yet when one searches the Oligocene for origins, not a great deal of choice is available, since the range of morphotypes is very limited. The *P. opima* group shows the beginnings of globorotalid development in its flattened spiral side, decreased inflation of chambers and, importantly, in the presence of a distinct extraumbilical aperture. True, several other forms in the Oligocene, such as *Globorotalia gemma* Jenkins, satisfy these requirements and have relatively smooth walls as well. A possible connection with the globorotalid wall cannot be discounted. However, the detailed nature of the *G. gemma* type of wall is obscure, and there is no evidence of a developmental sequence to the globorotalid wall. On the other hand, there is some evidence of a transition between a coarse honeycomb (or what others have called cancellate) and smooth wall. Fleisher (1974), for example, noted that a variety of *Globorotalia peripheroronda* illustrated by Blow (1969) is intermediate in texture between cancellate and smooth. In a study of early and middle

PLATE 2

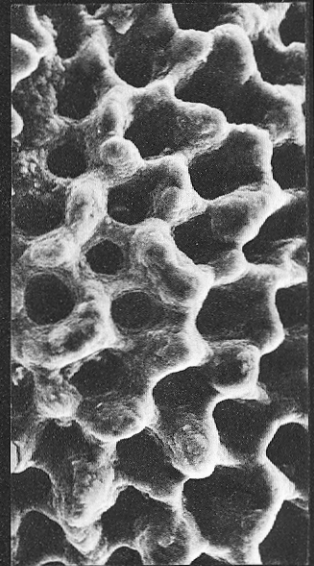
1. *Globorotalia opima* Bolli. $\times 200$. 1a. Detail of n-2 chamber; $\times 1,000$. Trinidad; Upper Oligocene, *Globorotalia opima* zone, type locality.
2. *Globorotalia opima* Bolli. $\times 200$. 2a. Detail of n-2 chamber; $\times 1,000$. Trinidad; Upper Oligocene, *Globorotalia opima* zone, type locality.
3. *Orbulina universa* d'Orbigny. $\times 200$. 3a. Detail of n chamber; $\times 1,000$. Trinidad; Middle Miocene, *Globorotalia mayeri* zone, cotype locality.
4. *Orbulina universa* d'Orbigny. $\times 135$. 4a. Detail of n chamber; $\times 1,000$. Trinidad; Middle Miocene, *Globorotalia mayeri* zone, cotype locality.
5. *Orbulina universa* form *suturalis* Bronnimann. $\times 150$. 5a. Detail of n chamber; $\times 1,500$. Trinidad; Middle Miocene, *Globorotalia mayeri* zone, cotype locality.



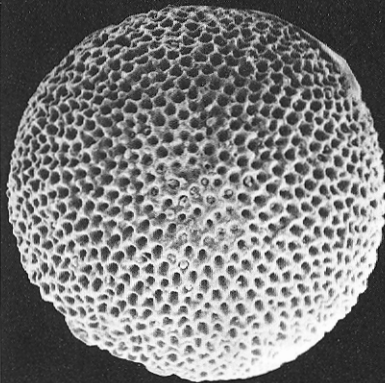
1a



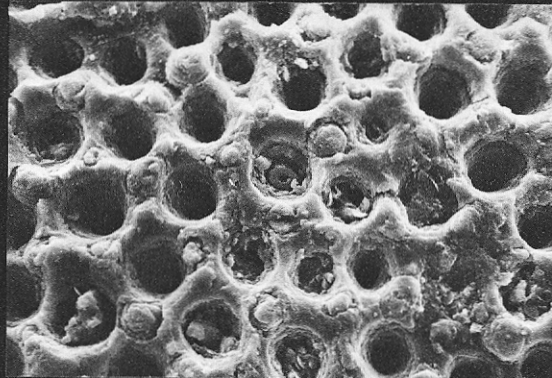
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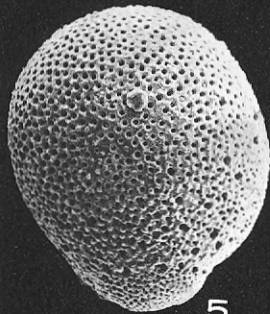
2a



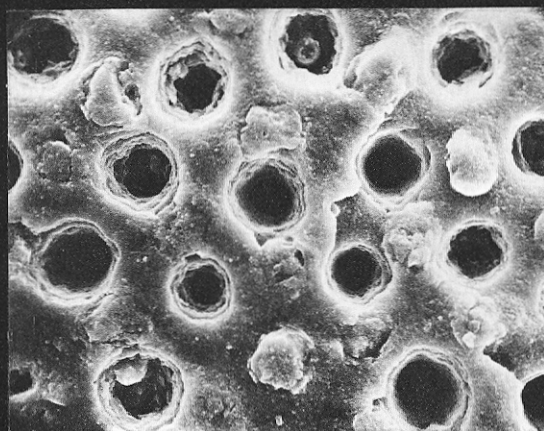
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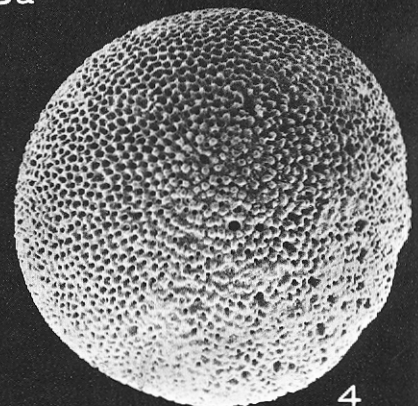
3a



5



5a



4

Miocene *Globorotalia* of Trinidad Cifelli and Glaçon (in press) found intermediate textured walls with honeycomb patterns not only in *G. peripheroronda*, but also in *G. praescitula* and in other early forms of *Globorotalia*. Among late Tertiary populations of advanced menardiiform species of *Globorotalia* it is not too uncommon to find individuals with slightly coarsened walls and pore patterns suggestive of a relic honeycomb texture (unpublished data).

ORBULINE FORMS

Modern representatives of *Orbulina universa* are totally lacking in ridge development, so that the spine bases stand in isolation on the wall surface. No photographs of modern *O. universa* are shown here, but good ones illustrating its texture are given by Bé and others (1976). Because of the abundance of spine bases, the modern *O. universa* has a hispid appearance when seen under low magnification. Viewed in detail, the spine bases can be seen to protrude from a very smooth, flat wall composed of sheetlike laminations. The laminations are visible inside the pores. Indeed, except for the intervening spine bases, with their projecting spines when preserved, the wall in its smoothness bears a close resemblance to the wall of *Globorotalia*.

In the course of examining SEM photographs of fossil forms, it came as a surprise to observe that *Orbulina universa* was not always characterized by its present kind of texture, and in fact, that older members of this species were honeycombed or quasi-honeycombed in texture. All of the specimens photographed here (Pl. 2, Figs. 3–5) are from the middle Miocene cotype locality of the *Globorotalia mayeri* Zone of Bolli (1957). Strongly developed ridges are shown in Pl. 2, Figs. 3, 3a. They occur throughout the test and connect completely to enclose individual pores in a honeycomb pattern. The ridge enclosures are mostly pentagonal in shape and spine bases protrude from each of the ridge corners. Pore areas are cylindrical and lamellae are visible within the actual pores. However, it may be significant that no terraced platelets can be seen in the ridges surrounding the pores. Also, the tops of the ridges appear to be of nearly equal height, forming a rather uniform flat surface. It appears that some deviation from the ridge forming process has occurred, and what is witnessed here is a transformation from a honeycomb to a smooth texture. Transformation is further indicated by the specimen shown in Pl. 2, Fig. 4. The left side of this specimen is distinctly ridged and honeycombed in texture,

but in the center of the specimen ridges are totally lacking, with the spine bases standing in isolation. The surface in the central area has a hispid appearance as in the modern *O. universa*. A much smoother surface is shown by a specimen of *O. universa* var. *suturalis* which comes from the same sample as the above specimens. Ridges are incompletely formed and only traces of a honeycomb pattern remain (Pl. 2, Fig. 5); in the central area ridges are absent. A magnified portion of the central area (Pl. 2, Fig. 5a) shows a flat, smooth surface with intervening spine bases and laminated pores.

Of course, it is not possible now to explain the mechanism responsible for the transformation from a honeycomb to a smooth texture. However, the process may involve some change in regulatory balance of the calcifying modes. As discussed earlier, the wall of spinose species is reinforced and thickened both by the addition of sheetlike lamellae that envelop the whole chamber and the deposition of platy crystallites that build around the spine bases and spread laterally to form terraced ridges. In the transformation to a smooth wall it would seem that there must be an increased activity in sheetlike deposition and a curtailment in deposition of platy crystallites. The fact that in Pl. 2, Fig. 3a the ridges are not tiered and are of about equal height suggests that there might have been at least a partial shift to sheetlike envelopment in their formation. Whatever the process, an immediate turnover in wall texture did not occur in *Orbulina universa* as honeycombed or quasi-honeycombed forms persisted throughout the Tertiary and into the Quaternary. A ridged form of *Orbulina universa* with a quasi-honeycomb pattern from a Quaternary DSDP sample in the tropical Pacific is shown by Krashenninnikov (1980).

POST-PALEOGENE GLOBOROTALIDS AND TURBOROTALIDS

The reason for proposing *Paragloborotalia* is that neither *Globorotalia* nor *Turborotalia* suitably accommodates spinose honeycombed textured turborotalids of Oligocene and later age. A review of the problem follows.

There is some ambiguity in the original meaning of *Globorotalia* because of an incompatibility between description and designated type species. The name *Globorotalia* itself suggests a certain dualism in concept, as it implies something like a globigerinid on one hand and something like a rotalid on the other. Cushman (1927) described this genus as follows, "Test tro-

choid, early chambers often like *Globigerina*, dorsal side flat, the ventral side broadly convex, aperture usually umbilicate, wall frequently roughened throughout, mostly pelagic." From this description there is really nothing to distinguish *Globorotalia* from *Globigerina* except the flattened dorsal (spiral) side. Close affinity with *Globigerina* was further implied in a later description by Cushman (1948) when he stated in part, "... earliest chambers often like *Globigerina* with a rough cancellated exterior . . . frequently spinose . . ." However, the designated species was *G. tumida* (= *Pulvinulinella menardii* var. *tumida* Brady), a Pliocene species that is quite unlike *Globigerina*. This species is distinctly smooth walled with compressed chambers, an acute, angular profile and a well formed keel. Cushman made no mention of an extraumbilical aperture in his description, but the significance of that feature was not appreciated until much later.

Later, Cushman and Bermudez (1949) attempted to rectify the ambiguity and overly broad morphologic limits of *Globorotalia* by dividing it into three subgenera. *Globorotalia* s.s. was centered around the type species (*G. tumida*) and included species with smooth walls, compressed chambers and angular profiles, although not all of them were keeled. The subgenus *Truncorotalia*, with the Recent *G. truncatulinoides* (*Rotalina truncatulinoides* d'Orbigny) as type species, accommodated species with sharply conical umbilical sides. The remaining globorotalid species, without distinctly compressed chambers or acute profiles, were grouped in the subgenus *Turborotalia*, with the late Eocene *G. centralis* Cushman and Bermudez as type species. Toumarkine and Bolli (1970) found that *G. centralis* is a junior synonym of *G. cerroazulensis* (also from the late Eocene), so the latter species is now generally considered to be the type species of *Turborotalia*. In this subgenus Cushman and Bermudez included both smooth and coarse walled forms. All three subgenera, like the original *Globorotalia*, were based solely on morphological considerations, with no regard for stratigraphic occurrences. Cushman (1948) recognized *Globorotalia* as ranging from Late Cretaceous to Recent, while the species listed by Cushman and Bermudez (1949) under the three subgenera range from Paleocene to Recent.

Truncorotalia has not been used very much by later workers, probably because few species have sharply conical profiles. Also, there is difficulty in deciding just how conical a profile needs to be for inclusion in *Truncorotalia*. For example, the placement of *Globorotalia hirsuta* in *Truncorotalia* by Cushman and

Bermudez is clearly open to question. Steineck and Fleisher (1978) recently revived *Truncorotalia* as a genus to encompass a phylogenetic lineage of early Miocene to Recent globorotalids.

Turborotalia has been used widely as either subgenus or genus. However, there have been problems in determining what *Turborotalia* should include. Since the angularity of profiles varies considerably among species, a clear distinction from *Globorotalia* cannot be made. Blow (1969) circumvented this problem by setting very sharp limits to *Globorotalia* and including in that genus only keeled species; the remaining globorotalids were placed in *Turborotalia*, no matter how acutely angular the profile. However, virtually all other workers have taken a broader view of *Globorotalia* and placed greater emphasis on the smoothness of the wall at the expense of profile angularity.

It is generally agreed at present that the Paleogene and Neogene globorotalid morphotypes are the end products of two distinct radiations. Most workers now follow the lead of McGowran (1968) in restricting *Globorotalia* to the Neogene and applying other generic designations to the earlier Paleogene homeomorphs. The early Neogene turborotalids, such as *opima* and *angulosuturalis*, which preceded the development of the Neogene globorotalids, have been assigned to either *Globorotalia* or *Turborotalia*. While these turborotalids agree well enough with the original descriptions of both genera, they cannot be reconciled with either of their type species. Texturally and morphologically, these early turborotalids are too distinct to be included in the same genus as *G. tumida*, a highly advanced globorotalid that occurs in the Pliocene. On the other hand, the type species of *Turborotalia*, *T. cerroazulensis*, occurs in the late Eocene and is a terminal form of the late Eocene radiation. As pointed out by Fleisher (1975), "*Turborotalia* should be retained only for the lineage culminating in *T. cerroazulensis* s.l." In addition, *T. cerroazulensis* has a smooth wall, comparable to that of the modern *Globorotalia*, as shown by the excellent SEM pictures of Toumarkine and Bolli (1975). It also has a subangular profile rather than the rounded profile of the Oligocene and later turborotalids. Indeed, that species stands out as a remarkably close homeomorph of the modern *G. crassaformis*.

There remains the question of *Neogloboquadrina*, which Fleisher (1975) proposed as a generic replacement for early to late Miocene species formerly assigned to *Turborotalia*. Despite earlier arguments to the contrary (Cifelli, 1973), *Neogloboquadrina* is regarded here as an acceptable genus. Recent study

(Cifelli, in press) of *N. dutertrei*, the type species, has shown a distinctive wall texture that clearly separates it from *Globigerina*. The texture of *N. dutertrei* is characterized by a honeycomb pattern of pore ridges very much like that of *Globigerinoides*. The chief difference lies in spinosity. Species of *Globigerinoides* are fully spinose and the pore ridges develop from tiered crystallites that first form around the spine bases and then spread laterally to connect with each other. Spines are not totally lacking in *N. dutertrei*, but they occur intermittently and fail to develop fully. Ridge formation is more obscure than in *Globigerinoides* as the ridges mostly, although not always, appear to form independently of spines. As a result, the ridge corners in *N. dutertrei* tend to be round and blunt rather than sharply angular as in *Globigerinoides*. In this respect the species described here, and now included in *Paragloborotalia*, show a textural affinity with *Globigerinoides* rather than with *Neogloboquadrina*. Textural affinity is also indicated by the neatly tiered structure of the ridges. In *N. dutertrei* the ridges are mostly smooth, and a tiered structure is not apparent.

The spiny, honeycomb texture is primitive and dates back to the Oligocene. The similar but essentially non-spinose texture of *Neogloboquadrina* is a later development, like the smooth texture of *Globorotalia* and quasi-smooth texture of *Orbulina*. Further study is required to determine where the divergence occurred.

PROPOSAL OF A NEW GENUS

Family GLOBOROTALIIDAE Cushman, 1927

Genus *Paragloborotalia* n. gen.

Type species. Globorotalia opima opima Bolli, 1957.

Diagnosis. Test trochoid, composed of about $2\frac{1}{2}$ whorls with $4\frac{1}{2}$ or more chambers in the peripheral whorl; flattened or slightly concave on the spiral side; profile rounded, periphery sublobulate to rounded; sutures broadly radial on both sides, depressed; aperture low, arched, umbilical to extraumbilical, sometimes lipped; wall coarse, spinose, honeycomb textured in the type species, with tiered ridges surrounding individual pores and spine bases protruding from ridge corners.

Remarks. In morphology and texture this genus corresponds to the original descriptions of *Globorotalia* Cushman and *Turborotalia* Cushman and Bermudez. However, as discussed above, *Paragloborotalia* cannot be reconciled with the type species of the above genera, either on phylogenetic, morphological or textural grounds. An Oligocene representative of *Paragloborotalia* belonging to the *P. opima* group prob-

ably was the globorotalid root stock from which *Globorotalia* developed in the middle Miocene. A connecting link between the two genera is seen in *G. praescitula* (Cifelli and Glaçon, in press). However, a good link between *Paragloborotalia* and *G. praescitula* is yet to be found. Early Miocene representatives of *Paragloborotalia* such as the form Cifelli and Glaçon (in press) identified as *G. siakensis* show no morphological or textural advancement over *P. opima*. *Paragloborotalia* is probably also ancestral to *Neogloboquadrina*, with divergence involving an almost entire loss of spinosity. A honeycombed ridge network is retained in *Neogloboquadrina*, but the ridges develop independently of spine bases. It is not known when the divergence may have occurred. Modern homeomorphs of *Paragloborotalia* include *Neogloboquadrina pachyderma* and *N. incompta* which display the same morphological features. However, the textural affinities of these species are clearly allied with *Neogloboquadrina*, in their general lack of spinosity and their independently developed ridge network.

CONCLUSIONS

The spinose honeycomb texture that characterizes the modern *Globigerinoides* is primitive and dates back at least to late Oligocene. Most likely it preceded the development of the genus *Globigerinoides*. Spinose honeycomb texture was much more common in the past than it is today and formerly occurred in globigerine, turborotalid and orbuline forms. A new genus, *Paragloborotalia*, is proposed for honeycomb walled turborotalid species of Oligocene and later age which are incompatible with the type species of either *Globorotalia* or *Turborotalia*. If the *P. opima* group is accepted as the Oligocene root stock of *Globorotalia* (choices appear to be limited), it follows that the smooth globorotalid wall was derived from a honeycombed spiny wall. *Globorotalia peripheroronda* and *G. praescitula* appear to be examples of species with intermediate textures. The modern, flat walled *Orbulina* also had honeycomb textured origins. Some evidence for a transition appears in the middle Miocene *Globorotalia mayeri* Zone. However, there was not an immediate textural turnover, as honeycombed or quasi-honeycombed forms of *Orbulina* occur as late as the Quaternary. None, however, has been observed in living populations. Whether *Globigerina* was derived from a honeycombed form of "*Globigerina*" of Fleisher (1974) or whether the two forms coexisted independently in the Oligocene is not known.

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