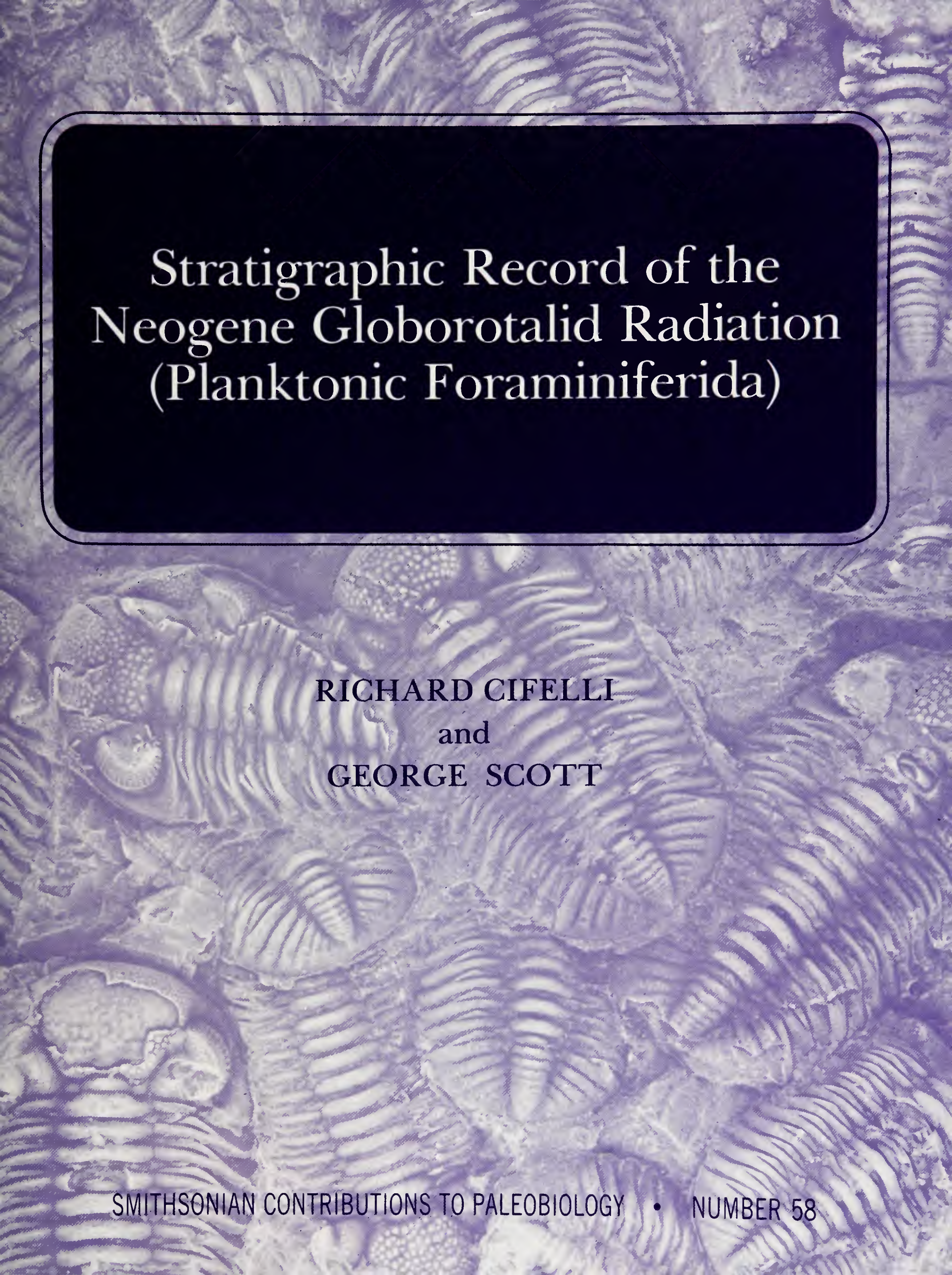

Stratigraphic Record of the Neogene Globorotalid Radiation (Planktonic Foraminiferida)

RICHARD CIFELLI
and
GEORGE SCOTT

SMITHSONIAN CONTRIBUTIONS TO PALEOBIOLOGY • NUMBER 58

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ABSTRACT

Cifelli, Richard, and George Scott. Stratigraphic Record of the Neogene Globorotalid Radiation (Planktonic Foraminiferida). *Smithsonian Contributions to Paleobiology*, number 58, pages 101, 43 figures, 1986.—The histories of lineages forming the Neogene globorotalid radiation in the planktonic foraminifera are reconstructed primarily from stratigraphic distributions. Data on major taxa are synthesized, with particular reference to the development of shell design, and related to biogeograpy and evolutionary strategies.

The radiation was established about the base of the lower Miocene by three groups (*Fohsella*, *Globorotalia zealandica* lineage, and *G. praescitula* plexus), which probably arose from separate paragloborotalid lineages.

Common trends (size increase, chamber compression, keel development, reduced wall relief) early in the radiation culminated in the evolution of disklike taxa which, since the middle Miocene, have been centered in the tropics. The later phase of the radiation (post middle Miocene) was marked by architectural diversification as spiroconical (e.g., *G. margaritae*), ventroconical (e.g., *G. truncatulinoides*), and globose (e.g., *G. inflata*) taxa arose. Architectural diversification may be linked with watermass differentiation in the late Neogene.

Neogene designs have close counterparts in the earlier, but phyletically isolated, Paleogene and Cretaceous radiations. There are also resemblances in ontogenetic strategies and lineage histories. Common adaptations are suggested, but specific functional explanations have not been established.

Periods of major redesign are recognized in most lineages and are not confined to speciation events. Examples of stasis in adult morphology occur particularly in taxa that have evolved compressed, keeled shells. Bifurcations in lineages are indistinctly represented by wide spectra of morphotypes. Within the radiation very rapid speciation events are conspicuously absent, although they possibly occurred at the origin of some lineages. The distinctly sluggish tempo of change may be due to large population sizes and their degree of intercommunication. Good examples of allopatric and parapatric speciation were not found, but the prevalence of polytypic taxa, often distributed in contiguous populations showing clinal variation, would favor the inception of parapatric speciation.

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Contents

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Richard Cifelli and George Scott

Introduction

Fossil planktonic foraminifera have been studied primarily from a geologic point of view. Research was stimulated through the expansion of oil exploration that followed the second world war and from a newly gained awareness by the industry of the advantages of long ranged, intercontinental correlations that could be obtained by means of the widely distributed planktonic foraminifera. Additional opportunities for study of the history of foraminifera in geologic context were provided by the Deep Sea Drilling Project (DSDP), which has resulted not only in an improved biostratigraphic framework and a calibrated time scale but also in solutions to problems in tectonic and climatic history.

The paleobiologic aspects of planktonic foraminifera, by contrast, have received relatively little emphasis so far. On occasion, biostratigraphers have considered the evolutionary implications of their work and proposed phylogenetic schemes (e.g., Walters, 1965; Berggren, 1966; McGowran, 1968; Blow, 1969; Jenkins, 1971; Srinivasan and Kennett, 1981b; Kennett and Srinivasan, 1983). For the most part, however, their summaries hardly do justice to the record available. Indeed, the documented record of the Cenozoic planktonic foraminifera is matched by few groups of organisms. This sort of record ought to be ideally suited for in-depth evolutionary studies that could provide a good background to assess current theories and models. There are at least two reasons why full advantage has not been taken of the planktonic record in this respect.

One reason is that biostratigraphers have higher priorities than evolution. Their zonations are constructed using events (appearances and extinctions) that occur in fixed stratigraphic order. Lineages tend to be treated as stratigraphic successions of morphotypes and species concepts are sometimes quite arbitrarily restricted to specimens closely resembling the type specimen. Usually, no information is given about population structure, and it is uncertain whether one or more morphotypes may be present in the development of lineages. Lineages that contribute events of little stratigraphic value are generally ignored, even though they may provide critical links in the line of development. Therefore, it is difficult to obtain insight into the dynamics of transformation from most biostratigraphic reports, even though they contain important documentation about species occurrences.

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The other reason for the lag in evolutionary interest is perhaps more compelling, but much more subtle, because it involves a question of attitude about foraminifera that is rarely confronted directly. As pointed out by Lipps (1981), ever since Carpenter (in Carpenter, Parker, and Jones, 1862) denied that foraminifera had undergone any significant change since the Paleozoic, a view upheld by Darwin, the foraminifera have been relegated to a role of "secondary citizens" in evolutionary biology. Chiefly responsible for the origin of this attitude was Dujardin (1835), who discovered that the foraminifera were single celled and relegated them to the "lowest forms of life." This attitude has persisted. Van Valen (1965) remarked of foraminiferal research that, despite material scarcely paralleled in abundance, little of value for the general study of evolution has appeared from it. Even today, probably few evolutionary biologists believe that the record of planktonic foraminifera can reveal much that is of importance. Lipps (1981) emphasized the backwardness of biologically oriented research. We will not argue the question of whether or not there is a fundamental difference in evolutionary potential between protozoans and metazoans, but merely point out that there is a demonstrable historic order in the development of planktonic foraminifera that compares favorably with that of metazoans (Cifelli, 1969). Whether the pattern of planktonic development is typical is yet to be resolved; the point is that the record of planktonic foraminifera is about as good a documentation as there is about the phyletic development of a group. Any evolutionary model that ignores, or cannot account for, this record is inadequate.

The quality of the planktonic foraminiferal record should be placed in perspective, because while it may be considered excellent, it is excellent only in a relative sense. It still has limitations. Relative to a group such as the ammonites, the planktonic record appears superior because ammonites are often concentrated in shell beds, perhaps a few tens of feet or less thick, which are separated by clays and silts, perhaps one hundred or more feet thick (e.g., Arkell, 1933). Planktonic foraminifera are generally found continuously, although not always abundantly, throughout marine sequences outside of very near shore, shallow facies; in pelagic facies they are very often remarkably continuous and abundant in distribution. A few grams of residue often contains a larger sample than the 352 (approximately, incomplete data) primate teeth from 59 samples used in an evolutionary study by Gingerich and Simons (1977, text-fig. 10). Moreover, because of their small size, a refined sampling of populations is possible, sometimes to a nominal resolution of about 1000 years, even in slowly deposited deep sea sequences (Schindel 1982). The planktonic record, however, is not always as it would seem. There may be facies influences on morphology. Size, extent of secondary calcification, and some aspects of form (e.g., axial shape in the group studied here) vary appreciably between open ocean and neritic environments. Occurrences of planktonic foraminifera are sporadic in the excellent marine Tertiary sequence of California and they are poorly represented in parts of the Mediterranean succession. Recovery of planktonic foraminifera from deep sea cores is sometimes poor because of local unconformities and dissolution of tests by diagenetic processes (e.g., Berger, 1971). Bioturbation may affect the resolution of the record, but more serious are the very large regional gaps between outcrop sections. Many important parts of these gaps are being filled by the DSDP, but even at eupelagic sites there may be extensive hiatuses (Moore and others, 1978; Keller and Barron, 1983). At such sites stratigraphic completedness (Sadler, 1981) may be as low as 1% at the 100-year scale of resolution (Schindel, 1982). Despite many local gaps or imperfections, however, there appears to be no global loss of the planktonic foraminiferal record over the last 20 m.y. that inhibits reconstruction of the history of the group we study. In a piecemeal fashion the resolution of the record, at one or more locations, is probably always better than 0.05 m.y.

We use this record to trace the history of the major Neogene to Recent globorotalid lineages. Although diverse architectures developed, the lineages are linked by several common trends and demonstrate particularly well the iterative pattern of planktonic foraminiferal evolution (Cifelli, 1969). A synthesis of the extensive biostratigraphic data about the lineages should assist in understanding their evolutionary patterns.

Recognition that a group has a good fossil record calls for comment on methodology and objectives. For Neogene biostratigraphers there is a need to review the morphology, distribution, and relationships of taxa used in zonations. While biostratigraphers can, and do, pursue their objectives without knowledge of phyletic history, there is little doubt that such information, together with an understanding of population variation and biogeography, can raise the accuracy and resolution of zonations. The scrutiny of the stratigraphic record needed to meet this objective is also appropriate for studying the history of globorotalid shell design and adaptation and for assessing the tempo of character evolution. Malmgren and Kennett (1981, 1982) provided good examples of the resolution attainable in character mappings of *Globorotalia* from the fossil record.

When Eldredge and Gould (1972) challenged the model of gradual phyletic evolution, they generated a need not only for new observations of the stratigraphic record of lineages but also for a re-examination of old ones. Although most of the data we mention were collected for biostratigraphic purposes, they warrant consideration in light of questions about evolutionary mode and tempo. Here, magnetostratigraphy now provides a sound chronologic basis for assessment of evolutionary rates. Therefore, without apology to methodologists like Cracraft (1974) and Patterson (1981), we interpret the phylogeny of Neogene globorotalids primarily from the stratigraphic record. Ideally, this is done by identifying sequences of populations in which variation fields overlap but, because of the small amount of biometric mapping, most estimates of continuity between samples are qualitative. However, the latter method is assisted by the density of the record and the relatively slow progress of character trends. Effectively, we are suggesting a version of phenetic linkage as outlined by Gingerich (1976). Evaluations of character polarities are used only when stratigraphic evidence is inadequate. This occurs particularly at the origin of the radiation.

The study focuses on evolution at the species level and, within the radiation, the record is often adequate to provide evidence of taxonomic transitions. However, we do not consider that phylogeny can be literally read from the rocks. Differences between our interpretations and those of Kennett and Srinivasan (1983) are witness to the equivocal nature of the record in some instances, but we consider that the gross form of the phyletic tree can be estimated from the stratigraphic record. Paul (1982) provided a theoretical justification for this approach. Comparative morphology provides a secondary approach to the assessment of phylogeny. Its use is promoted by the prevalence of simple unidirectional trends in chamber design throughout globorotalid lineages. In several examples, the polarities of important trends (increasing compression of chambers, development of keel) are clearly defined by stratigraphic evidence, and accord with architectural and structural considerations. Polarities so confirmed are relevant to studies of other lineages that have poor or inadequately researched stratigraphic records. We also attempt to discriminate characters that are relatively stable (effectively plesiomorphic in cladistic terminology) from those in which major architectural changes occur. The former are useful in identifying lineages; some transformations in the latter group are remarkably similar among lineages, and we consider their functional role through reviews of biogeography and comparisons with earlier globorotalid radiations.

While this study is eclectic and lacks the internal consistency of cladistic methodology, it allows for multiple approaches to the estimation of ancestry. We do not attempt to minimize convergences (cf. Eldredge and Cracraft, 1980); neither do we eschew character reversals (a *bête noire* of cladistic theory). Indeed, there is good stratigraphic evidence of such an occurrence in the origin of a major Neogene lineage. We recognize the limitations of the fossil record but do not consider they inhibit valid inferences about ancestor-descendant relationships.

Only an overview of the Neogene globorotalid radiation is provided here. The treatment is uneven and some taxa have been omitted, either because we lack knowledge of them or because they appeared to be of minor evolutionary significance. The study is further biased by our limited knowledge of lineage histories in some regions (e.g., Indian Ocean). A major formal systematic revision of the group is desirable. While we do not attempt this, attention is drawn to several outstanding problems in lineage relationships that such a study must address.

Biostratigraphers and evolutionists remain relatively isolated groups who pursue quite different research objectives and often neglect each others' theory and data. This is mutually disadvantageous. We hope this study allows both groups to judge the value of a broader conspectus of the fossil record of a planktonic foraminiferal group.

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The Neogene Succession of Globorotalids

Root Stocks

The development of the globorotalids, perhaps the highlight of the Neogene planktonic radiation, had modest beginnings because of the severe reduction of similar designs at the close of the Paleogene. By early Oligocene, all lineages that had earlier achieved a globorotalid architectural design were exterminated and few clues were left to the course of future development. Inferences from comparative morphology are essential. The Oligocene faunas are characterized by simple, generalized forms, reminiscent of the assemblages found in temperate to subarctic regions today (Cifelli, 1969). Prominent among Oligocene faunas is *Paragloborotalia*, a genus that in many respects compares closely with the modern *Neogloboquadrina pachyderma* and *N. incompta*. *Paragloborotalia* has inflated chambers, a spherical profile, and a coarse wall that is ridged and often honeycombed (Figure 1*b–c*, *f–g*). At least some species of *Paragloborotalia* are spinose, with a texture comparable to that of the modern *Globigerinoides* (Cifelli, 1982). The coarse wall and inflated chambers are not at all suggestive of a globorotalid affinity, but some connection is indicated by the flattened spiral side and extra-umbilical extension of the aperture.

A smooth wall, an important feature of advanced globorotalids, occurs in some Oligocene forms, such as *Globorotalia munda*. However, this wall is more like the kind found in *Globigerinita* than in the globorotalids, as it has minute pores and pustules distributed more or less evenly on all chambers (Figure 1*a*). There is no evidence that forms having this type of wall ever developed in a globorotalid direction. Fleisher (1974:1033) proposed the genus *Tenuitella* for such species, and it is likely that this group developed independently.

Walters (1965), McGowran (1968), and Kennett and Srinivasan (1983) proposed the Oligocene group of species centered around *Paragloborotalia opima* (e.g., *P. nana*, *P. pseudocontinuosa*, and *P. semivera*) as a globorotalid root stock and, in view of the limited options available, this interpretation serves as a reasonable first approximation. However, with one possible exception (Srinivasan and Kennett, 1981b), transformation series have not been identified and specific con-

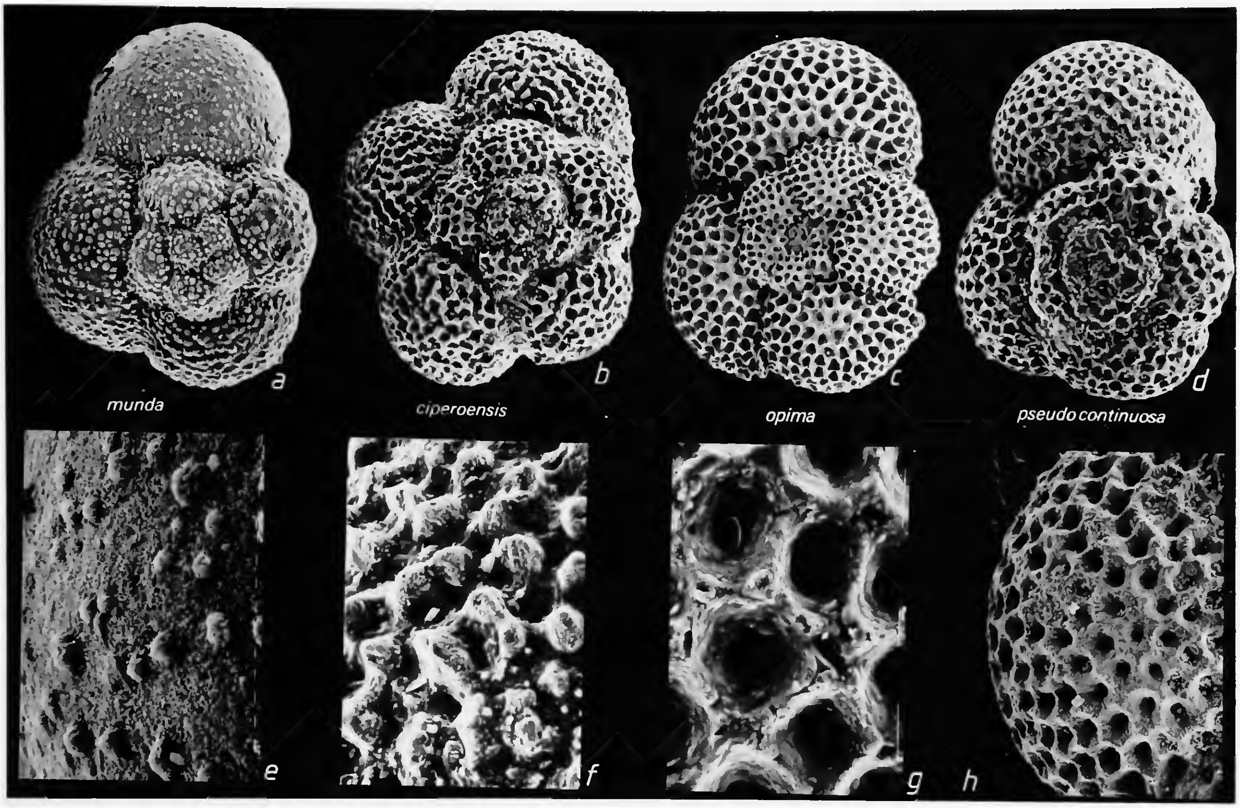


FIGURE 1.—*a, e, Globorotalia munda* Jenkins, S127/f422, Waitaki Valley, New Zealand, lower Oligocene, topotype, (*a*, × 260; *e*, × 1430); *b, f, Paragloborotalia ciperoensis* (Bolli), 18-1-2 (R. Cifelli), ?Trinidad (*b*, × 180; *f*, × 750); *c, g, Paragloborotalia opima* (Bolli), 40-3 (R. Cifelli), ?Trinidad (*c*, × 130; *g*, × 660); *d, h, Paragloborotalia pseudocontinuosa* (Jenkins), N2/f554, Parengarenga Harbour, New Zealand, lower Miocene, topotype (*d*, × 200; *h*, × 355).

nections remain obscure. Although we focus on the paragloborotalids, it may be premature to regard them as the only potential ancestral group. While the later chambers of *Globorotaloides* (a widespread taxon in the Oligocene) are globigerine, the early chambers closely resemble those of *Globorotalia*. Did some globorotalids arise by neoteny? This merits investigation (N. deB. Hornibrook, pers. comm., March 1984), despite the prevalence of recapitulatory patterns in globorotalids.

One of the major unresolved questions in globorotalid evolution concerns the actual number of connections with the paragloborotalids. In the early Miocene, three distinct globorotalid lines with self-contained histories can be recognized. Was the early Miocene the only time that transformation from paragloborotalids occurred? There is really no good reason to assume that this was the case, because the paragloborotalids were not totally replaced by the globorotalids at the end of the Oligocene. For example, the typically Oligocene *Paragloborotalia opima* group is succeeded in the Miocene by species variously referred to as *Globorotalia mayeri, G. siakensis,* and *G. continuosa*, which show no globorotalid advancement and therefore belong with *Paragloborotalia.* Bolli and Saunders (1982) viewed the latter two species as junior synonyms of *G. mayeri* and extended the range of *G. mayeri* down into the late Oligocene, emphasizing that the paragloborotalids can be viewed as a long ranging group with the potential for repeated globorotalid development. In the late Cenozoic there

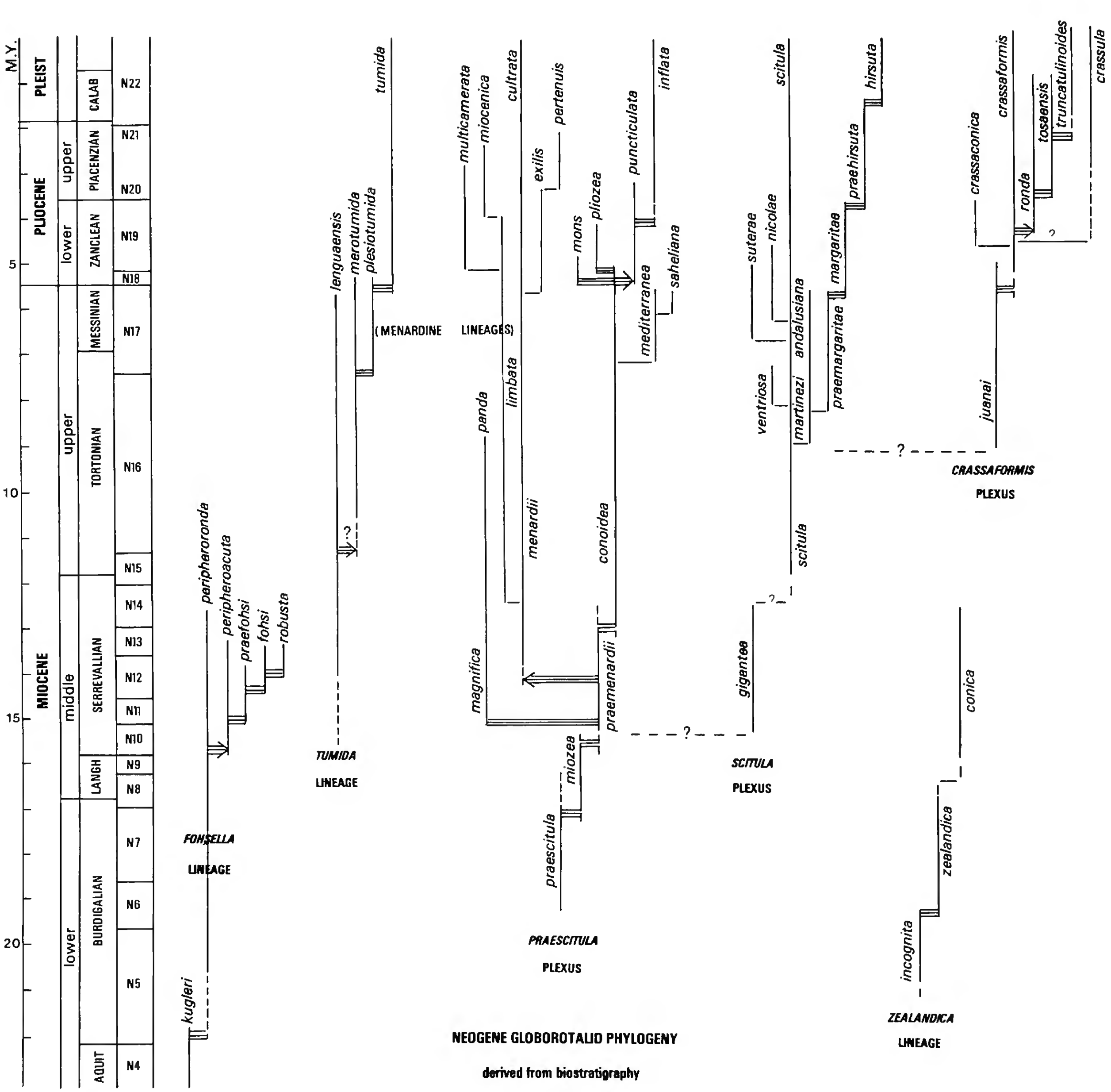


FIGURE 2.—Phylogeny of Neogene globorotalids showing major groups and selected taxa. (Species ranges in *Fohsella* lineage partly after Blow (1969); in menardine taxa after Berggren and Amdurer (1973); in *G. tumida* lineage partly after Blow (1969) and Srinivasan and Kennett (1981a, 1981b); in *G. praescitula* plexus partly after Catalano and Sprovieri (1971), Berggren (1981), and Hornibrook (1981b); in *G. scitula* plexus partly after Catalano and Sprovieri (1971), Wernli (1977), Perconig and others (1980), Berggren (1981), and Hornibrook (1981b); in *G. crassaformis* plexus partly after Rögl (1974), Stainforth and others (1975), Zachariasse (1975), and Berggren (1981); calibration of zonation after Berggren (1981).)

are several advanced globorotalid groups whose origins are obscure and the possibility of independent development from paragloborotalid ancestors cannot be ruled out. A tree with a single root has been proposed from biostratigraphic data (Steineck and Fleischer, 1978). However, our reconstruction (Figure 2) takes cognizance of the limited stratigraphic and morphological evidence that there are probably multiple roots.

Major Evolutionary Trends

As a basis for examining the historic development of the Neogene globorotalids, we review their major advances over the paragloborotalids: (1) The wall surface is nonspinose and smooth, although pustules are commonly present; the ridged, honeycomb topography of paragloborotalids is obliterated (Figure 3). (2) Whereas paragloborotalid chambers are quasi-spherical as in globigerinids, globorotalid chambers are compressed and the axial profile is angular (Figure 3); compression increases during ontogeny. (3) A keel is developed as a fold in the chamber wall (Figure 4); in the earlier globorotalids this feature is a late ontogenetic development, but in more advanced forms it occurs through most of the test; there is no comparable structure in paragloborotalids. (4) The shape of the chambers on the spiral face (Figure 5) is modified from broadly radial (I-type) to either narrowly radial (T-type, characteristic of *Fohsella*) or elongate in the direction of coiling (A-type or B-type, characteristic of *Globorotalia*); a flaring (C-type) chamber develops later (characteristic of the *G. menardii* group).

These advances began near the base of the Miocene (Zone N4) and were fully achieved by the middle Miocene (Zone N12), when compressed, fully keeled, smooth-walled globorotalids had developed. At this stage, globorotalid architecture was fully established, and later developments primarily concerned details of chamber form and coiling geometry.

The first deviation from the paragloborotalid morphotype involved a change in the shape of the chamber on the spiral side, to narrowly radial in *Fohsella*, and to elongate in the direction of coiling in *Globorotalia* (e.g., *G. incognita*). The earliest representatives tend to have chambers that are intermediate in shape. In the major *Globorotalia* plexus *(G. praescitula)*, the new shape was fully established in the earliest representatives (Figure 6*o*). Once established, the new chamber shapes remained relatively stable.

Closely correlated with these spiral side changes is compression of chambers. Once the chambers were transformed in shape, some deviation from the paragloborotalid axial profile is visible. This change was gradual, as both the early *Fohsella* and *Globorotalia* are only slightly compressed and their profiles deviate but little from the spherical profiles of the paragloborotalids (Figure 7, compare *G. incognita* with *Paragloborotalia opima*; Figure 8*m*). Later, they became increasingly subangular to angular and, finally, acute.

Flattening of the wall also occurred early, but a fully smooth surface was not attained until the profiles became acute and keels were formed. Transformation may have involved a change in regulatory balance of the calcifying processes. Wall relief lowered from honeycombed to flattened, and eventually became smooth as chambers became reinforced less by ridge development and more by the addition of sheet-like laminations. In *Fohsella*, flattening and smoothening occurred in a reasonably uniform fashion, as the wall is at first coarse, then generally becomes decreasingly honeycombed with succeeding species and finally smooth with the arrival of the keeled form. In the principal *Globorotalia* plexus, development was more variable. The earliest forms of *G. praescitula* are quite smooth-walled, with only slight honeycomb texture (Figure 6*o–s*); but these may be succeeded by forms with coarser textures and more clearly defined ridges. As in *Fohsella*, a totally smooth wall was not achieved until the profile became acute and a keel formed. Once fully achieved, the smooth wall was always retained and there was no rever-

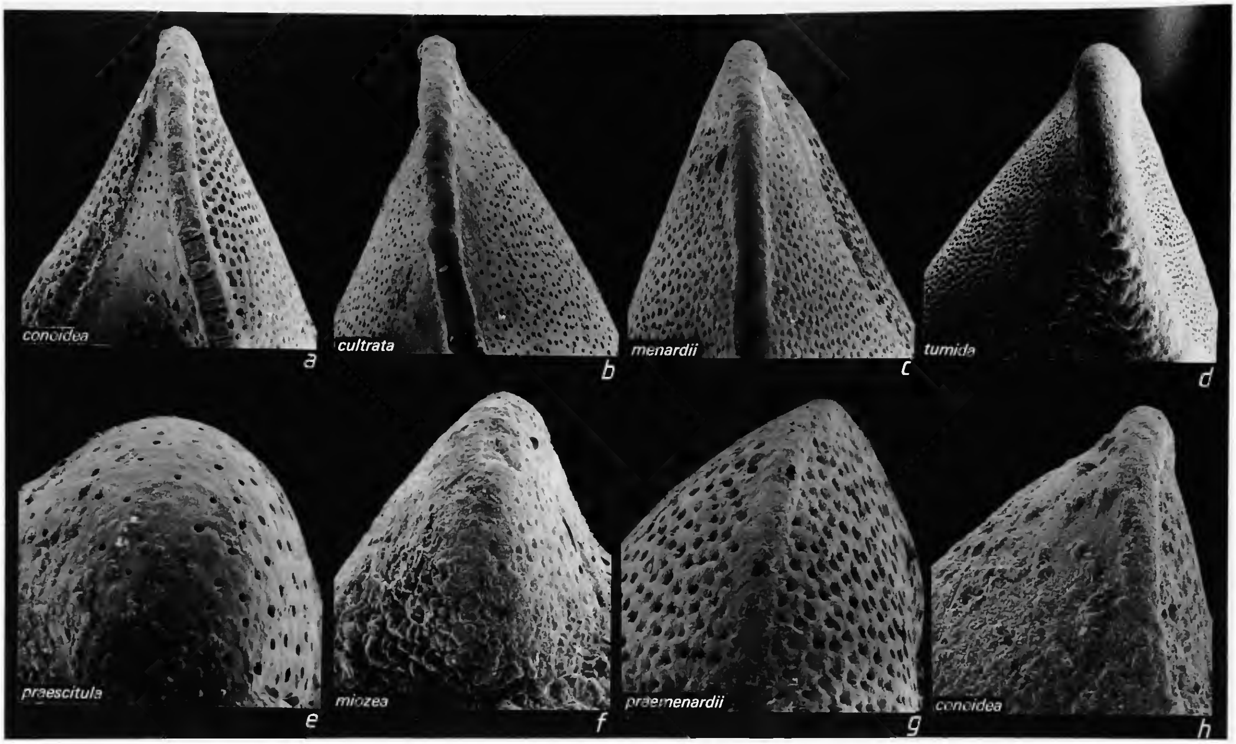


FIGURE 3.—*a*, *h*, *Globorotalia conoidea* Walters (*a*, cotype locality *Paragloborotalia mayeri* Zone, Trinidad, middle Miocene, Trinidad example of "form 3" morphotype of Tjalsma (1971), × 345; *h*, N98/f565, Waimata Valley, New Zealand, topotype, middle Miocene, × 245); *b*, *Globorotalia cultrata* (d'Orbigny), Atlantic Ocean, 22°07′N, 81°08′W, 270 fathoms, Recent (× 240); *c*, *Globorotalia menardii* (Parker, Jones, and Brady), type locality *Paragloborotalia mayeri* Zone, Trinidad, middle Miocene (× 240); *d*, *Globorotalia tumida* (Brady), Atlantic Ocean, 22°07′N, 81°08′W, 270 fathoms, Recent (× 60); *e*, *Globorotalia praescitula* Blow, S137/f615, Oamaru, New Zealand, lower Miocene (× 455); *f*, *Globorotalia miozea* Finlay, F5089, Greymouth, New Zealand, middle Miocene, topotype, (× 240); *g*, *Globorotalia praemenardii* Cushman and Stainforth, locality 13 (P. W. Jarvis), Lower Green Clay, Cipero Section, Trinidad (× 340).

FIGURE 4.—Dissections of last-formed chambers: *a*, *Globorotalia miozea* Finlay, S68/f31, Dovedale Stream, New Zealand, lower Miocene (× 310); *b*, *c*, *Globorotalia praemenardii* Cushman and Stainforth, S44/f717, Stillwater Creek, New Zealand, middle Miocene (*b*, × 650; *c*, × 900); *d*, *Globorotalia conoidea* Walters, T26/f175, Whakatahine Stream, New Zealand, upper Miocene (× 490).

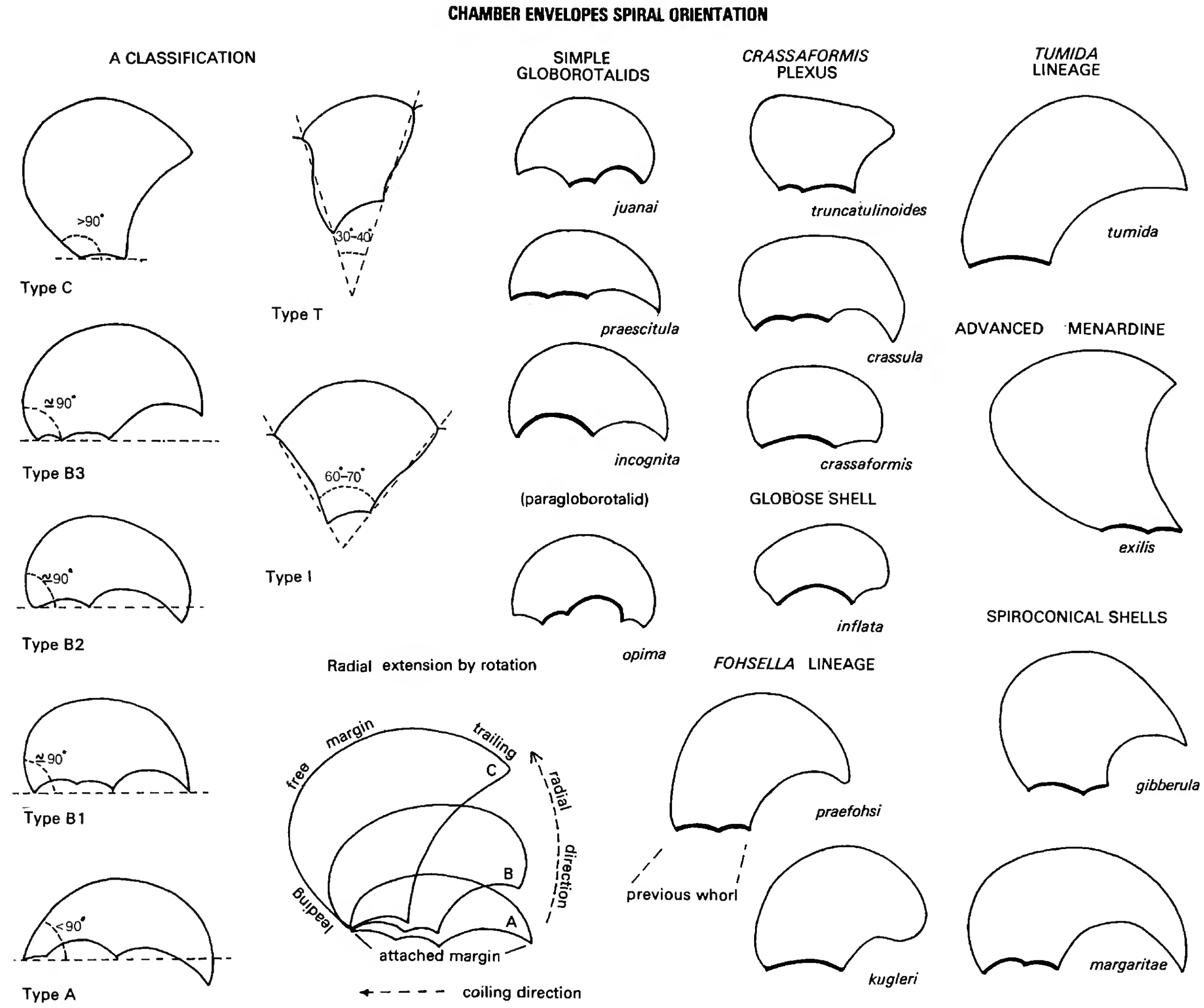


FIGURE 5.—*Left,* Classification of spiral shape of chambers (after Cifelli and Glaçon, in press) based on the angular position of the leading margin and location of the trailing margin (types A-C) and the angle between these margins (types I, T). Types A-C describe the amount of outward (radial) rotation of the chamber envelope. Type C, utilized by menardine taxa, increases the diameter of the shell and is a technique for producing a large shell. *Right,* Some examples of chamber envelopes (last-formed or final chamber drawn from SEM micrographs). The segment of the attached margin abutting the middle whorl is thickened and its straight-line length is approximately constant in the drawings. This scaling illustrates the radial elongation of late-formed chambers in large biconvex, tumid, and discoidal taxa (Figure 7). In contrast, in the ventroconical *Globorotalia truncatulinoides,* in which the ventral surfaces are greatly extended, the spiral surface is relatively small. The slightly elongate, crescentic shape of a phyletically early taxon (*G. incognita*) quite closely resembles the semicircular envelope of *Paragloborotalia opima,* a possible member of its ancestral group. A-type crescentic chambers occur early in the *G. praescitula* plexus and are transformed to B and C types in most advanced members. Radial elongation of quasi-T-type chambers occurs in the *Fohsella* lineage and similar chambers evolved in *G. tumida.* As with type C, this is a technique for increasing the radial diameters of shells. Phyletically simple shapes occasionally occur late in the radiation. The envelope of *G. juanai* resembles that of a paragloborotalid and, although it is regarded as a scituline, it may represent a separate line of descent (Figure 2).

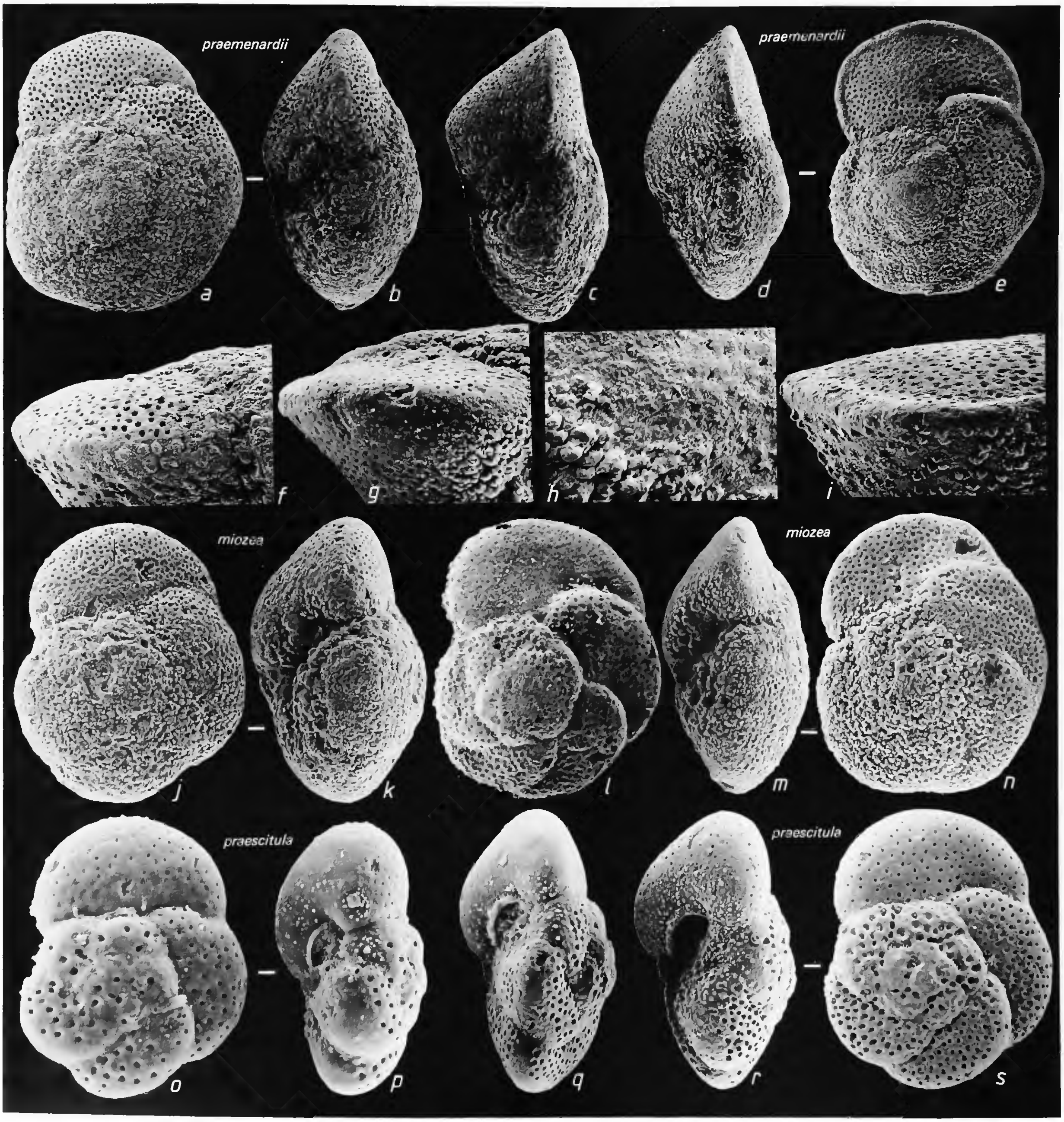


FIGURE 6.—*a–f, i, Globorotalia praemenardii* Cushman and Stainforth, J32/f 7589, Greymouth, New Zealand, middle Miocene (*a,b*, × 100; *c*, × 90; *d,e*, × 80; *f*, × 220; *i*, × 205); *g,h, j–n, Globorotalia miozea* Finlay: *g–h, l–n*, F5089, Greymouth, New Zealand, topotypes, middle Miocene (*g*, × 205; *h*, × 300; *l*, × 120; *m,n*, × 115); *j,k*, S68/f241, Waipara, New Zealand, lower Miocene (× 85). *o–s, Globorotalia praescitula* Blow: *o,p*, S136/f1159, 91–92 ft (27.76–28.06 m), Awamoa Drillhole, New Zealand, lower Miocene (× 245); *q*, S136/f1159, 11.5 ft (3.51 m), Awamoa Drillhole, New Zealand, lower Miocene (× 170); *r,s*, S137/f615, Oamaru, New Zealand, lower Miocene (× 185); (*p–r* are in ascending stratigraphic order, left to right).

sion towards a honeycomb texture. In *G. zealandica* lineage partial smoothing of the wall was achieved rapidly.

Once the globorotalid test became fully developed, subsequent architectural changes were restricted primarily to chamber design and particularly to the axial profile. Design changes within the spiral face of chambers were relatively minor (Figure 5). C-type chambers arose in the menardine branch of the *G. praescitula* plexus while, in contrast, quasi-rectangular shapes arose in the *G. crassaformis* plexus, notably in *G. truncatulinoides*. But most of the praescituline descendants remained conservative and retained the B-type chamber without change.

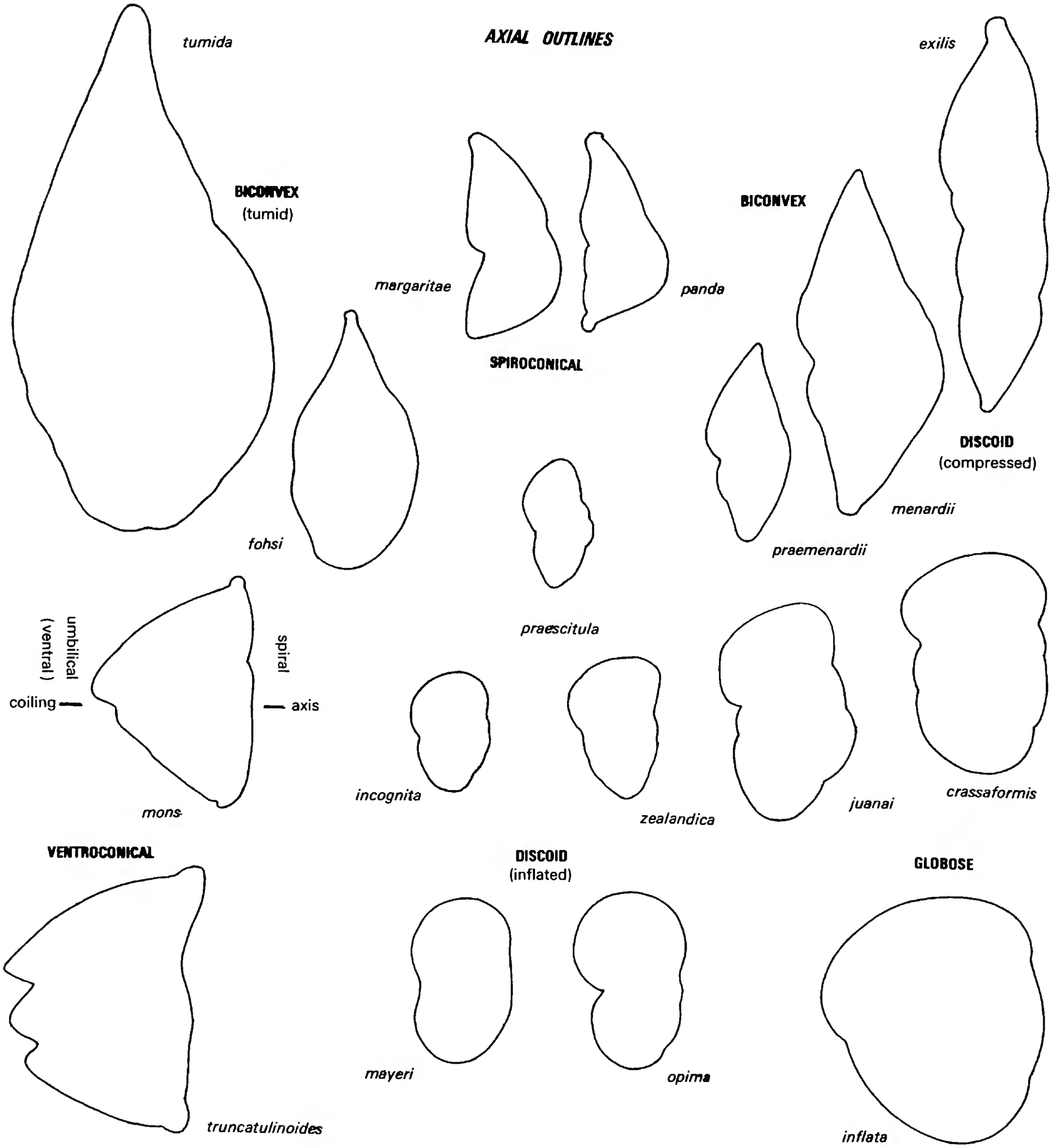
Spiral chamber shape is related to the number of chambers in the outer whorl. *Fohsella* is generally multi-chambered, with six or more chambers in the outer whorl. A radially elongate shape permits chambers to be closely packed. *Globorotalia* normally has only four to six chambers in the outer whorl and rarely only three. The few short-lived menardine Pliocene species that experimented with arrangements of more than six chambers, such as *G. multicamerata* and *G. exilis*, developed radially elongate chambers that closely approximate those of *Fohsella*.

The axial profile became modified in two principal directions: (1) The axial compression of chambers, which produced a disk-like shell, and (2) the radial compression and extension of the umbilical side of chambers, which produced axially elongated chambers, culminating in a truncated cone. Both architectures are most strongly developed in mid-late ontogeny. Ultimate expressions of the two trends are *Globorotalia cultrata* and *G. truncatulinoides*, but there are intermediaries. Throughout the radiation, the spiral side, with a few important exceptions, remained flat or gently convex. The menardine, disk-like form became a stable design and little architectural change occurred in the *G. menardii* group. On the other hand, the *G. conoidea* group, though conservative in other respects, retained greater plasticity and the early-middle Miocene trend of globorotalid development was reversed in one branch.

In most lineages the keel, once evolved, was retained by all descendants. Indeed, Blow (1969) considered that the keel was a fixed structure, incapable of complete suppression. However, in the *Globorotalia inflata* lineage, which arose from the compressed and keeled *G. conoidea* (a main branch of the *G. praescitula* plexus), radial inflation of chambers resulted in reduction and eventual elimination of the keel. The axial profile of *G. puncticulata* sensu stricto (Pliocene) resembles that of *G. zealandica* from the lower Miocene. The latter is phyletically close to the paragloborotalids; the former arose from a globorotalid ancestor in which the keel had been universal for about 8 m.y. A similar but less pronounced reversal may have also occurred in the scitulines, although their record is less clear.

No doubt there are some like Blow (1969) who look upon reversals of trend as biologically indefensible. Yet, what else can be read from the stratigraphic record? Starting in the latest Oligocene or earliest Miocene, there is a singular trend towards the development of an acute profile and keel, along with a smooth wall, that culminated in the middle Miocene. These acutely profiled, mostly keeled forms are the sole globorotalids available for ancestry of the later representatives of *Globorotalia*. If there was not a reversal, then an independent connection with a later paragloborotalid must be envisaged. This is not demonstrable for the *G. inflata* lineage.

However, an actual case of direct transformation from a late paragloborotalid may be represented by a form such as *G. anfracta* Parker (e.g., Poore, 1979, pl 2: figs. 8, 9). This species has a totally smooth wall, but a spherical profile and chambers that are broadly radial. If a ridged, honeycombed texture were superimposed on the surface, one would, with little hesitation, refer it to *Paragloborotalia*. Yet, although smooth, the wall is not a typical globorotalid type. It is very thin and glassy in appearance throughout the test, like the walls of early formed, unreinforced chambers. Immature, honeycombed forms that have not yet reinforced any of their chambers by secondary calcification may show a very similar smooth, glassy surface (Cifelli, 1982, pl. 1: fig.


AXIAL OUTLINES
tumida
BICONVEX
(tumid)
fohsi
margaritae
panda
SPIROCONICAL
praescitula
BICONVEX
exilis
menardii
praemenardii
DISCOID
(compressed)
umbilical
(ventral)
coiling
spiral
axis
mons
VENTROCONICAL
truncatulinoides
incognita
zealandica
juanai
crassaformis
DISCOID
(inflated)
mayeri
opima
GLOBOSE
inflata

←

FIGURE 7.—Axial outlines (in the plane of the coiling axis) of taxa representing major Neogene globorotalid architectures. Drawings, from micrographs, are to a common scale and are of representative, mature specimens. The form of the axial outline in these trochospiral shells is largely determined by the shape of chambers in the outer whorl, their rate of expansion, and by the rate of vertical translation of whorls along the coiling axis. There is much greater variation in axial shape of globorotalid shells than in spiral shape (defined by the equatorial outline of the outer whorl). The difference may relate to the preferred orientation of the organism in water, but there has been no research. Lower Miocene taxa (*Globorotalia praescitula, G. zealandica, G. incognita*), which occur early in the Neogene radiation, have shapes similar to the inflated discoidal form of paragloborotalids like *Paragloborotalia opima* and *P. mayeri*. Occasionally, this form occurs later in the radiation (e.g., *G. juanai*). The dominant axial architectures have compressed chamber margins. The primitive discoidal shape (inflated) is stretched radially to a large diameter in compressed discoidal taxa. Radial extension is assisted by the use of C-type chambers (Figure 5). Biconvex and tumid shapes develop when moderately inflated ventral surfaces of chambers approximately correspond with curvature of the spiral surface of the shell produced by translation of whorls along the coiling axis (*Fohsella fohsi, G. praemenardii, G. menardii, G. tumida*). Spiroconical profiles form when the rate of translation of whorls is high (quasiconical spiral surface), and the ventral surface is depressed (*G. margaritae, G. panda*). In ventroconical shells the rate of translation of whorls is low (flattish spiral surface), but ventral surfaces of late-formed chambers are highly elevated (*G. mons, G. truncatulinoides*). In the globose *G. inflata*, relatively low whorl translation is associated with rapid increment in size of the radially inflated chambers. While the diagram suggests common morphological pathways, comparison with Figure 2 shows that several taxa with very similar profiles are placed in separate lineages (e.g., *F. fohsi* and *G. tumida*; *G. mons* and *G. truncatulinoides*; *G. margaritae* and *G. panda*). Only a simple transformation seems to be required to redesign *P. opima* into *G. inflata*, but the record (Figure 2) shows that the latter descended from biconvex to ventroconical populations with compressed peripheries. Lines of descent are sometimes much more complex than analysis of the form of end members might suggest. Generally, modification of the phyletically primitive, inflated discoidal profile is associated with pronounced increase in size. This, together with good stratigraphic evidence of convergence in axial shape, suggests that modification to the primitive forms may be size-required responses that have followed a few common plans.

1). The wall of *G. anfracta* lacks the distinctive laminations of *Globorotalia* and there is a total absence of pustules. Therefore, this distinctive species may very well have quickly transformed from a late paragloborotalid by a retardation of shell growth.

In perspective, reversals in trends and loss of advanced structures were minor components of the radiation. They demonstrate the plasticity of chamber form and the potential for advanced lineages to change architectural directions. In fact, few did so. The dominant feature of the radiation is canalization of evolutionary advance along a few, well-defined routes.

Origins of the Early Lineages

The Neogene globorotalid radiation began with the appearances of *Fohsella kugleri, Globorotalia praescitula*, and *G. incognita* in the early Miocene. These forms are the first to show a clear deviation from paragloborotalid architecture, and they are the progenitors of three separate stocks that achieved various degrees of success during the Neogene. *Fohsella kugleri* appeared first, in Zone N4, and was preceded in the late Oligocene (Zone N2) by *F. mendacis*, a form that still lacked well-developed globorotalid features. *Globorotalia praescitula* and *G. incognita* both appeared later, in Zones N5–N6.

Jenkins (1971) recognized *Fohsella peripheroronda* as the most primitive *Fohsella* and derived that species directly from *Paragloborotalia bella*, an early Miocene form with an inflated profile, which shows some advancement towards a globorotalid in the flattening of the wall surface. Arguments against *P. bella* are that the chambers are sometimes elongate in the direction of coiling, which is more suggestive of *Globorotalia*, and the number of chambers in the outer whorl is lower than in *Fohsella*. An early form displaying distinct profile angularity is *F. kugleri*, which appeared close to the Oligocene-Miocene boundary (Blow, 1969:350, about 23 m.y. ago on the time scale of Ryan and others, 1974, table 7). Kinship of *F. kugleri* to the succeeding *Fohsella*

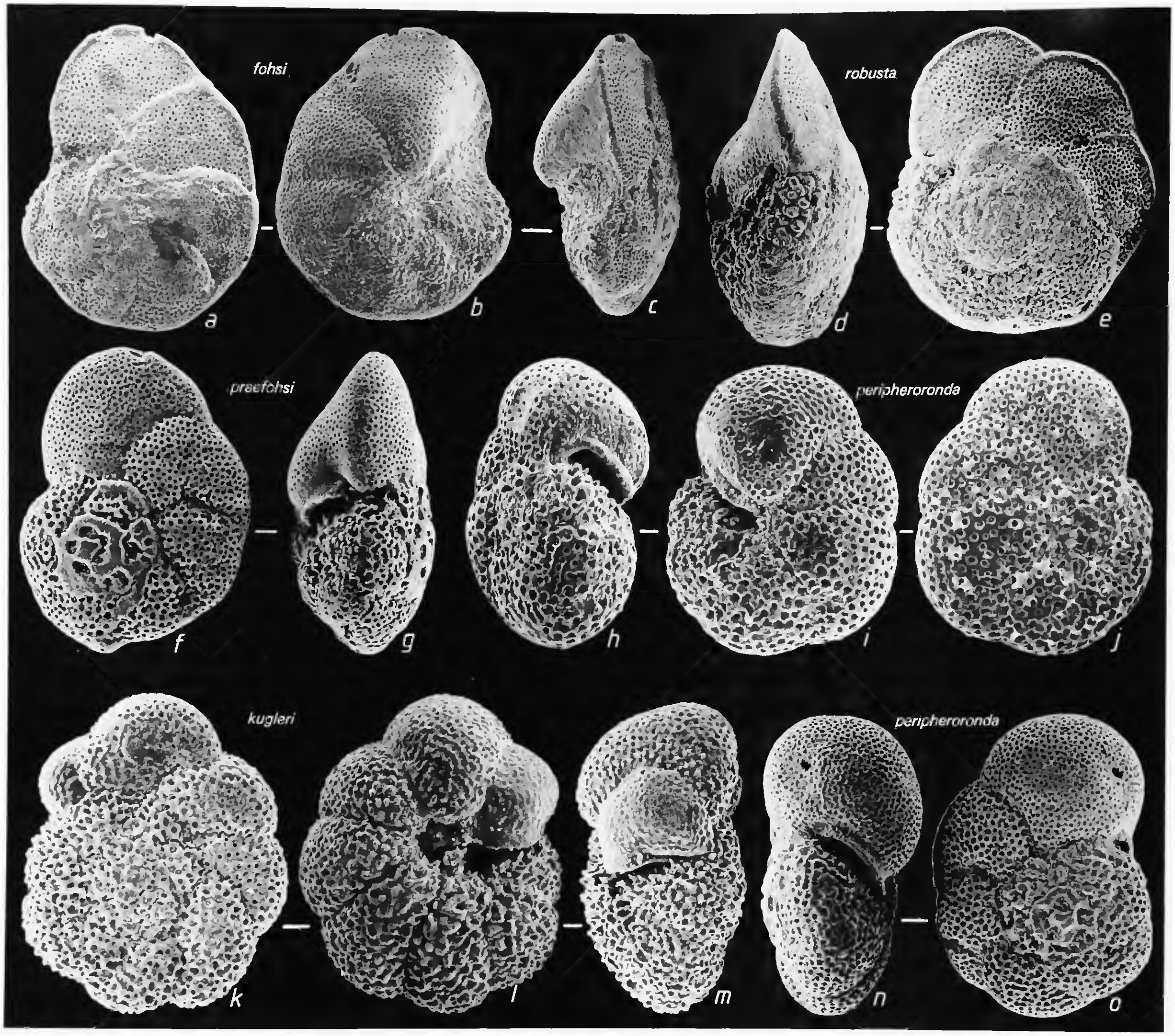


FIGURE 8.—*a–c, Fohsella fohsi* (Cushman and Ellisor), type locality *Fohsella lobata* Zone, Trinidad, middle Miocene (× 90); *d,e, Fohsella robusta* (Bolli), near type locality *F. lobata* Zone, Trinidad (× 95); *f,g, Fohsella praefohsi* (Blow and Banner), cotype locality *Fohsella fohsi* Zone, Trinidad, middle Miocene (× 115); *h–j,n,o, Fohsella peripheroronda* (Blow and Banner) (*h–j*, type locality *Globigerinatella insueta* Zone, Trinidad, lower Miocene (× 150); *n–o*, locality 12 (P.W. Jarvis), Upper Marl, Cipero Section, Trinidad, middle Miocene (× 115)); *k–m, Fohsella kugleri* (Bolli), type locality *F. kugleri* Zone, Trinidad, lower Miocene (× 160).

species was suggested by Stainforth and others (1975:279) and the connection appears very close. *Fohsella kugleri* has the same narrow, radially elongate, T-type chambers that are characteristic of *Fohsella* and that show the beginnings of distinct profile angularity (Figure 8*k*—*m*). The principal difference between *F. kugleri* and descendant forms is its coarsely ridged texture, with projections from the ridge corners, suggesting that the species was spinose in its living state (Cifelli and Glaçon, in press).

In texture, *Fohsella kugleri* compares favorably with *Paragloborotalia ciperoensis* (Figure 1*f*), a possible ancestor of *Fohsella*. Both species lack the regular honeycomb pattern of Oligocene forms, such as *P. opima*, where the ridges spread laterally to enclose single pores (Figure 1*g*). Some honeycomb patterning is formed on chambers of *F. kugleri* and *P. ciperoensis*, but not on all parts, and the spine-like projections may stand in isolation without ridge support. Where ridges do develop, they spread erratically and sometimes join to enclose two or more pores (Figures 1*f*, 8*k–m*). *Paragloborotalia ciperoensis* is a quasi-globigerine form with a large, open umbilicus, but there is some extension of the aperture towards the periphery. There is also minor flattening of the spiral side. This species is comparable to the modern *Neogloboquadrina dutertrei*, which shows similar quasi-globigerine features.

Fohsella kugleri has a narrow but distinctly open umbilicus, which conceivably could be derived from *P. ciperoensis*. However, there is no evidence of a transition, as the very primitive fohsellid, *F. mendacis*, has the same narrow umbilicus as *F. kugleri*. Primitiveness of *F. mendacis* is shown by its chamber shape, which varies between the broadly radial I-type, characteristic of *Paragloborotalia* and the radially elongate T-type, characteristic of *Fohsella* (Blow, 1969, pl. 38: figs. 7, 8). Also *F. mendacis* has a tapered profile that is neither distinctly spherical nor angular (Blow, 1969, pl. 38: fig 5). The wall is coarse and irregularly ridged as in *P. ciperoensis* and *F. kugleri*. *Fohsella pseudokugleri* shows no additional stages in development. Chambers on the holotype of this species are consistently more radial than in *F. mendacis*, but appear to fall within the range of variation of the latter. Possibly, *F. pseudokugleri* is a junior synonym of *F. mendacis*. Keller (1981) reported intergradations among *P. kugleri, P. pseudokugleri,* and *P. mendacis*. Therefore, while early *Fohsella* compare closely with the paragloborotalids and a connection with *P. ciperoensis* is suggested, the actual line of descent remains obscure, both from comparative morphology and from the stratigraphic record.

The species showing the closest paragloborotalid-globorotalid connection is *Globorotalia incognita* (Figure 9*a,e*). Srinivasan and Kennett (1981b:518) reported a transition between *G. incognita* and *Paragloborotalia continuosa*, but they did not show the chamber transformation. The loop-shaped aperture of *G. incognita* suggests affinity with *P. semivera* and *P. pseudocontinuosa*, and possibly *P. acrostoma*. Early representatives of *G. incognita* have distinct honeycombed walls and subspherical profiles that are barely distinguishable from the spherical profiles of *Paragloborotalia* (Figure 7). The only major advance of *G. incognita* is a definite elongation of chambers in the direction of coiling, seen on some individuals. With the appearance in the lower part of Zone N6 of the descendant *G. zealandica*, a globorotalid shell form with a partially flat wall is achieved.

Globorotalia praescitula is remarkably advanced from the outset. Even the earliest representatives are distinctly globorotalid with chambers that are all distinctly elongate in the direction of coiling. The wall is nearly smooth, with honeycombing retained only on the earliest chambers. Features shared in common with paragloborotalids are an elongate, narrow aperture and the four to five chambers in the outer whorl. Some tendencies toward a globorotalid shell form can be seen in late-occurring *Paragloborotalia* species, such as *P. bella*, which tend to have flattened, although distinctly honeycombed, walls and chambers that are somewhat elongated. However, *G. praescitula* represents a clear break with *Paragloborotalia* and its origin has rightly been termed cryptic (Jenkins, 1965:268). The derivation from any particular paragloborotalid is speculative. In light of the Oligocene–early Miocene DSDP sequences that have been studied, the chances of finding additional links become increasingly remote but should be searched for. The chamber shape and flat wall of *G. praescitula* represents a major redesign that may have occurred through rapid speciation.

This view of the origin of *Globorotalia praescitula* disagrees with those of Keller (1981), Srini-

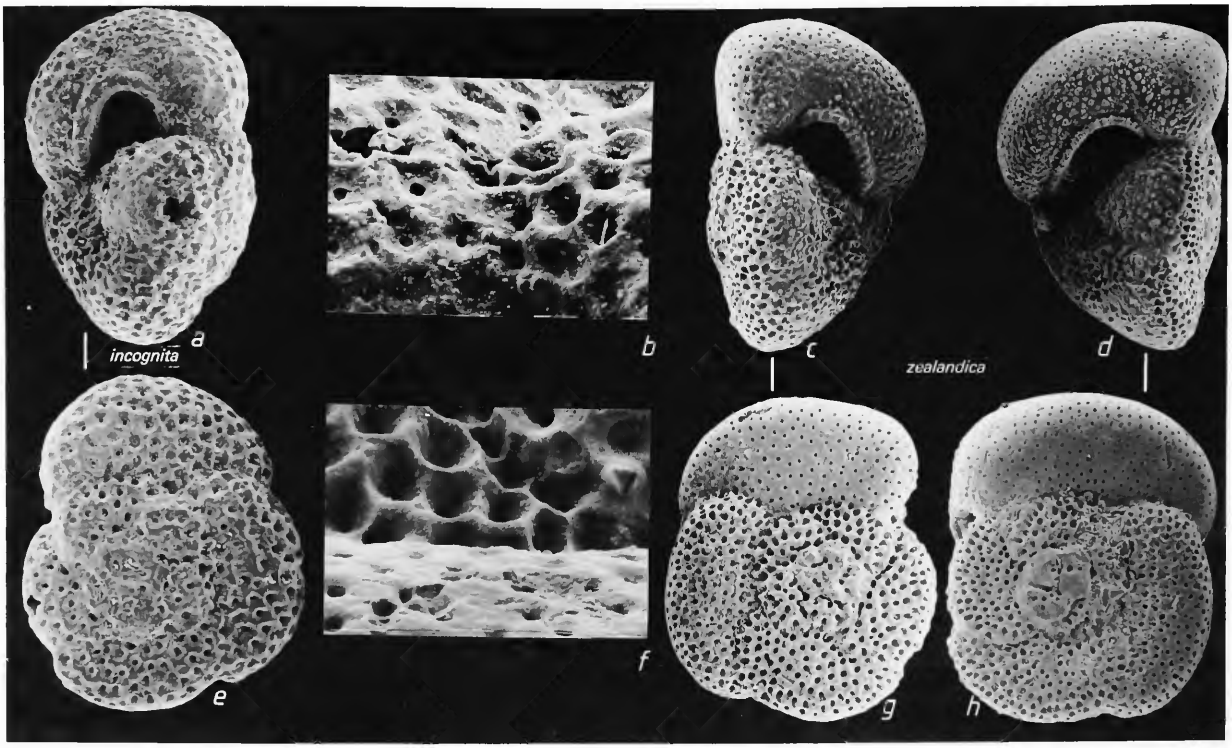


FIGURE 9.—*a,b,e*, *Globorotalia incognita* Walters, S136/f1159, 48.5–49.5 ft (14.79–15.10 m), Awamoa Drillhole, New Zealand, lower Miocene (*a,e*, × 195; *b*, × 550); *c,d,f–h*, *Globorotalia zealandica* Hornibrook, S137/f615, Oamaru, New Zealand, lower Miocene (*c,g*, × 145; *d,h*, × 130; *f*, × 765).

vasan and Kennett (1981b) and Kennett and Srinivasan (1983). Keller (1981, fig. 3) depicts *G. praescitula* arising via *G.* cf. *miozea* from *G. incognita*. Srinivasan and Kennett (1981b, fig. 10) show *G. praescitula* branching from *G. zealandica*. In these papers the entry of *G. praescitula* is shown to be subsequent to the evolution of *G. zealandica* sensu stricto. In New Zealand and at DSDP Site 516 in the South Atlantic (Berggren and others, 1983) the reverse occurs, suggesting-that the sequences studied by Srinivasan and Kennett and by Keller do not contain the early history of *G. praescitula*. Pending further data, we discount their reconstruction.

Fohsella Lineage

Formerly, the members of this group were designated as subspecies of *Globorotalia fohsi*, but they are treated here as a lineage totally distinct from *Globorotalia*. Trinomial nomenclature is not used as the relationship of the members is sufficiently indicated by their inclusion in the genus *Fohsella*.

Bolli (1950; 1957) recognized the following sequence in Trinidad:

Fohsella robusta
Fohsell lobata
Fohsella fohsi
Fohsella peripheroronda (originally *Globorotalia barisanensis*)

This species group was later revised by Blow and Banner (1966), who added *Fohsella peripheroacuta* and *F. praefohsi* as intermediaries between *F. peripheroronda* and *F. fohsi*. Blow and Banner also considered *F. robusta* and *F. lobata* as varietal forms of *F. fohsi* and made no taxonomic distinction among them. Bolli (1967) accepted the addition of Blow and Banner's two new species to the *Fohsella* group but rejected the grouping of *F. lobata* and *F. robusta* with *F. fohsi.* Bolli was supported by Stainforth and others (1975:276, 280) who pointed out that *F. lobata* and *F. robusta* are not only larger, but show greater advancement in keel development. From examination of holotypes and other material we are in agreement with this conclusion. In addition to having better developed keels, *F. robusta* and *F. lobata* tend to have smoother walls. However, we are uncertain about the distinction between *F. robusta* and *F. lobata,* and so we tentatively call these most highly advanced globorotalid forms of the *Fohsella* lineage *F. robusta.* To the above group of species, *F. kugleri* and *F. mendacis* are added here as the ancestral forms. Srinivasan and Kennett (1981a:410) previously assigned *Globorotalia kugleri* to *Fohsella.*

It might appear that the *Fohsella* lineage (Figure 8) would serve as an example of phyletic gradualism, since its development is seemingly marked by a unidirectional, progressive series of increasingly advanced forms culminating in a single type of globorotalid shell. However, branching occurred along the line of descent, as well as significant variation in the rate of developmental change. The early representative of *Fohsella, F. kugleri,* is a small lobulate form with five or more chambers in the peripheral whorl and a narrow, open umbilicus. It has an arched, rather broad profile but is distinctly subangular, rather than rounded as in *F. mendacis.* The wall is very coarse, with well-developed ridges surrounding single pores or distributed irregularly among the pores (Figure 8*k—m*). Occasional spike-like projections protruding from the surface may be relic spine bases.

Fohsella peripheroronda (Figure 8*h–j,n–o*) shows small, but distinct advances over *F. kugleri.* Keller (1981) and Srinivasan and Kennett (1981a) reported intergradations between these taxa. The test of *F. peripheroronda* is more compact, with a more rounded, circular periphery, and a profile that is perhaps a little more subangular, although still distinctly arched. There is some flattening of the wall in *F. peripheroronda,* but a ridged texture is retained throughout the test. Most of the flattening occurs in the final chambers; the early chambers are almost as coarse as the chambers in *F. kugleri.*

Fohsella peripheroronda is a long-lived species, which was cosmopolitan in the tropical and temperate regions during the greater part of its range. About the level of Zone N10 a split in the parent population occurred, with one part retaining relatively primitive features and the other part evolving into a rapid succession of increasingly advanced species. The split was accompanied by geographic partitioning, as the evolving stock became increasingly restricted to the tropics (Figure 34) and the parental *F. peripheroronda* retracted to higher latitudes. In New Zealand, the relatively primitive *F. peripheroronda,* or a close descendant, extends into Zone N14, but for the most part this species was unsuccessful after the split and beyond the Southwest Pacific is poorly known above Zone N10. Middle Miocene populations transitional between *Fohsella peripheroronda* and *Paragloborotalia mayeri* were noted by Jenkins (1966b:27, 1971:119) from this region. Nominally, this is an important instance of a globorotalid evolving into a paragloborotalid. However, *P mayeri* has a long history in the tropics prior to the level of origin postulated by Jenkins in the Southwest Pacific. Hoskins (1984) contrasted the honeycombed surface textures of New Zealand specimens of *P. mayeri* with the smooth interpore spaces on the shells of *F. peripheroronda* and argued that they were not related.

The evolving *Fohsella robusta* stock was short-lived. Although paralleling and achieving the same globorotalid architecture as *Globorotalia,* it become extinct soon after the time of most rapid and important change. The evolving species seldom wandered far beyond the tropics, and they became increasingly restricted in distribution (Jenkins, 1965; Saito, 1977; Figure 34). *Fohsella peripheroacuta* is the first species of the evolving branch and its principal advance over *F. peripheroronda* is the acquisition of a distinct, acutely angular profile that compares favorably with the profile of *Globorotalia miozea* and *G. archeomenardii.* Transformation may have been rapid but was of long enough duration to leave a geologic imprint. Jenkins and Orr (1972:1102) reported a transition between *F. peripheroronda* and *F. peripheroacuta* in DSDP cores from the Equatorial Pacific.

The wall surface of *Fohsella peripheroacuta* is considerably smoother than in *F. peripheroronda,* although a relic honeycomb texture is retained. Like *F. peripheroronda,* the honeycomb texture is most strongly developed in the earlier chambers. In the final chamber or two, the wall may be lacking visible ridges (Stainforth and others, 1975; fig. 117:3). The peripheral margin of *F. peripheroacuta* is either totally or partially perforate (Stainforth and others, 1975; fig. 117:1,4; Quilty, 1976, pl. 12: figs. 3, 4). A globorotalid feature introduced by *F. peripheroacuta* is the development of pustules around the apertural area (Stainforth and others, 1975, fig. 117:3).

The succeeding forms, *Fohsella praefohsi* (Figure 8*f–g*) and *F. fohsi* (Figure 8*a–c*) are very similar to *F. peripheroacuta,* and these three species have sometimes been grouped together as *F. fohsi.* The figures of Stainforth and others (1975) cited above as examples of *F. peripheroacuta* were grouped with *F. fohsi* by those authors. The globorotalid advancement shown by these succeeding forms is in the development of an imperforate peripheral rim and weak keel. There seems to be no dispute that this development occurred sequentially; but the problem is that development appears to have been rapid and with wide variation, so that the successive stages can seldom be distinguished in stratigraphic sequences.

Both *Fohsella praefohsi* and *F. fohsi* are about the same size as *F. peripheroacuta* with equivalently acute profiles and almost totally smooth walls. There is some increase in radial elongation of the test, especially in *F. fohsi.* An imperforate rim is formed in *F. praefohsi* but is well developed only in the final chambers. The rim may be accompanied by some weak keel formation, as suggested by the sectioned specimens of Blow and Banner (1966, pl. 2: figs. 6, 7). In *F. fohsi* a distinct rim extends around the entire test. There is some keel development in *F. fohsi,* but it is weakly formed and is not found on all specimens.

Fohsella robusta (Figure 8*d–e*) is appreciably larger than its predecessors. This form also displays a small reversal in evolutionary direction, as it has a circular outline like the earlier *Fohsella* species rather than the radially elongate outline of *F. fohsi,* its immediate predecessor. *Fohsella robusta* is a fully developed globorotalid, with an acute profile and a distinct keel bounding the peripheral margin. There is variation among populations, and some individuals may lack a keel around the early chambers; but other individuals have keels that extend around the entire test. The wall is smooth, but a strong development of pustules sometimes conceals the primary surface. This form is totally comparable in architecture to the advanced forms of *Globorotalia. Fohsella robusta* evolved rapidly and has a limited stratigraphic range. It made its first appearance in Zone N12, the same zone in which *F. fohsi* first appeared, and became extinct in Zone N13.

Using the scale of Ryan and others (1974) as a reference, the estimated sequence of events (approximately in millions of years before present) in the evolution of *Fohsella* is as follows:

F. kugleri (first appearance) Zone N4 (base) 23 m.y.
F. peripheroronda (first appearance) Zone N5 (middle) 21 m.y.
F. peripheroronda (last appearance) Zone N14 (lower) 12.5 m.y.
F. peripheroacuta (first appearance) Zone N10 (base) 15.5 m.y.
F. praefohsi (first appearance) Zone N11 (base) 15 m.y.
F. robusta (first appearance) Zone N12 (middle) 14 m.y.
F. robusta (extinction) Zone N13 (early) 13 m.y.

While this scale can be used only as an approximation, it does underscore the pattern of development, which was one of a long period of stasis and a short interval of rapid change. It took *F peripheroronda* some 3 m.y. to evolve from *F. kugleri,* even though the architectural change amounted to very little. Another 5.5 m.y. elapsed before *F. peripheroacuta* branched off from *F. peripheroronda.* Here, a significant advance occurred, but it is possible that the transformation was compressed within a short interval of time. The branching did not result in the complete replacement of the parental stock as *F. peripheroronda* survived in its original form for about another three million years, somewhat longer than the descendant lineage. Once branching occurred, the advances in shell form were rapid, with the succeeding *Fohsella* species appearing at intervals of about 0.5 m.y. The terminal *Fohsella, F. robusta,* survived for only slightly more than 0.5 m.y. The status of some of the short-lived fohsellid taxa is uncertain. We have followed current biostratigraphic usage but, as we note later, several may represent arbitrarily defined morphotypes within populations.

In summary, *Fohsella* developed in the late Oligocene–early Miocene from a coarse walled paragloborotalid, possibly like *Paragloborotalia ciperoensis.* Some of the early development may have occurred through rapid speciation. However, the actual transformation in shell design probably did not occur through a quantum jump, because *Fohsella mendacis* has intermediate paragloborotalid-globorotalid features. Once the basic globorotalid type of shell was achieved, there was a long period of stasis during which *Fohsella* was first represented by *F. kugleri* and then succeeded by the little modified, long-ranging *F. peripheroronda.* Throughout this time, *Fohsella* was cosmopolitan and showed no regional concentration in distribution that would suggest a watermass preference. In the middle Miocene branching occurred, with a rapid (in a geologic sense) succession of populations developing along the branch that culminated in a fully developed, keeled globorotalid (*F. robusta*). With branching occurred biogeographic partitioning, as the parental *F. peripheroronda* retracted from the tropics, while the newly evolved species became increasingly restricted to the tropics (Figure 34). The seemingly anomalous occurrence of *F. fohsi* and *F. lobata* reported by Bartlett (1968) from Nova Scotia may be a reflection of Miocene watermass structure (Cifelli, 1976a).

Despite rapid development of a shell design fully equivalent to that of *Globorotalia,* the *F. robusta* branch did not flourish and soon became extinct. Olsson (1972:183) attributed the development and extinction of the *Fohsella robusta* branch to climatic causes. He correlated a maximum size increase with the peak of a warming cycle, and keel development and extinction with cooling at the end of the cycle. However, it is overly simple to view the oceans as a homogeneous entity that becomes equally warmed or cooled in all places. In fact, the regional separation of the *Fohsella* parental stock and its branch suggests that differentiation of watermasses occurred in the middle Miocene. Also, the development of the menardines, a group strongly preferring the tropics, occurred about the time of extinction of *Fohsella,* and so one would presume that suitable warm-water habitats were available. Indeed, competitive exclusion by *G. menardii* is a possibility. The increasing stenotopy of the *F. robusta* branch may also be significant. Cracraft (1982) suggested, for example, that stenotopy raises susceptibility to extinction.

Globorotalia zealandica Lineage

Although this is a minor lineage, with a short history, it provides an interesting record of a design that deviated from the main line of early globorotalid development and presaged a later architectural trend. The early taxon, *Globorotalia incognita,* is differentiated from paragloborotalids like *Paragloborotalia opima* by several modest but distinctive alterations of chamber shape. In spiral view, chambers are elongated in the direction of coiling so that chamber length (coiling direction) exceeds height (radial direction). In *P. opima* (Figure 1*c*) and allies the chamber margins are semicircular, but in *G. incognita* they are transformed to a broad, crescentic arch (Figure 9*e*). The leading edge may show greater curvature than the trailing edge, creating slight asymmetry in the margin. Convexity of the spiral surface of chambers (axial orientation) is weaker than on the umbilical surface (Figure 9*a*). This produces a primitive version of the characteristically flattened, or compressed, spiral surface of globorotalid shells. Umbilically, chambers in the outer whorl are commonly slightly extended to form a low, broad, convex surface without trace of compression near the periphery. The umbilicus is closed. The aperture is a high arch, sometimes like that in *P. acrostoma,* and greater than in *P. semivera.* However, *G. incognita* retains the strongly ridged, honeycombed texture that characterizes the paragloborotalids.

The evolution of globorotalid chamber form is advanced further in the succeeding species, *Globorotalia zealandica* (Figure 9*c,d,f–h*), which appears in New Zealand at about Zone N6 (Hornibrook, 1981b). The spiral margin is often less arched and some outlines are subquadrate. In axial orientation, the central portion of the spiral surface of late-formed chambers is nearly flat, while the ventral surface is usually more strongly raised than in *G. incognita.* The periphery varies from subangular to broadly convex. In advanced specimens of *G. zealandica* both spiral and ventral components of chamber shape closely resemble those in Pliocene *G. crassaformis* and *G. puncticulata.* There is also some advance towards the smooth wall texture typical of the globorotalids. Honeycombing is absent on the last-formed chamber, and the wall between pores has only very low amplitude undulations. The penultimate and earlier chambers, however, retain moderately well-developed honeycomb texture. This tends to be strongest on chambers of the inner whorls, but chamber by chamber increments are not obvious. Shells from open ocean environments may be encrusted.

This history, based on temperate Southwest Pacific sequences, conflicts with that of Keller (1981) who studied tropical and subtropical North Pacific sequences. She considered that *Globorotalia incognita* descended, via an intermediate, from *Paragloborotalia continuosa,* as earlier suggested by Walters (1965, fig. 5) and Jenkins (1971:133), and recently reported by Srinivasan and Kennett (1981b:518), at about the middle of Zone N4. In contrast to the New Zealand record, however, she identified *G. zealandica* at a slightly earlier horizon and suggested that it descended directly from *P. continuosa.* On the other hand, her figures of *G. zealandica* (Keller, 1981, pl. 3), do not compare well with the New Zealand form (Figure 9*g, h*). They have a fully ridged texture and chambers that are broadly radial, rather than elongate, in the direction of coiling. These specimens offer no evidence of *G. zealandica* development.

Evidence that the lineage was distributed widely around the southern oceans is indicated by records of *Globorotalia incognita* from the Southwest Atlantic (Tjalsma, 1977, DSDP Site 329) and *G. zealandica* from the Southeast Atlantic (Berggren and Amdurer, 1973, DSDP Site 18; Jenkins, 1978, DSDP Site 360; Pujol, 1983, DSDP Site 516). The specimen shown by Jenkins (1978, pl. 1: fig. 19) may show the textural modification seen in Southwest Pacific populations. However, that the lineage was not recorded from the lower Miocene sequence at DSDP Site 362 (Southeast Atlantic latitude 20°S) by Jenkins (1978), or from Indo-Pacific sequences at similar latitudes (e.g., Shafik and Chaproniere, 1978), or from the equatorial DSDP Site 289 (Srinivasan and Kennett, 1981b), suggests that it primarily inhabited higher latitude water in the Southern Hemisphere, a view also advanced by Pujol (1983:628).

There are several North Atlantic records, again from higher latitudes. Specimens shown by Poore (1979, pl. 7:figs. 10–12, DSDP Site 408, 64°N) have the chamber form, textural, and apertural features of Southwest Pacific populations of *Globorotalia zealandica,* as does one of the specimens in Jenkins (1977, pl. 4: fig. 11, English Channel 49°N). King (1983:11) recorded it from the North Sea and there is also a tentative record of *G. zealandica* in Poore and Berggren (1975, DSDP Site 116, 57°N). None of these works record the presence of both taxa. There is an absence of records in the lower Miocene of the Aquitaine Basin (e.g., Jenkins, 1966a; Poignant and Pujol, 1976). In the lower Miocene assemblages from southern Spain, Molina (1979) identified *Paragloborotalia semivera, P.*

nana, and related taxa as in the Southwest Pacific but did not find *G. incognita* or *G. zealandica.* However, Tjalsma (1971, fig. 25) recorded *G. zealandica* from this region in higher faunas containing *Orbulina.* This report draws attention to the need for further study of the later history of the lineage. The middle Miocene *Globorotalia conica* closely resembles *G. zealandica,* and Southwest Pacific records of the former (Jenkins, 1971:134) include one that was originally identified as *G. zealandica* by Hornibrook (1961:143). Possibly the lineage continued into the middle Miocene.

The origin of the lineage involved only modest changes to the chamber shape of the paragloborotalid ancestor. As yet, only Srinivasan and Kennett (1981b:518) have reported connecting populations (suptropical Southwest Pacific). However, it is premature to conclude that the lineage arose in this region because of the possible difficulty in distinguishing the slightly innovative architecture of *Globorotalia incognita* in large paragloborotalid assemblages (e.g., Molina, 1979). The character transformations in *Globorotalia incognita* that led to *G. zealandica* are greater and better defined than those of the initial divergence. The New Zealand record indicates that textural change and chamber redesign occurred concurrently, although not necessarily jointly on a particular individual, in a short stratigraphic interval. The distinguishing architectural characters of *G. zealandica* occur only on chambers formed late in ontogeny. In some individuals, usually small, late-formed chambers retain the shape of *G. incognita.*

The evolutionary pattern suggested by the New Zealand record is step-like, in which two taxa of relatively stable morphology are linked, in an ancestor-descendant sequence, by a brief interval in which late ontogenetic innovations in form and texture occurred. Although there are specimens in *Globorotalia zealandica* populations that have not progressed beyond the *G. incognita* grade of evolution, there is no evidence of distinct populations of the latter taxon after the appearance of *G. zealandica.* The record suggests phylogenetic transformation rather than divergence.

In the perspective of the Neogene globorotalid radiation, this lineage represents an early experiment in the evolution of an inflated discoidal shell with only moderate advancement on the globular axial profile of the paragloborotalids. Spirally, chamber and shell shapes are as advanced as in later globorotalids (e.g., *Globorotalia crassaformis*) but, in *G. zealandica,* wall texture remained incompletely rectified. While the periphery of some late-formed chambers became narrowly rounded (Figure 9*d*), advanced compression and keel development did not arise. However, axial chamber shape may be significant here as the later globose globorotalids (e.g., *G. puncticulata, G. inflata, G. crassaformis*) are similarly keel-less. The lineage is thus distinguished from its two lower Miocene contemporaries by its architectural direction towards ventrally inflated chambers rather than towards the compressed biconvex design. The latter design reached its acme in the middle Miocene whereas globose designs, presaged by *G. zealandica,* arose afresh in the major Pliocene lineages.

Globorotalia praescitula Plexus

Globorotalia praescitula is the stem species of the major component (in longevity, architectural innovation, and taxonomic diversity) of the Neogene globorotalid radiation. *Globorotalia praescitula* plexus is used here to include the main descendants, as can be reasonably inferred from the stratigraphic records of intergrades and transformations of taxa. It refers to a minimally monophyletic group with limits that are somewhat arbitrarily defined. Thus, the plexus includes the widely divergent menardines because the approximate time and mode of transformation in that group seem fairly clear, but excludes the scitulines, and the *G. crassaformis* plexus, because their origins are still obscure. They are considered separately. Some taxa in the plexus have been placed in separate genera or subgenera by Steineck and Fleischer (1978) and Kennett and Srinivasan (1983), but here we are concerned primarily with tracing ancestry rather than with classification.

Despite a certain amount of variability suggesting a species group rather than a single species, *Globorotalia praescitula* (Figure 10) retains a good degree of interregional identity and uniformity. Therefore, it seems appropriate to consider it as a world-wide taxon from which later *Globorotalia* emerged. *Globorotalia praescitula* has been recorded from the tropical Atlantic region (Blow, 1959:221), the temperate North Atlantic (Poore, 1979:471), South Atlantic (Berggren and others, 1983:678), Mediterranean (Bizon and Glaçon, 1978:691), the temperate North Pacific (Oda, 1977:60), and temperate Southwest Pacific (Walters, 1965:115).

Srinivasan and Kennett (1981a:410–411) apparently overlooked this cosmopolitant distribution when they restricted *G. praescitula* to a stem species of a tropical lineage leading to the menardines and proposed *G. incognita* as the stem species of a temperate lineage leading to *G. conoidea* and descendants. Subsequently, however, Srinivasan and Kennett (1981b:518) and Kennett and Srinivasan (1983:108) proposed that *G. praescitula* descended from the temperate *G. zealandica* and was ancestral to *G. miozea*. We consider that *G. praescitula* evolved independently of the *G. zealandica* lineage. It appeared in New Zealand prior to *G. zealandica* sensu stricto and has more advanced wall topography.

In its typical form from the Caribbean (Blow, 1959:221), *Globorotalia praescitula* has a small, compact test with slightly more than four chambers in the peripheral whorl and a distinctly angular, but not acute, profile. In axial view (Figure 10*b*) the periphery appears blunted, and the spiral side is just slightly convex. Wall relief is low but there is a clear honeycomb texture in all but the final chambers. Pores are large and occur throughout the entire test. There is no visible reduction in porosity at the peripheral margin. Chambers are elongate in the direction of coiling and are asymmetrical (B-type). The aperture is elongate and narrow. In the Caribbean some of the early Miocene sequence is poor, obscuring the early development of *G. praescitula*. According to the locality data given by Blow (1959:221) the holotype and paratypes come from a horizon referable to Zone N7. Recent examination of material from Trinidad has revealed an occurrence of this species in Zone N6 (type locality of the *Catapsydrax stainforthi* Zone). Berggren and others (1983) considered that it

FIGURE 10.—*Globorotalia praescitula* Blow: *a*, BN141, base of section 6.75 km east of Ancona, Italy, lower Miocene (× 170); *b*, Tocuyo Formation Eastern Falcón, Venezuela, paratype (USNM 625714), lower Miocene (× 190); *c*, locality 309 (H.M. Bolli), *Globigerinatella insueta* Zone, Trinidad, lower Miocene (× 280); *d*, S136/f615, Oamaru, New Zealand, lower Miocene (× 230).

appeared near the base of Zone N7 in the South Atlantic sequence at DSDP Site 516.

The development of *Globorotalia praescitula* can be followed in the New Zealand early Miocene sequences where this species first appears at the base of the Altonian Stage (about Zone N6–lower N7). Earliest representatives found in shelf facies (Figure 6*o,p*) are sparse and small but distinctly praescituline, except for a subspherical axial profile that deviates but little from the spherical profile of the paragloborotalids. Chambers are crescentic and distinctly elongated in the direction of coiling, representing a major transformation from the slightly elongated chambers seen in some paragloborotalids, like *Paragloborotalia bella*. Another major transformation is seen in the texture of the wall, which is nearly flat. A slight honeycomb texture is suggested, but it is confined to the chambers of the early whorl. Like the Caribbean types, New Zealand early representatives contain rather large, evenly spaced pores, except in the final chamber where pore size is reduced considerably. An apparent difference, however, is that pore density tends to be reduced around the peripheral margin and extends to the umbilical surface. This feature persists in descendant forms. It is common but variable in extent (Figures 6*p*, 10*d*). An imperforate band has not been observed on individuals from the Caribbean.

Two principal trends can be seen in the development of *Globorotalia praescitula* in New Zealand, where it is ubiquitous in middle shelf to bathyal facies of the Altonian Stage.

Axial Profile: All populations show variation in profile, but the earliest ones (Figure 6*p*) tend to be subspherical and lack the angularity of typical globorotalids. In later forms from the Altonian Stage (Zones N6–N7), most outlines are considerably more compressed. At this stage the spiral side is weakly convex and runs into a sector of rapid curvature at the periphery. The umbilical side inclines downward towards the coiling axis and often is partly linear. This results in a subangular to angular profile that compares favorably with the profiles of the Caribbean forms from the same zonal level. This basic form was retained by descendants; it was varied only in the degree of compression at the periphery and in the inclination of the ventral segment of the chamber wall.

Size Increase: Earliest individuals are small (under 200 μm diameter) with 4–4.5 chambers in the outer whorl and a total of about 12 chambers. Larger shells (over 400 μm diameter) occur in later populations. Extension of ontogeny to include about 15 chambers occurred very quickly, but the major mechanism of enlargement was probably by increase in chamber growth rates between the successive chambers. Size increase possibly occurred gradually as a phyletic trend.

Texturally, New Zealand representatives of *Globorotalia praescitula* made little progress toward total reduction of wall topography. Actually, there is even an apparent slight reversal, as the earliest representatives are the smoothest. The only indications of honeycomb texture on them are gentle undulations and low, broad mounds around the pores of the inner whorls (Figure 6*o–p*). In later Altonian populations, ridges constructed on the early whorls are reminiscent of the honeycomb texture of the paragloborotalids (Figure 6*q,s*). However, there is a conflict in the interpretation of these textures. According to one view (R.C.), the undulations and ridges are actually vestigial traces of a paragloborotalid honeycombed texture. The fact that the wall in these early New Zealand forms is mostly flat shows that the transformation in texture occurred neither in a single step nor through a progressive series of changes. During the transformation, the regulatory balance between ridge-forming and sheet-like calcification included a period of instability so that relic honeycombed textures were retained to a greater extent in some populations than in others. The paratype of *G. praescitula* has a rather coarse, ridged texture (Figure 10*b*) that provides a good link with a paragloborotalid ancestor, even though it may be younger (in Zone N7) than the New Zealand forms. According to another view (G.H.S.), the undulations and ridges on the early New Zealand forms (Figure 6*s*) may be no more than simulations of ridged, honeycombed textures and may not necessarily be a paragloborotalid relic. Their absence entirely from some of the earliest specimens, and from late-formed chambers of more advanced specimens, support this interpretation. Furthermore, the constructional ridges often fuse together over the earliest chambers (Figure 6*s*), a feature not seen in *Paragloborotalia*.

In the Mediterranean, developmental trends in *Globorotalia praescitula* are similar to those in New Zealand, although comparison is somewhat complicated by a "timing" problem. Planktonic foraminiferal markers for a biostratigraphic framework are lacking at the DSDP core Site 372 where the early Mediterranean occurrences of *G. praescitula* are recorded (Bizon and Glaçon, 1978). *Globorotalia praescitula* first appears in the upper part of the *Sphenolithis belemnos* Zone (NN3), which is about equivalent to the base of the planktonic foraminiferal Zone N7. Therefore, *G. praescitula* possibly appeared later in the Mediterranean than in the Caribbean or New Zealand where records extend down into Zone N6.

As elsewhere, the Mediterranean appearance of *Globorotalia praescitula* is cryptic and cannot be connected in a gradational series with an ancestor. Even the earliest forms have distinctly elongated chambers in the direction of coiling and, like New Zealand representatives, are symmetrically crescentic. However, in later populations chamber shape changes from symmetric to asymmetrical (Bizon and Glaçon, 1978, pl. 1,2). Profiles are variable and early populations include some that tend to be subspherical, although they are generally subangular and compare more favorably with the Caribbean profiles than the ones in early New Zealand populations. The spiral sides of the Mediterranean forms are flat to convex. Convexity is found not only in early populations but in later ones as well. Wall surface is low, comparing favorably with the New Zealand forms, but a relic honeycomb texture is visible in most of the chambers. Pores are rather large and evenly distributed. However, as in New Zealand, there is a tendency towards imperforation or semiperforation around the peripheral margin and adjacent umbilical region. This tendency persists in descendant forms. There is no difference in wall texture between early and later Mediterranean populations. The principal change from early to later populations of Mediterranean *G. praescitula* involves, as in New Zealand, the extent of compression at the chamber periphery. This results in an acute profile (Bizon and Glaçon, 1978, pl. 1,2). There also appears to be some increase in size of the test between early and later populations.

NEW ZEALAND RECORD OF *GLOBOROTALIA MIOZEA*

A useful perspective on the development of *Globorotalia miozea*, which we consider to be the descendant of *G. praescitula*, is available in New Zealand, the region from which that species was first described. The taxa show a gradational relationship. Hornibrook (1961:144) noted the larger size of *G. miozea* (he identified *G. praescitula* as "*G. miozea* small variety"), but discrimination solely on this basis would be arbitrary. However, populations of the upper Altonian Stage (about Zone N7) exhibit several other changes which, either singly or in combination, are more useful in identifying the appearance of *G. miozea*. The transformations are neither abrupt nor necessarily concurrent: (1) Chambers became more compressed at the periphery (Figure 6*k,m*) and the profile sometimes became angular, particularly in crust-free specimens; there was a tendency towards umbilical elevation of the axial profile, a tendency that was continued in some descendants of *G. miozea*. (2) Not strictly architectural but nonetheless important, was the initiation of crust formation, a feature that is particularly characteristic of Southwest Pacific populations. (3) A change in coiling direction occurred (Walters, 1965, fig. 4; Jenkins, 1971, table 58); sinistrally coiled shells became dominant in the upper Altonian Stage and this mode remained dominant in Miocene descendants. (4) The number of chambers in the outer whorl increased, with some individuals having five; B-type spiral chamber outlines (Figure 6) became typical.

Of the above changes, the increased chamber compression resulting in an acute profile was the most significant, as it marked the inception of the evolution of the keel, the culminating architectural structure in *Globorotalia* development. The earliest stage in the evolution of the keel detectable in New Zealand representatives of *G. miozea* is the presence of a narrow, translucent rim at the angular periphery of compressed chambers. Under reflected light it appears contiguous with the intercameral suture and is made distinct by its highly reduced pore density (Scott, 1973a, pl. 2: figs. 8,9). It has no topographic expression and cannot be distinguished by scanning electron microscopy. This rim is comparable to the one seen in *Fohsella fohsi* and represents a comparable stage in keel development. The structure is most obvious on the latest chambers but commonly extends back to those formed in mid-ontogeny. In New Zealand, a rim first appears in *G. miozea* populations near the entry of *Praeorbulina* or early in Zone N8. Initially, all gradations from absence to clear definition of the structure occur, possibly depending on the angularity of the junction between spiral and umbilical walls.

The interval between the appearances of *Praeorbulina glomerosa curva* and *Orbulina suturalis* (Zone N8), corresponds with the period in which rim formation spread in *Globorotalia miozea* populations to become a common character of the species; the type population is from this interval. Concurrently, a primitive keel appeared, recognizable as a distinctive topographic feature at the peripheral margin. The keel develops as a fold or a crimp in the chamber wall at the junction of the umbilical and spiral surfaces (Scott, 1973a, pl. 2: figs. 1–4), forming a cord-like structure. As with the origin of the rim, keel formation was initially weak and variable (Figure 6*f,i*). Scanning electron microscopy is needed to discriminate the weak ridges formed on the earliest keeled specimens. At this stage, the keel is more obvious on the spiral side of the peripheral margin. However, the amplitude of the fold increases and, in populations associated with the appearance of *Orbulina universa* (in Zone N9), some cord-like structures occur. We use the development of a keel to mark the appearance of the *G. praemenardii* morphotype. Specimens figured as *G. miozea* by Kennett and Srinivasan (1983, pl. 26: figs 1–3) are at this stage (compare with topotypes in Figure 6*j–n*).

The axial shape of *Globorotalia miozea* is commonly biconvex but there is wide variation. Chambers in some individuals extend umbilically, presaging the architecture that became typical of *G. conoidea* populations. Other shells, often crust free, show less umbilical extension (Walters, 1965, fig. 8*f–h*), and a few have flat or even slightly concave umbilical surfaces as in *G. panda*. Compression of chamber peripheries is also widely variable but tends to be correlated with the axial form of the shell. It is weakest in umbilically extended chambers and strongest in those with relatively flat umbilical surfaces. Usually, there are about five chambers in the outer whorl with six-chambered variants occasionally present. These variants tend to be large with wide, radially extended chambers and raised trailing edges (advanced B-type form).

ENCRUSTATION

In New Zealand, the first occurrence of *Globorotalia miozea* often equates with the onset of encrustation. Indeed, the earliest representatives of *G. miozea* are little more than rather large, encrusted counterparts of *G. praescitula* and appear in the Altonian Stage. Thereafter, encrustation is a characteristic feature of New Zealand *G. miozea* and its descendants. While onset of encrustation helps to define the first occurrence of *G. miozea*, it did not coincide with any major change in shell design. It possibly arose late in a phase of chronoclinal increase in size, and it could be argued just as easily that encrustation originated in the late stages of *G. praescitula*. Encrustation is a highly variable phenomenon in *G. miozea* and cannot be used as a governing taxonomic criterion. New Zealand populations of *G. miozea* commonly contain crust-free as well as heavily encrusted specimens, with ratios between the morphotypes and the amount of encrustation varying considerably. Nor can the crusted and uncrusted forms be separated satisfactorily by other morphologic criteria. Jenkins (1971, table 38: sample 651) referred small uncrusted specimens to *G. praescitula*, large uncrusted specimens to *G. praemenardii*, and encrusted ones to *G. miozea*. All are probably intrapopulational variants, not easily discriminated except for size and incidence of crust. We do not consider such reports as evidence of speciation in *G. praescitula*.

The evolution of the crust is an interesting problem, as yet unresolved. At least initially, crusted forms of *G. miozea* tended to be larger than crust-free ones, which suggests that an ontogenetic factor is involved, while the very nature of the phenomenon seems to call for some environmental explanation, such as bathymetry and/or temperature. That bathymetry was a control is implied by the fact that encrusted specimens do not occur in shallow shelf, inshore Altonian facies. Whether a bathymetric explanation can be upheld by analogy with the distribution of modern planktonic species remains unclear. Kennett (1976) reviewed the problem and, while he concluded that encrustation was an ontogenetic feature associated with deeper and/or colder water, the evidence remains equivocal. For example, Hecht and Savin (1970) studied the oxygen composition of the crust and entire shell of *Sphaeroidinella dehiscens* and found that crust registered a warmer temperature than the whole shell. Their conclusions were challenged by Bé and van Donk (1971). In the water column, encrusted forms of the subtropical species *Globigerinoides conglobatus* are commonly captured in oblique plankton tows from 0–200 m, while encrusted forms of *Neogloboquadrina dutertrei* are recovered from similar types of tows in tropical regions (Cifelli, 1982). Of course, this evidence does not completely negate a bathymetric and/or cool water control of encrustation because it is possible that, in towing down to 200 m, the critical depth had been passed and the encrusted specimens were recovered in the lower depth range. On the other hand, Bé (1980:294) found that laboratory cultured specimens of *G. sacculifer* became calcified during gametogenesis, where neither depth nor temperature was a factor.

This review could be pursued at length, but there would be no advantage, as a satisfactory conclusion cannot be reached at present. Unquestionably, encrustation occurs ontogenetically, but the relationship of this phenomenon with the environment, or with life processes, remains unclear. Probably no single generalization can be made and individual species may have their own peculiar habits. Certainly, the development of crust in Southwest Pacific populations of *G. miozea* and its long persistence in descendants is a rather unique historic feature among planktonic foraminifera. Following the model of Hart (1980), this development in *G. miozea* possibly resulted from colonization of the lower depths for part of its ontogeny during the early Miocene when that section of the water column provided a vacant niche. Migration could have been induced by the increase in size and extended ontogeny of *G. miozea* over its praescituline ancestor. The first invasions may have occurred fortuitously as "buoyancy costs" arising from the evolution of large shells. Such an explanation, of course, would have to allow that migration to lower depths did not occur uniformly throughout the oceans, because in the tropics encrusted forms are scarce. However, it is not possible to arrive at a good estimate of the relative importance of encrusted versus crusted forms in various regions from published accounts, because encrustation has sometimes been used as the principal criterion for identification. Uncrusted counterparts have sometimes been referred to as unkeeled forms of *G. praemenardii* (e.g., Jenkins, 1971).

NORTHERN REPRESENTATIVES OF *GLOBOROTALIA MIOZEA*

A major question at this point is whether *Globorotalia praescitula* was succeeded by world-wide populations referable to *G. miozea* or whether *G. praescitula* was followed by divergent tropical and temperate lineages. We have previously noted that Srinivasan and Kennett (1981a, 1981b) proposed inconsistent views about this question. The issue involves matters of taxonomy and levels of variation considered allowable. Certainly, what divergence may have occurred amounted to very little, because the developmental trends in the tropics following *G. praescitula* closely parallel those in the temperate Southwest Pacific. Also, while the pace in development may not have been identical, changes occurred at about the same time. The developmental trends involve profile changes that lead to the formation of a keel. At the partially keeled stage, Caribbean populations of *G. praemenardii* are not clearly separable morphologically from New Zealand populations of *G. miozea* and a two-lineage hypothesis was not upheld by Scott (1972). Whereas Kennett and Srinivasan (1983) envisaged a tropical-temperate divergence in *G. praescitula* populations, we locate the major branch in the plexus later, between *G. conoidea* (fully keeled B-type chambers, moderately elevated on the umbilical side) and *G. menardii* (fully keeled C-type chambers and compressed, discoidal shell).

In the Caribbean, *Globorotalia praescitula* is succeeded by a form that Bolli (1957) called *G. archeomenardii* (Figure 11*k–o,r–t*). It is a small form, little larger than *G. praescitula*, with a very acute profile that usually has a rim around the peripheral margin and, sometimes, even a partial keel. In his description, Bolli (1957:120) mentioned that *G. archeomenardii* has a convex spiral side, but the taxonomic importance of that feature should not be overemphasized. It is common (Figure 11*r*), but many individuals do not show it at all. *Globorotalia archeomenardii* in turn is succeeded by *G. praemenardii* (Figure 11*a–j*), which is an appreciably larger form but otherwise very similar. The holotype of *G. praemenardii* has a weak keel that extends around the entire shell (Blow, 1969, pl. 6: figs. 1–3), but, as in New Zealand, populations are variable and include rimmed or even unrimmed forms as well. Blow (1969:368) noted that *G. praemenardii* has a more depressed shell than *G. archeomenardii* and a more circular spiral outline (compare Figure 11*f* with Figure 11*k*). He thought that the two forms could often be distinguished in this way. But such separation can sometimes be difficult (compare Figure 11*a* with Figure 11*o*). Blow (1969:369) recognized a transition between *G. archeomenardii* and *G. praemenardii* at about the boundary between Zones N9 and N10.

Forms transitional between *Globorotalia praescitula* and *G. archeomenardii* occur in the Caribbean about the level of Zone N8, which is somewhat higher than the time of transition from *G. praescitula* to *G. miozea* as identified in New Zealand. Earlier, Scott (1972) referred a Zone N8 Caribbean population to *G. praescitula* with which it shows close affinity in its totally perforate profile. However, advancement is shown by strong compression and acuteness of the profile, which appears more developed than in the New Zealand forms of *G. miozea*. In the *G. barisanensis* Zone of Bolli, or Zone N9, rims and some partial keels appear on *G. archeomenardii*, which is about contemporaneous with the development of these features on *G. miozea* in New Zealand. Throughout the development of *G. praescitula–G. archeomenardii–G. praemenardii* the pores remain large.

The major differences in development between the Caribbean and Southwest Pacific populations involve size and encrustation. In the Southwest Pacific populations size increase is evident by Zone N8, but in the Caribbean an increase does not occur until Zones N10–N11. Populations showing size increase in the Caribbean are the ones that have been referred to *Globorotalia praemenardii*, while the older, smaller forms have been referred to *G. archeomenardii* (e.g., Blow, 1969). *Globorotalia praemenardii* populations do show an advancement in keel development, but the keel is weak and not

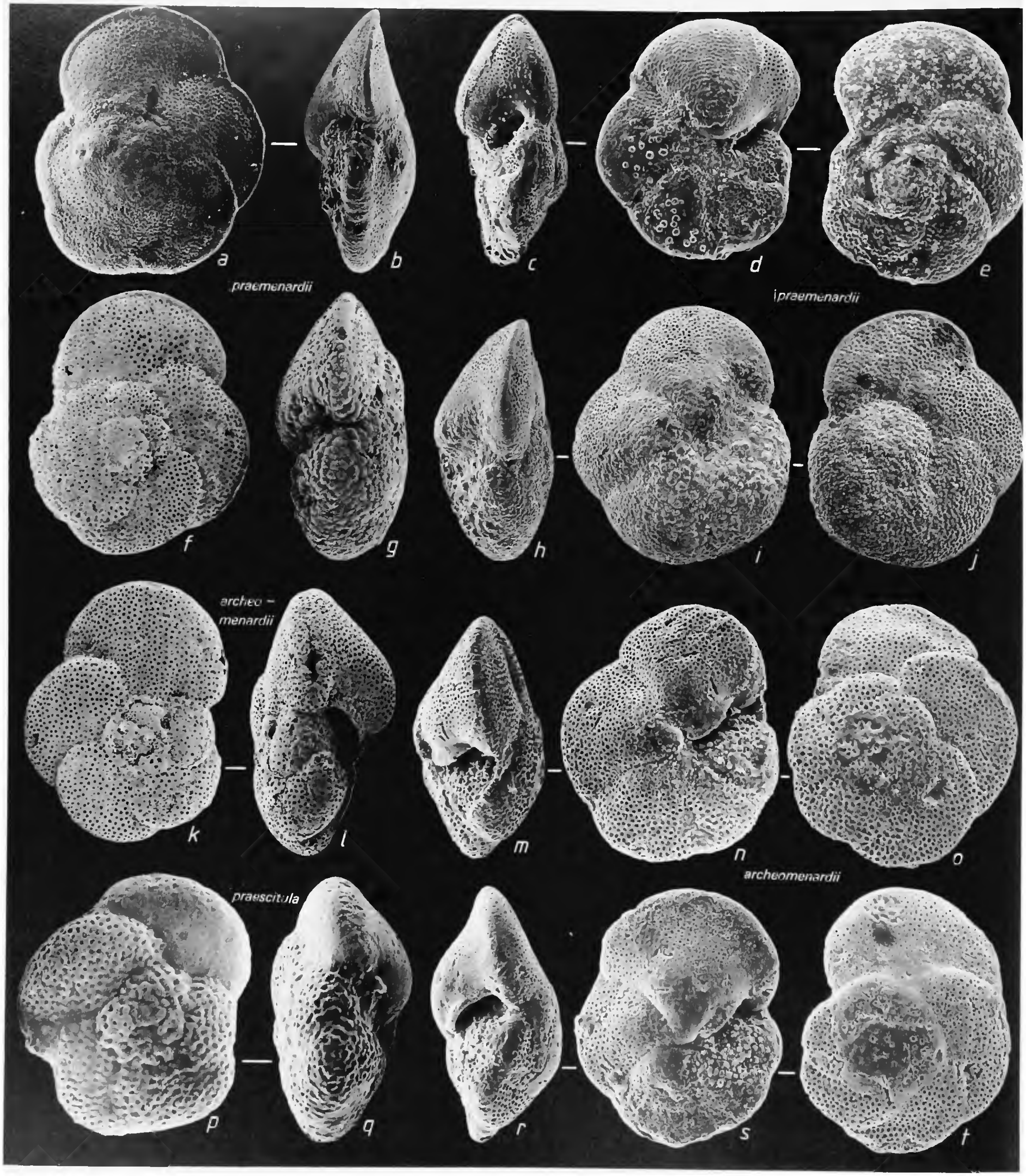


FIGURE 11.—*a–j*, *Globorotalia praemenardii* Cushman and Stainforth (*a,b*, type locality *Fohsella robusta* Zone, Trinidad, middle Miocene (× 105); *c–e*, cotype locality *F. fohsi* Zone, Trinidad, middle Miocene (× 100); *f*, locality 13 (P.W. Jarvis), Lower Green Clay, Cipero Section, Trinidad, middle Miocene (× 90); *g*, locality GG20379 (BMNH), Santo Domingo, middle Miocene (× 125); *h–j*, type locality *F. lobata* Zone, Trinidad, middle Miocene (× 80)); *k–o,r–t*, *Globorotalia archeomenardii* Bolli (*k,l*, locality 12 (P.W. Jarvis), Upper Marl, Cipero Section, Trinidad, middle Miocene (× 160); *m–o,r–t*, type locality *F. peripheroronda* Zone, Trinidad, middle Miocene (*m–o*, × 145; *r–t*, × 150)); *p,q*, *Globorotalia praescitula* Blow, Tocuyo Formation Eastern Falcón, Venezuela, paratype (USNM 625714), lower Miocene (× 170)).

much better defined than the rim of *G. archeomenardii*. The available evidence suggests that *G. archeomenardii* populations are smaller in size than *G. miozea* while *G. praemenardii* is fully comparable to the latter. Encrustation is mostly lacking in the Caribbean populations but, as discussed before, this is a variable feature in the Southwest Pacific populations and is of dubious taxonomic value.

In the North Atlantic, morphotypes of *Globorotalia miozea* (Poore, 1979, pl. 6: fig. 12) and of *G. praemenardii* (Poore and Berggren, 1975, pl. 1: figs. 4–6) occur together through Zones N11–N13 (approximately), a distribution resembling that in the Southwest Pacific.

In the Mediterranean, a similar developmental trend leading from the primitive *Globorotalia praescitula* to *G. miozea* with rims and partially formed keels occurs at DSDP Site 372 (Bizon and Glaçon, 1978). Forms transitional between *G. praescitula* and *G. miozea*, or primitive *G. archeomenardii*, occur in association with *Praeorbulina glomerosa* or at a level equivalent to Zone N8. These forms, referred to as *G. archeomenardii* (Bizon and Glaçon, 1978, pl. 3: fig. 7), have a very acute profile, like the Caribbean forms, and a peripheral margin that is partially imperforate and even slightly rimmed. They tend to be somewhat larger than *G. praescitula* and are succeeded by still larger forms that have distinct rims and partially formed keels. Bizon and Glaçon (1978) referred some of these forms to *G. magnifica*, a spiroconvex species that shows close relationship with *G. panda*. However, some individuals figured by Bizon and Glaçon are clearly biconvex and of the same evolutionary grade as *G. praemenardii* (Bizon and Glaçon, 1978, pl. 4: fig. 5). Encrusted forms of *G. miozea* were identified from the same core section. Partially keeled forms referable to *G. praemenardii* are well represented at levels equivalent to Zone N12. As in the Southwest Pacific and the Caribbean, these forms are not readily separable from an unkeeled *G. miozea* population.

Surface outcrops of the lower and middle Miocene in the Mediterranean region are inadequately exposed to establish a developmental sequence. However, the succession of forms in the Gaudalquivar Basin of southern Spain that Tjalsma (1971:57) referred to as *Globorotalia menardii* forms 1–5, are relevant. The earliest of these forms, *G. menardii* form 1, is comparable to advanced *G. praescitula* or early *G. miozea* (4.5–5 chambers in the outer whorl). It has chambers elongate in the direction of coiling and a profile that is subangular, but not acute. There is no indication of a peripheral rim. The succeeding *G. menardii* form 2 is clearly more advanced and compares well with *G. archeomenardii*. This form has a distinctly acute profile. Some specimens (e.g., Tjalsma, 1971, pl. 4: fig. 5*c*) are without a keel, while it is weakly developed on others (Tjalsma, 1971, pl. 4: fig. 4*b*). Tjalsma's *Globorotalia* forms 3–5, are fully keeled forms and will be considered later. The Mediterranean region is in need of more sampling and study.

SUMMARY OF THE EARLY HISTORY OF THE PLEXUS

We suggest that the same developmental stages in the evolution of the axial profile and keel (Figures 3*e–g*, 4) can be followed in sequences from the Southwest Pacific, Caribbean, and Mediterranean regions and that they occurred at approximately equivalent horizons. There was a world-wide, progressive trend in the evolution of *Globorotalia* during the early to middle Miocene, despite some regional differences in size, shape, and encrustation. Importantly, the same, progressive development in profile and keel can be followed at both tropical and temperate latitudes. Because development was so cosmopolitan, we think that the single lineage concept for the evolution of *Globorotalia* is better supported than that of parallel tropical and temperate lines of descent (Kennett and Srinivasan, 1983:103, 120). Furthermore, in each region there is a common pattern of gradual transformation, substantial intrapopulation variation, and intergradation.

The taxonomy of the lineage is currently in an unsatisfactory state because of synonymies arising from studies of contemporaneous populations in different regions, wide local variation, and the rather inconspicuous, gradual evolution of the keel. Blow and Banner (1966) used the stages in development of profile and keel for the subdivision of the *Fohsella* lineage and we suggest that this method might also provide a workable taxonomy of the *Globorotalia praescitula* lineage, as follows.

Globorotalia praescitula: rounded periphery, rimless; 4–4.5 A- or B-type chambers in outer whorl.

Globorotalia miozea: moderately compressed periphery, usually rimmed, rarely with very weak keel; 4.5–5 chambers in outer whorl; chambers of the B-type. *Globorotalia archeomenardii* may warrant recognition as a smaller, more compressed, regional subspecies.

Globorotalia praemenardii: compressed, angular periphery, usually rimmed and often with a weak keel on late-formed chambers; about five B-type chambers in outer whorl. Such specimens have been previously identified in New Zealand as *G. miozea*. Careful inspection by scanning microscopy may be required to determine the presence of a keel.

It should be stressed that all of the morphotypes, as defined above, may occur in individual assemblages at about Zones N9–N12. The value of identification by major morphotype, as opposed to the mere presence of an advanced form, needs to be assessed.

EARLY SPIRALLY CONVEX FORMS

Most globorotalid shells are either biconvex or more convex on the umbilical side than the spiral side. Individuals in which the spiral side is more convex than the umbilical are more often the exception rather than the rule. Forms with a very rapid translation of whorls along the coiling axis, such as the benthonic *Patellina corrugata* or the planktonic *Globigerinita bradyi* did not develop out of the basic globorotalid architecture. The closest globorotalid form is *Globotruncana contusa* from the Cretaceous radiation. Among modern *Globorotalia*, only *G. hirsuta* is spirally convex.

In the Neogene radiation, spiral convexity first developed in the *Globorotalia praescitula* plexus during the middle Miocene (Figure 12*a–d*), subsequently redeveloped at about the beginning of the Pliocene in *G. margaritae* (Figure 12*h–j*) and, still later, appeared occasionally in populations of *G. cultrata* (Figure 12*k–l*). Architecturally, these forms are very close, but the stratigraphic record indicates that they are products of convergent trends.

When they first appear in the middle Miocene, spiroconical shells are closely associated with populations of *Globorotalia miozea* and *G. praemenardii*. *Globorotalia panda* was named from the Southwest Pacific and *G. magnifica* from the Mediterranean, but both show similar patterns of variation; we tentatively regard them as a single branch of the *G. praescitula* plexus.

Earliest spiroconical forms (about Zone N12) from New Zealand, referred to *Globorotalia panda* by Jenkins (1971:97), display moderate to strong spiral convexity, but the ventral surfaces are commonly slightly raised rather than depressed (Figure 12*d*). The periphery tends to be more strongly compressed than in the contemporary *G. praemenardii* and the keel is more prominent. However, most characters intergrade with those of *G. praemenardii*, and it is only the combination of spiral convexity and well-formed keel in a few individuals that allows recognition of *G. panda*. The record therefore suggests a morphotype within the main *G. miozea–G. praemenardii* populations rather than a separate species or even a subspecies.

Later (about Zones N14–N16), populations of *Globorotalia panda* can be recognized in New Zealand that are clearly differentiated from *G. conoidea* and *G. menardii*. The periphery is acute and bounded by a prominent, thick keel. Spirally, chamber shape resembles the B-type but is generally more elongate, as in *G. margaritae* (compare Figures 6, 12*a,i*). In some specimens spiroconical shape is accentuated by a depressed, or flat, ventral surface (Figure 12*b*). Similar shells occur in the Southeast Atlantic (Jenkins, 1978, pl. 2: figs. 3–5).

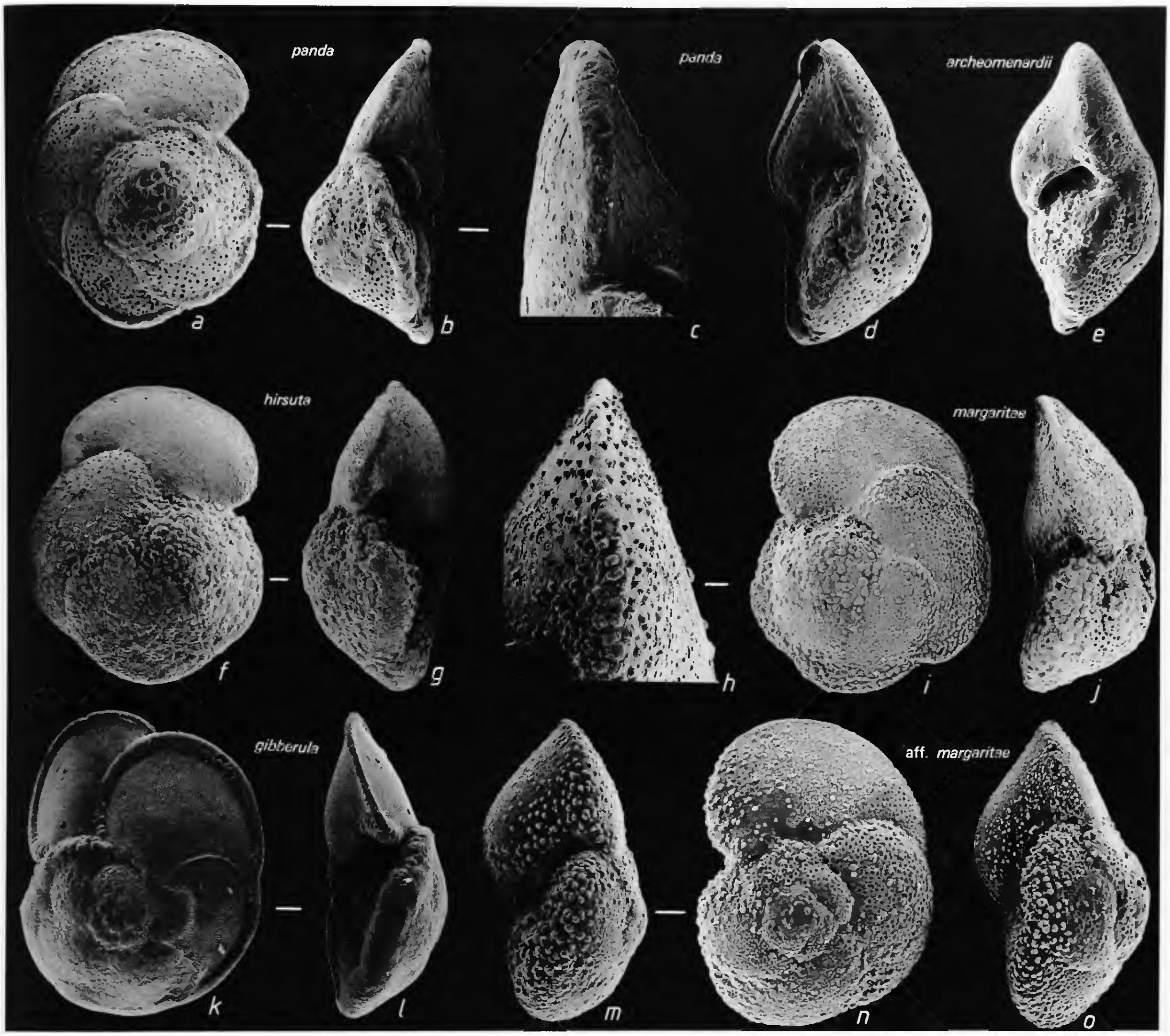


FIGURE 12.—*a–d*, *Globorotalia panda* Jenkins (*a–c*, Y18/f92, Gisborne, New Zealand, upper Miocene (*a,b*, × 100; *c*, × 195); *d*, N80/f1405, Mata River, New Zealand, middle Miocene (× 110)); *e*, *Globorotalia archeomenardii* Bolli, type locality *Fohsella peripheroronda* Zone, Trinidad, middle Miocene (× 145); *f,g*, *Globorotalia hirsuta* (d'Orbigny), DSDP Site 284, 1-1-35, Southwest Pacific, Quaternary (× 45); *h–j*, *Globorotalia margaritae* Bolli and Bermúdez, Chain Station 115-6-67, South Atlantic, Pliocence (*h*, 346 cm, × 195; *i*, 346 cm, × 80; *j*, 323 cm, × 95); *k,l*, *Globorotalia cultrata gibberula* Bé, locality RC 9-150 (surface sediment), Indian Ocean, Recent (× 45); *m–o*, *Globorotalia* aff. *margaritae* Bolli and Bermúdez, Chain Station 115-6-67, 507 cm, South Atlantic, upper Miocene (*m,n*, × 90; *o*, × 95).

While many Trinidad individuals of *Globorotalia archeomenardii* have a moderately convex spiral surface (Figure 12*e*; Bolli, 1957, pl. 28: fig. 11; Blow, 1969, pl. 47: figs. 1–4), this feature fails to develop to any significant degree. There is no subsequent record of morphotypes like *G. panda* in that region and, indeed, Caribbean populations of *G. praemenardii* tend to be less convex, spirally, than the preceding *G. archeomenardii* (Figure 11).

The Mediterranean record of spiroconical forms is more comparable with that of the Southwest Pacific. Bizon and Glaçon (1978) proposed *Globorotalia magnifica* for a spirally convex form with a distinct keel and they noted similarities with *G. panda* and *G. praemenardii*. Their illustrations show only a moderate development in spiral height, ventral depression and keel, which suggests that *G. magnifica* is closer in affinity to early forms of *G. panda* (Figure 12*d*) than to later, fully developed forms (Figure 12*a,b*). Some weak-keeled specimens of *G. magnifica* (e.g., Bizon and Glaçon, 1978, pl. 4: fig. 5) compare with ones from New Zealand identified as *G. praemenardii* (Figure 6*a,b*). The range attributed to *G. magnifica* (about Zones N10–N12) further suggests that this form refers to an early segment of the *G. panda* branch. *Globorotalia ichinosekiensis*, described by Takayanagi and others (1976) from strata of about Zone N14 age in Japan is possibly a synonym of *G. panda*.

While further work on the middle Miocene spiroconical forms is needed, present records indicate a gradational and perhaps rather gradual divergence from *Globorotalia praemenardii* populations. In both hemispheres the distribution was extratropical. In New Zealand and adjacent deep sea sites (Srinivasan and Kennett, 1981b, figs. 4, 5) the extinction of *G. panda* occurred in Zone N16, significantly before the entry of *G. margaritae*.

GLOBOROTALIA CONOIDEA–GLOBOROTALIA MENARDII DIVERGENCE

The appearances of *Globorotalia conoidea* and *G. menardii* mark the separation of *Globorotalia praescitula* plexus into two distinct lineages. It is a major divergence (Figure 2). Both species are fully keeled and represent culminations of the globorotalid architectural form. *Globorotalia conoidea* remained close to the parental stock and is hardly more than a fully keeled *G. praemenardii*, with a tendency towards vaulting on the ventral side. *Globorotalia menardii* underwent a change in shell design by the development of flaring, C-type chambers, increased axial compression, and a reduction in pore size. The bifurcation is accompanied by the first biogeographic differentiation in the plexus, as *G. menardii* developed in the tropics and all of its descendants continued to show a strong preference for that habitat (Figure 35). *Globorotalia conoidea* and its successors tended to avoid the lower latitudes and are characteristic of subtropical and temperate regions (Srinivasan and Kennett, 1981b). However, there is considerable overlap in the distribution of these two groups, particularly in the northern hemisphere.

THE CONSERVATIVE BRANCH, *GLOBOROTALIA CONOIDEA*

The origin of *Globorotalia conoidea* involved neither rapid character transformations nor introduction of novel structures. Fixation of keel construction in late ontogeny is the major evolutionary advance of this species over *G. praemenardii*. Walters (1965) distinguished *G. conoidea* from *G. miozea* (in which he included specimens we regard as *G. praemenardii*) by its larger size and high umbilical side, as well as by the presence of a distinct keel. However, in New Zealand there is no consistent size difference, and individuals with vaulted umbilical surfaces occur in both *G. miozea* and *G. praemenardii* populations. The New Zealand record shows that *G. conoidea* preserved much of the variation spectrum of *G. miozea* and *G. praemenardii* except for the fixation of the keel (Scott, 1975). Architecturally minor, but significant, changes were reductions in the convexity of the spiral surface of chambers, in the depression of sutures, and in offset between chambers. While some early populations of *G. conoidea* are strongly conical, ventrally biconvex shells persisted. Some populations from northeastern New Zealand also include large, disk-like forms. Walters (1965) treated populations of biconvex forms as *G. miozea* sensu lato, while Jenkins (1971, pl. 6: fig. 138) identified crust-free biconvex specimens like that in Figure 13*n–o* as *G. miotumida*. Both are here regarded as variants of *G. conoidea*. While the umbilical surfaces of *G. conoidea* are, on the whole, clearly

FIGURE 13.—*a–c*, *Globorotalia pliozea* Hornibrook (*a*, DSDP Site 284, 14-4-20, Southwest Pacific, Pliocene (× 70); *b–c*, DSDP Site 284, 14-6-20, Southwest Pacific, Pliocene (*b*, × 80; *c*, × 70)); *d–g Globorotalia mons* Hornibrook (*d,e*, DSDP Site 284, 15-6-20, Southwest Pacific, topotype, Pliocene (× 65); *f,g*, DSDP Site 284, 16-3-20, Southwest Pacific, upper Miocene (× 85)); *h–r*, *Globorotalia conoidea* Walters (*h–j*, DSDP Site 284, 16-3-20, Southwest Pacific, upper Miocene (*h*, × 80; *i*, × 100; *j*, × 80) (*h* represents the ventrally elevated morphotype described as *G. conomiozea* by Kennett, 1966; *k–o*, N98/f565, Waimata River, New Zealand, topotypes, middle Miocene *k,l*, × 100; *m* × 105; *n,o*, × 100); *p–r*, cotype locality *Paragloborotalia mayeri* zone, Trinidad ("form 3" morphotype of Tjalsma, 1971, middle Miocene, *p,q* × 95; *r* × 105)), *s,t*, *Globorotalia mediterranea* Catalano and Sprovieri, JT1911A, Falconara, Sicily, upper Miocene (× 75).

more vaulted than in *G. miozea*, the axial shape oscillated within wide limits. Late in the history of *G. conoidea* in the Southwest Pacific (about Zone N17), there was an acme of highly conical, quasitruncatuline forms. Kennett (1966) proposed *G. conomiozea* for these (Figure 13*h*) but, commonly, gradation in degree of ventral elevation with *G. conoidea* forms occurs within a single assemblage, and we do not think that *G. conomiozea* is specifically separable. Vincent (1981:345) has a similar view. Records from the Southwest Atlantic (Pujol, 1983, Table 4, DSDP Site 516) of *G. conomiozea* almost always associated with *G. conoidea* in consecutive samples over a substantial interval in the upper Miocene may indicate intraspecific variation.

The number of chambers in the outer whorl also fluctuated in the history of *Globorotalia conoidea*. In recollections from the type locality, an early horizon (about Zone N14), 4–4.5 chambered forms are dominant. In later populations five-chambered forms are dominant, and some individuals have six chambers; similar variation occurred in *G. miozea*. However, late in the species history, the number of chambers declined progressively and the four-chambered form again became predominant. This trend in reduction is associated with the acme of the highly conical *G. conomiozea* variants and probably occurred throughout the southern oceans. There is evidence of it in the South Atlantic (Scott, 1983) and the Southwest Pacific (Malmgren and Kennett, 1981).

In the Pliocene, variation in the ventral elevation of shells appears to be much more bimodal among Southern Hemisphere populations than the late Miocene ones. *Globorotalia mons* (Figure 13*d–g*) is strongly ventroconical, while *G. pliozea* (Figure 13*a–c*) retains the convex shape of many of the earlier *G. conoidea* populations. In both species, the umbilicus is narrower and the aperture lower than in the preceding populations of *G. conoidea*, including the truncatuline, *conomiozea*, form. In *G. pliozea*, an elongate, A-type chamber is typical and, like *G. mons*, four chambers are included in the outer whorl. The Pliocene descendants of *Globorotalia conoidea* are widely distributed in the temperate regions of the Southern Hemisphere. Scott (1983) recorded them from the South Atlantic Rio Grande Rise. *G. pliozea*, at least, seems to occur in the Indian Ocean (Boltovskoy, 1974: pl. 11: figs. 8,15,17; recorded as *G. conoidea*). *Globorotalia conomiozea subconomiozea* Bandy, described from Pliocene sediments in a submarine core, may be a very close relative of *G. pliozea*. The Pliocene specimens from North Pacific DSDP Site 310, illustrated by Keller (1978, pl. 1: figs. 1–10) as *Globorotalia conomiozea* and *G. conoidea*, may resemble *G. mons*. The extinction of *G. pliozea* in the upper Pliocene appears to close the record of the *G. conoidea* group in the Southern Hemisphere.

The relationships of species recorded from the Mediterranean region as *Globorotalia menardii* form 3, *G. dalii*, *G. mediterranea*, and *G. conomiozea* are uncertain. A close relationship with *G. conoidea* is indicated by the retention in these species of a shell design like those of *G. miozea* and *G. praemenardii*, with elongate, B-type chambers and large pores (Figure 13*p–t*). However, there are some regional differences between the development of the Mediterranean and Southwest Pacific populations. The earliest of the above Mediterranean species, *G. menardii* form 3, like *G. conoidea*, is hardly more than a strongly keeled *G. praemenardii*. In the Mediterranean, it immediately succeeds *G. praemenardii* at a level equivalent to Zone N13 where it occurs side by side with *G. menardii* (Bizon and Glaçon, 1978). *Globorotalia menardii* form 3 also occurs at about the same level, and alongside *G. menardii*, in the Caribbean (Cifelli and Glaçon, in press). *Globorotalia menardii* form 3 probably can be regarded as an infra-specific form of *G. conoidea*. The only apparent difference is that *G. menardii* form 3 tends to have a narrrowly biconvex rather than a vaulted profile. However, Zachariasse (1975:101) noted that this species may also have a moderately convex umbilical side (Zachariasse, 1975, pl. 2: fig. 5*b*). Distinctly vaulted forms have not been recorded from the Caribbean or other tropical regions.

It is more difficult to establish the possible relationships of the later occurring *Globorotalia dalii* and *G. mediterranea* (Figures 13*s,t*, 17*f,g*), which do not appear in the Mediterranean until Zone N17. Both species show a distinct vaulting of the umbilical side, and the more vaulted forms of *G. mediterranea* have been assigned to *G. conomiozea* by Mediterranean workers (e.g., Zachariasse, 1975:105; D'Onofrio and others, 1976, pl. 4: figs. 1,2). However, Scott (1980b) noted that none of the Mediterranean populations show the same developmental trends as the New Zealand populations of *G. conoidea*. The Mediterranean forms, while distinctly vaulted, are always domed and never conical as in the quasitruncatuline *conomiozea* morphotype. Also, the Mediterranean populations do not show the reduction to four chambers in the outer whorl (Figure 39) that characterizes the later populations of *G. conoidea* in New Zealand. *Globorotalia saheliana* (Figure 17*a,b*) may be related to these keeled Mediterranean populations. Catalano and Sprovieri (1971:241) described the keel as weak and limited to the outer whorl. On the specimen figured (Figure 17*a,b*), it is absent from the last two chambers and very weak on the preceding chamber. This variability and the radial inflation of chambers also occur in *G. puncticulata sphericomiozea*. However, southern populations of the latter contain only four chambers in the outer whorl while *G. saheliana* has at least five. Again, the contrast in northern and southern populations is apparent. Further, specimens resembling *G. mons*, one of the Pliocene descendants of *G. conoidea*, have not been illustrated from the North Atlantic (Poore and Berggren, 1974, 1975; Poore, 1979). This may also apply to *G. pliozea*. Some isolation is suggested among populations of *G. conoidea* in the late Miocene (Figure 43).

We have interpreted *Globorotalia conoidea* broadly for, although there is a large amount of variation in axial form, it seems to be gradational and there are strong interregional resemblances in spiral chamber shape, keel development, and aperture. We summarize our view of the various taxa associated with *G. conoidea* as follows.

Globorotalia miotumida: crust-free variants in Southern Hemisphere; possibly a senior synonym of *G. conoidea*.

Globorotalia menardii form 3 of Tjalsma: infraspecific variant, usually more compressed than Southern Hemisphere form of *G. conoidea*.

Globorotalia dalii, G. mediterranea, G. conomiozea (of Mediterranean usage): closely interrelated forms, varying primarily in axial shape; greater similarity with *G. menardii* form 3 and early southern populations of *G. conoidea* than with uppermost Miocene populations in the latter region.

Globorotalia iwaiensis: possibly a synonym of *G. conoidea*.

Globorotalia miozea rifensis: synonym of *G. conoidea*; fully developed keel; probably the equivalent of *G. menardii* form 3 of Tjalsma.

Globorotalia saphoae: greater ventral elevation of chambers than on other Mediterranean morphotypes; very closely resembles southern *G. conoidea* (e.g., Figures 13*k,l*, 17*h,i*; Feinberg and Lorenz, 1973, pl. 2: fig. 10; Scott, 1973a, pl. 2: fig. 3).

THE INNOVATIVE BRANCH, *GLOBOROTALIA MENARDII*

With the appearance of *Globorotalia menardii*, the only major modification of the elongate, B-type chamber was introduced. The new, C-type chamber (Figure 5) is broad and flaring, with a raised trailing edge and a leading edge that joins the spiral surface at either a right or obtuse angle. Tjalsma (1971) and Zachariasse (1975) distinguished two forms (4 and 5) of *G. menardii* according to the angle of intersection, but the angular range is slight. Both compare favorably with the Mediterranean lectotype of *G. menardii* proposed by Stainforth and others (1978).

The C-type arrangement allows more chambers to be included in a whorl. The design also moves the greatest spiral dimension of chambers in a radial direction (Figure 5), so tending to increase overall test diameter. Therefore, the C-type chamber might be viewed as a strategy for producing a larger shell without significantly extending ontogeny. The hydromechanical penalty of large size was reduced in the menardines by the good form resistance of the axially compressed shell (Scott, 1973b). The new form was well suited to the exploitation of tropical waters. The C-type chamber became the trademark of tropical *Globorotalia* but was never adopted by species endemic to regions outside of the tropics.

Most of the early representatives of *Globorotalia menardii* are modern in appearance, with typical C-type chambers and pores that are reduced in size. However, some early individuals are intermediate with *G. praemenardii*. Blow (1969:369) noted the intergradation and proposed that *G. menardii* be applied to specimens in which the sutural limbation extended into the middle whorl. Limbation is produced by keel formation; hence Blow was attempting to employ the progressively earlier inception of the keel in ontogeny. He considered that, in joint *G. praemenardii–G. menardii* populations of Zones N11–N13, progressively more specimens achieved early initiation of the keel in ontogeny. Application of the C-type chamber criterion also points to gradational relationships among *G. praemenardii*, *G. menardii*, and *G. conoidea*. Bizon and Glaçon (1978, pl. 8) illustrated specimens with C-type chambers but with weak keels restricted to the later chambers of the outer whorl (*G. praemenardii* level of keel development). Conversely, Cita and others (1978, pl. 5: figs. 1–3) show specimens with strong keels (some with limbation, meeting Blow's *menardii* criterion) but with B-type chambers. These are associated with individuals that they referred to *G. conoidea*. From the perspective of the later record of the plexus, it is certain that major divergences occurred in Zones N11–N13, but the level of analysis thus far fails to indicate well-defined speciations. That little use has been made of events in the plexus in the middle Miocene biostratigraphic classifications reflects the complexity of population variation.

We deal with the menardine lineage briefly and superficially, because the taxonomy of this group is intricate and connections between species in many cases remain obscure. There were no important changes in shell design after the appearance of *Globorotalia menardii*, but the lineage was innovative in many minor ways. A number of species or distinctive variants (Figure 14*d,e*) developed by changes in the number of chambers in the outer whorl, the shape of the peripheral margin, and the rate of size increase in chambers. There were also changes in the shape of the axial profile, but they were much more limited than in the *G. conoidea* lineage. The menardines never developed a highly vaulted ventral profile; most species have compressed, biconvex axial profiles with the greater convexity on the umbilical side. Some individuals are moderately domed (Zachariasse, 1975, pl. 4: fig. 11b). That, however, is about the extent of vaulting, and the menardines never exploited this type of shell form as did *G. conoidea*. In the short-lived Pliocene species, *G. miocenica*, a dome-like appearance is exaggerated by the presence of a flat spiral side. The common tendency of the menardine group has been to develop a thin, disk-like shell (Figure 7). Examples of this shell form are found in Miocene populations of *G. menardii* but are more common after the Miocene (Figure 14*b–c*). The disk shape is achieved during ontogeny, particularly in the final volution of the test (Scott, 1973b).

Normally, the menardines have five to six chambers in the outer whorl. During the Pliocene there was experimentation, particularly in the Atlantic (Parker, 1973; Keigwin, 1982), to develop multichambered species with more than six chambers in the outer whorl. All of these species (e.g., *Globorotalia multicamerata*, *G. miocenica*, *G. pertenuis*) include individuals with seven or more chambers in the outer whorl; *G. pertenuis* includes individuals with as many as 11 or more. Olsson (1973) showed that growth during ontogeny was complex. The menardines were no more successful with the multichambered experiment than other planktonic foraminifera. All of the Pliocene forms with seven or

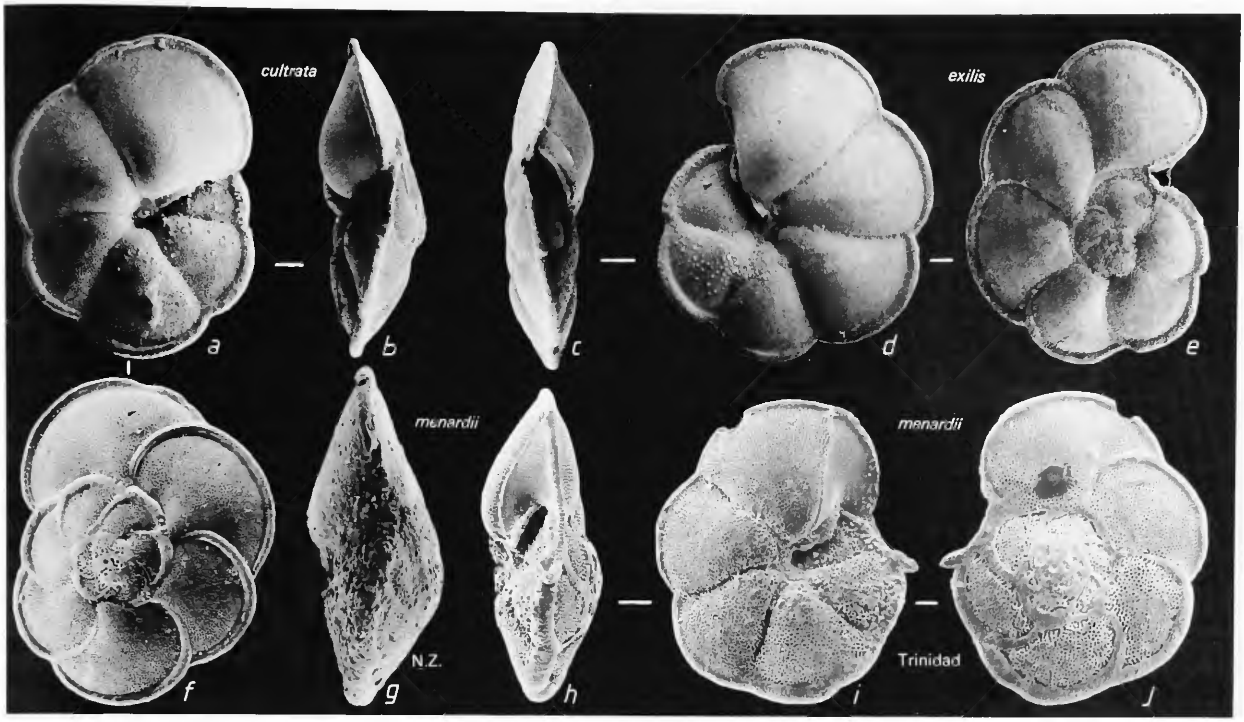


FIGURE 14.—*a,b,f, Globorotalia cultrata* (d'Orbigny), Atlantic Ocean 22°07'N, 81°08'W, 270 fathoms, Recent (× 60); *c–e, Globorotalia exilis* Blow, Folly Point, Jamaica, Pliocene (× 55); *g–j, Globorotalia menardii* (Parker, Jones, and Brady) (*g*, X18/f15, Hangaroa River, New Zealand, upper Miocene (× 110); *h–j*, cotype locality *Paragloborotalia mayeri* Zone, Trinidad, middle Miocene (× 70)).

more outer chambers were short-lived and became extinct before the end of the Pleistocene. Connections among these species and their roots are obscure, although Berggren and Amdurer (1973) postulated a phylogeny (Figure 15).

The historic development of the menardines was intricate and is reflected in the unsatisfactory state of their taxonomy. There are several major unresolved questions. Following Stainforth and others (1975), *Globorotalia menardii* refers to the middle to upper Miocene populations that developed from *G. praemenardii* (Figure 14*g–j*). Many post-Miocene tropical populations, which tend to be strongly compressed (Figure 14*b*), are placed in the modern *G. cultrata*, but the relationship of this taxon to its close Miocene precursor, and to other Pliocene menardines, is poorly known. Fleisher (1974:1026) found it impossible to consistently distinguish between *G. menardii* and *G. cultrata*, and suggested that they might be ontogenetic variants. A larger problem is the similarity between the *G. menardii–G. cultrata* group and *G. tumida*. These may represent end members of an almost interconnecting morphocline. Brady (1884:692) thought that *G. tumida* might be only a variety of *G. menardii*. Schmidt (1934:52) and Ericson and others (1961:263) considered them conspecific, while Thompson (1982:372) remarked that most Pacific specimens of *G. menardii* are intermediate with *G. tumida*. Brönnimann and Resig (1971:1276) proposed *G. tumida lata* for one such morphotype. Variants in which flexuose chambers are formed in late ontogeny have been assigned to both groups. (*G. menardii flexuosa* Srinivasan, Kennett and Bé; *G. tumida flexuosa* (Koch)). Rögl (1974:752) recorded *G. menardii, G. tumida*, and *G. cultrata* as a single group in a Timor Sea

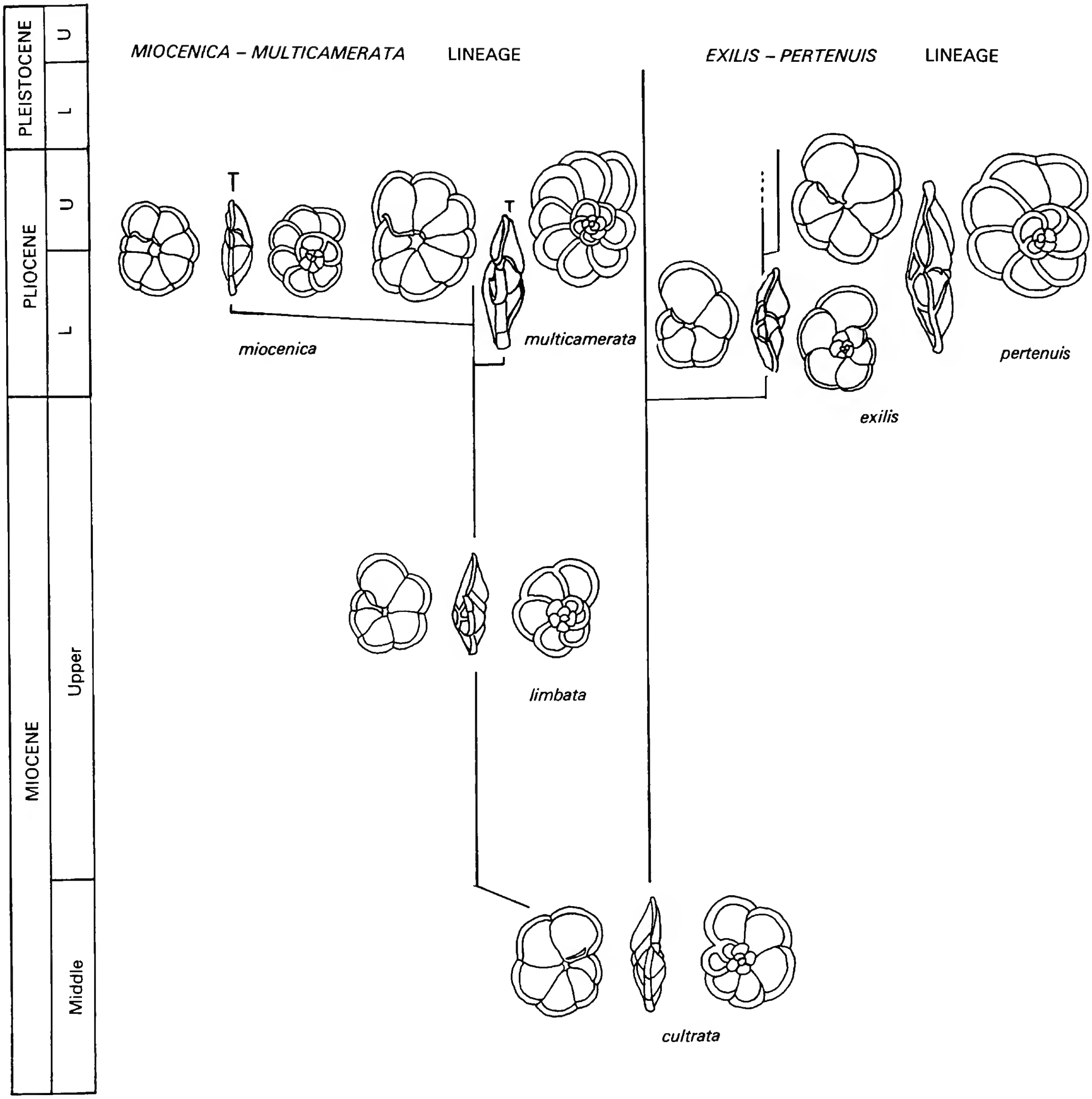


FIGURE 15.—Phylogeny of some Pliocene-Pleistocene menardine taxa redrawn from Berggren and Amdurer (1973). (Miocene populations of *Globorotalia cultrata* are probably referable to *G. menardii*.)

sequence, noting that they showed no significant difference in occurrence. In census work, specimens of *G. cultrata* or *G. menardii* are occasionally counted with *G. tumida* (Poore, 1981).

Nevertheless, despite these indications of intergradation, *Globorotalia tumida* has been shown by Banner and Blow (1965:1352) to have a separate ancestry from *G. menardii–G. cultrata* and to have appeared near the base of the Pliocene. Reports indicating their subsequent integradation require, initially, detailed study of population variation and, as Cosijn (1938:57) urged, an understanding of life histories in living material. Are there discontinuities? This problem, perhaps the most longstanding in globorotalid taxonomy, remains unresolved. Certainly, it is premature to place *G. tumida* and *G. menardii* in different subgenera (cf. Kennett and Srinivasan, 1983:120, 151).

The Scitulines

Among the remaining Miocene *Globorotalia* are the scitulines, a seemingly natural morphologic group of architecturally simple forms. Zachariasse (1975) included *G. scitula, G. subscitula, G. gigantea, G. ventriosa,* and *G. suterae* in the scitulines, but *G. juanai* and *G. cibaoensis* probably should also be added to this group. All show a close morphologic affinity to *G. miozea* or *G. conoidea* but are distinctive in that they have symmetrically crescentic, A-type chambers, generally without keels. They are reminiscent of early representatives of *G. praescitula.* In other respects too, such as axial compression, the scitulines are enigmatically primitive and they give the appearance of being a group of evolutionary "throwbacks." They are taxonomically difficult and have been interpreted in various ways (Perconig and others, 1980). Species limits and ranges are poorly known and the lines of descent are obscure. Despite their broad morphologic affinities, it is not by any means certain that the scitulines represent a phyletic group. Blow (1969), for example, treated such forms as *G. scitula, G. gigantea,* and *G. cibaoensis* as links along the line of descent of *G. miozea.* What is clear is that the oldest scituline, *G. gigantea* (middle Miocene) is architecturally more advanced than some later representatives (late Miocene), even though the later forms are more diverse. Some later Miocene scitulines have a somewhat coarsened wall surface that is suggestive of a relic, honeycombed texture. The relatively primitive appearance of this texture suggests that they could have developed independently of *G. gigantea,* through a later Miocene paragloborotalid. If this is the case, then the non-acute profiles of the late Miocene forms are the result of a repetition rather than a reversal of an evolutionary trend. A possible link with a late Miocene paragloborotalid is provided by a form such as *G. juanai,* but the stratigraphic record is insufficiently known to determine the actual course of scituline development or to determine if there is a discontinuity between *G. gigantea* and the later scitulines.

In light of the general obscurity of the scitulines, we review some of the important species. *Globorotalia scitula* (Figure 16*f–h, k–o*) is a modern form that Brady (1882:716) described from a dredge haul near the Faröe Islands. In modern sediments and in the water column *G. scitula* is seldom numerically abundant, but it is cosmopolitan. The species is characterized by symmetric, A-type chambers, with four almost equally sized chambers making up the outer whorl; there is no tendency towards radial extension of the shell. Examination of Recent *G. scitula* specimens in the Smithsonian USNM collections, identified by various workers, reveals an acute profile which, while variable, is never quite as acute as in *G. gigantea.* Also, no rim has been observed on the peripheral margins of the Recent specimens. The wall of the modern form is most often glossy and smooth with small, widely spaced, pores. However, some populations of *G. scitula* may have a coarsely porous surface (Saito and others, 1981:138).

In the Miocene sequence of Venezuela, Blow (1959:219–221) recognized two scitulines, identifying one as *Globorotalia scitula* and designating the other as *G. scitula gigantea,* a new taxon. At the time, he regarded *G. scitula* as ancestral to *G. gigantea* because it occurred lower in the section. Blow's figured specimen (1959, pl. 19: fig. 126) of *G. scitula* is from a level equivalent to Zone N11 and the holotype of *G. gigantea* from a level equivalent to Zone N12. Later, Blow (1969:355) reversed his view and regarded *G. gigantea* as ancestral to *G. scitula.* He gave the lower range of *G. gigantea* as Zone N6 and *G. scitula* as Zone N9. Impressed with the similarity

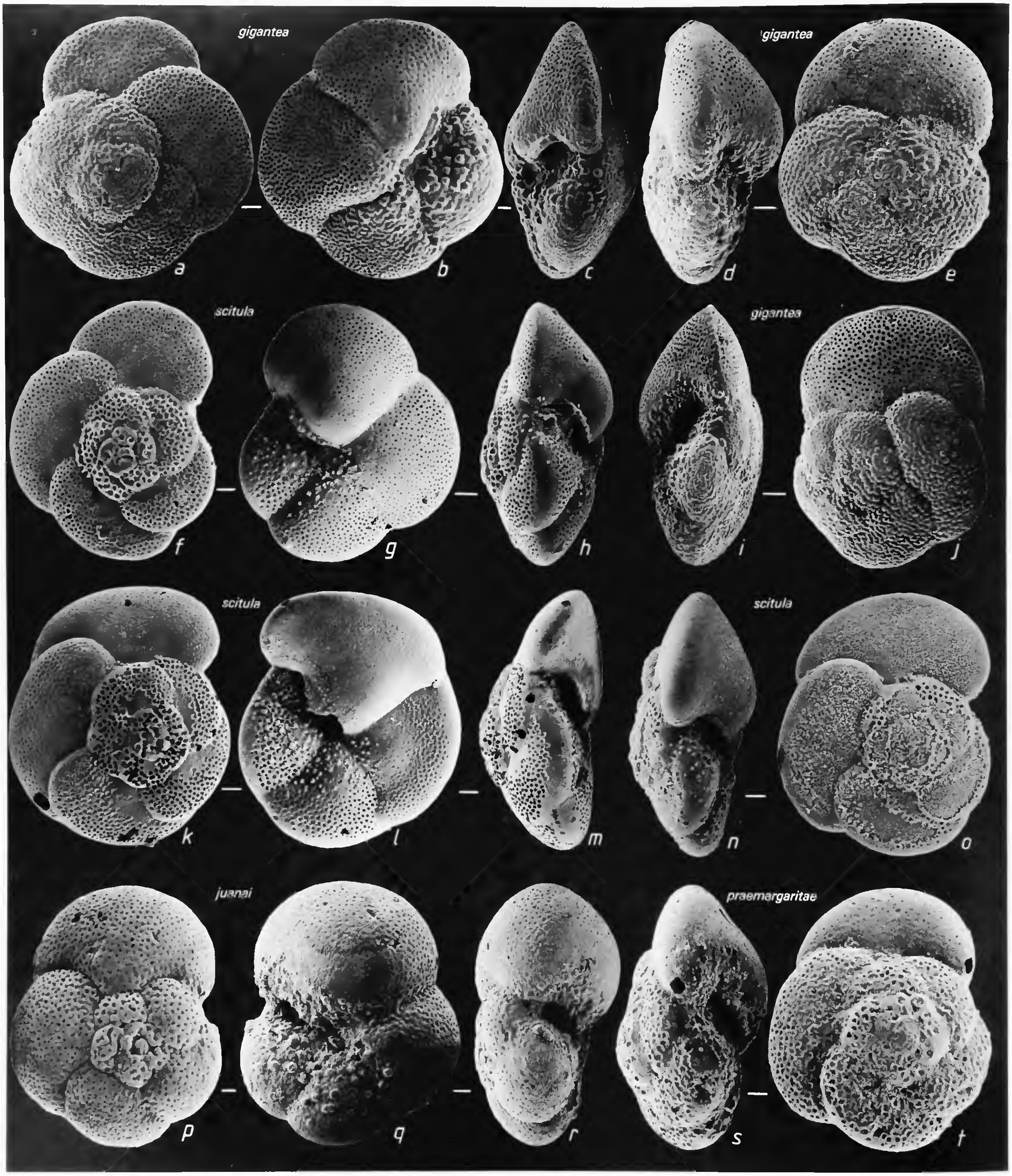


FIGURE 16.—*a–e,i,j*, *Globorotalia gigantea* Blow (*a–c*, Pozón, Venezuela, paratype (USNM 625716), middle Miocene (× 85); *d,e,i,j*, cotype locality *Paragloborotalia mayeri* Zone, Trinidad, middle Miocene (*d,e*, × 120; *i,j*, × 100)); *f–h,k–o*, *Globorotalia scitula* (Brady) (*f–h*, Guide Station 1, 32°08′N, 129°06′W, Pacific Ocean, 740 fathoms, Recent (× 110); *k–m*, DSDP Site 284, 1-1-100, Southwest Pacific, Quaternary (× 95); *n,o*, DSDP Site 284, 22-5-20, Southwest Pacific, upper Miocene (× 105)); *p–r*, *Globorotalia juanai* Bermúdez and Bolli, Well Cubagua-1, 2691–2703 ft (820.76–824.42 m), Venezuela, paratype (USNM 221849), middle Miocene (× 130); *s,t*, *Globorotalia praemargaritae* Catalano and Sprovieri, Section Rossi (Enna), Sicily, upper Miocene (× 135).

between *G. gigantea* and *G. miozea*, Blow made *G. gigantea* the connecting link between *G. praescitula* and *G. miozea*. Examination of the original material leaves little doubt that the form which Blow (1959: pl. 19: fig. 126) identified as *G. scitula* is the same as his *G. gigantea*. The holotype of *G. gigantea* is larger than the hypotypes of his *G. scitula*, but the unfigured paratypes are overlapping in size; there are no other distinguishing features. *Globorotalia gigantea* is also about the same size as modern *G. scitula*, a species with which it shows a very close morphologic affinity. It has the same symmetrical, A-type chambers with four almost equally sized chambers in the outer whorl and a quadrate test outline. While the wall of *G. gigantea* is never glossy, it is flat and smooth, fully comparable to the walls of advanced globorotalids. The only apparent feature distinguishing *G. gigantea* from modern *G. scitula* is its profile, which is often very acute, partially rimmed, and occasionally weakly keeled (Figure 16*i–j*). It is not surprising that Blow (1969:355) linked this species with *G. miozea*, because *G. gigantea* is as fully developed a globorotalid as the more advanced forms of *G. miozea*. However, the symmetric chambers and quadrate test of *G. gigantea* not only point to a specific difference but also suggest divergence from the *G. miozea* stock.

Evidence as to whether divergence may have occurred early or late remains equivocal. The symmetric, A-type chambers suggest a connection with the early representatives of *Globorotalia praescitula*, but the acute, rimmed profile and smooth wall point to a connection to more advanced forms (i.e., *G. archeomenardii* or *G. praemenardii*). Therefore, there seem to be several possibilities for the development of *G. gigantea*. A separation of stocks may have occurred at the time that the asymmetrical, B-type chamber was introduced in *G. praescitula*, with a *G. gigantea* lineage retaining the A-type chamber and following a course of development independent of the later *G. praescitula* and *G. miozea*. In this case, there must have been a very near parallel series in the development of *Globorotalia*. Considering the close parallel in development between *Fohsella* and *Globorotalia*, this possibility cannot be discounted. Another possibility is that *G. gigantea* bifurcated from a later *G. miozea* population through an evolutionary reversal that involved chamber shape only. A third alternative, that *G. gigantea* developed directly from a paragloborotalid ancestor, seems unlikely because of the advanced features displayed by *G. gigantea* and the lack of connecting links. The early record of *Globorotalia gigantea* is critical to an interpretation of its development. Blow (1969:354) gave the lower range of *G. gigantea* as Zone N6 but provided no documentation. Indeed, there is still no good evidence that this species appeared much before Zone N11, at least in the Caribbean region. Blow's (1959) figured specimens of *G. gigantea* (his pl. 16: fig. 127) and *G. scitula* (his pl. 19: fig. 126) both from Venezuela are from a level equivalent to Zone N11 or slightly higher. Bolli (1957) recorded a first occurrence of *G. gigantea* (as *G. scitula*) in Trinidad at a level equivalent to Zone N11. This is confirmed by our observations. The occurrence of *G. gigantea* in the Mediterranean recorded by Tjalsma (1971:63) and Zachariasse (1975:108) cannot be from horizons older than Zone N11. It is possible that specimens Blow (1969:354–356) identified as *G. gigantea* in the earlier horizons, down into Zone N7, actually belong to *G. archeomenardii*, but this would not account for the Zone N6 record of *G. gigantea*. If the early records (Blow, 1969:354) are correct, then *G. gigantea* probably did develop independently from an ancestral stock that retained a primitive type of chamber. If the early records are wrong, then *G. gigantea* probably developed from *G. miozea* through an evolutionary reversal in chamber shape.

In the Caribbean, *Globorotalia gigantea* is well represented from Zone N11 to Zone N13 or N14, but the upper limits of the species remain as obscure as its lower limits. While Blow (1969:354) placed the upper range of *G. gigantea* in Zone N15, there appears to be a dearth of reports of any scitulines from this stratigraphic interval. Tjalsma (1971:63, fig. 26) very questionably assigned *G. gigantea* to Zone N15 in the Mediterranean, but the form he figured

(Tjalsma, 1971, pl. 7: figs. 3–5) is not a typical scituline, as it has more than four chambers in the outer whorl and they increase rapidly in size. Typical scitulines next appear in Zone N16 and later horizons and seem to be particularly well represented in the Mediterranean. Whether real or an artifact of compendious taxonomic treatment of a stratigraphically unimportant group, there seems to be a discontinuity in the record between the early and later scitulines.

Some later scitulines appear architecturally and structurally primitive relative to the earlier *Globorotalia gigantea.* Of all the scitulines figured by Zachariasse (1975) from the Mediterranean late Miocene, none show any trace of a rim, while the profiles tend to be broad and even arched or vaulted. Also, the coarsely perforate surfaces are rather roughened in appearance, in contrast to the smooth, flat surface of *G. gigantea.* The form that Zachariasse (1975, pl. 13: figs. 1–3) identified as *G. gigantea* from the late Miocene Mediterranean, like Tjalsma's (1971, pl. 7: figs. 3–5) form, has more than four chambers in the outer whorl. However, the chambers are symmetrical and the resemblance to *G. gigantea* is clearly very close. Yet a rim is totally lacking, and the surface of the wall is rather coarse. The *G. scitula* figured by Zachariasse (1975, pl. 72: figs. 1–3) has a less acute profile. It compares very favorably with the modern, coarse-walled form of *G. scitula,* such as that described by Saito and others (1981:138). *Globorotalia subscitula* is virtually an identical form except that it has a glossy, largely nonporous wall. This form first occurs in the Mediterranean in the Pliocene, and it appears to be the same as that which most workers identify as *G. scitula* in modern sediments and from the water column.

Two other scitulines that occur in the later Miocene of the Mediterranean are *Globorotalia ventriosa* and *G. suterae* (Figure 17*e,j*). They closely resemble *G. scitula* with which they are found associated in Zone N16, but they are distinguished by their tendency towards a broad extension of the umibilical side and inclusion of five chambers in the outer whorl. Especially in *G. suterae,* where the ventral side is distinctly raised (Zachariasse, 1975; pl. 11: fig. 5b), this development is parallel to that in *G. conoidea.* However, unlike *G. conoidea, G. suterae* totally lacks a keel or rim. *In G. nicolae,* another upper Miocene Mediterranean form (Figure 17*c,d*), there is also marked radial inflation of chambers. The elevation of ventral surfaces in these taxa is reminiscent of the profiles in the earlier *G. zealandica* and the later *G. crassaformis,* testimony to the persistent development of this type of shell design. Relationships between *G. suterae, G. nicolae,* and *G. praemargaritae* were suggested by Wernli (1977, pl. 5). Several of these scitulines occur primarily at Mediterranean and adjacent North Atlantic sites, and their distribution elsewhere may be limited.

Possibly belonging to the scitulines is *Globorotalia cibaoensis,* but this species has been interpreted in various ways (Blow, 1969; Parker, 1973; Berggren and Haq, 1976; Perconig and others, 1980). Bermúdez (1949:285) described this species from late Miocene deposits of the Dominician Republic. It has reasonably symmetric chambers but, unlike the later scitulines, it has an occasional, partially formed rim (Cifelli and Belford, 1977:104) and a rather thickened, blunt profile.

The most primitive upper Miocene scituline is *Globorotalia juanai,* described by Bermúdez and Bolli (1969:171–172) from Venezuela. The spiral profile of chambers (Figure 5) is barely elongated and is close to the paragloborotalid shape. Axial compression of Venezuelan specimens is slight (Figure 16*r*) and little greater than on a primitive specimen of *G. praescitula* (Figure 6*p*). Some Southwest Pacific specimens (Scott, 1983, pl. 2: fig. 25) also have ridged, honeycomb-like surfaces on early formed chambers, as in *G. praescitula.* Chamber form, particularly, is more primitive than in contemporary *G. scitula* and a separate origin is postulated (Figure 2).

Globorotalia juanai, or similar upper Miocene scitulines (e.g., *G. suterae, G. praemargaritae*), may have played a significant role in the origin of several important groups that appear in the

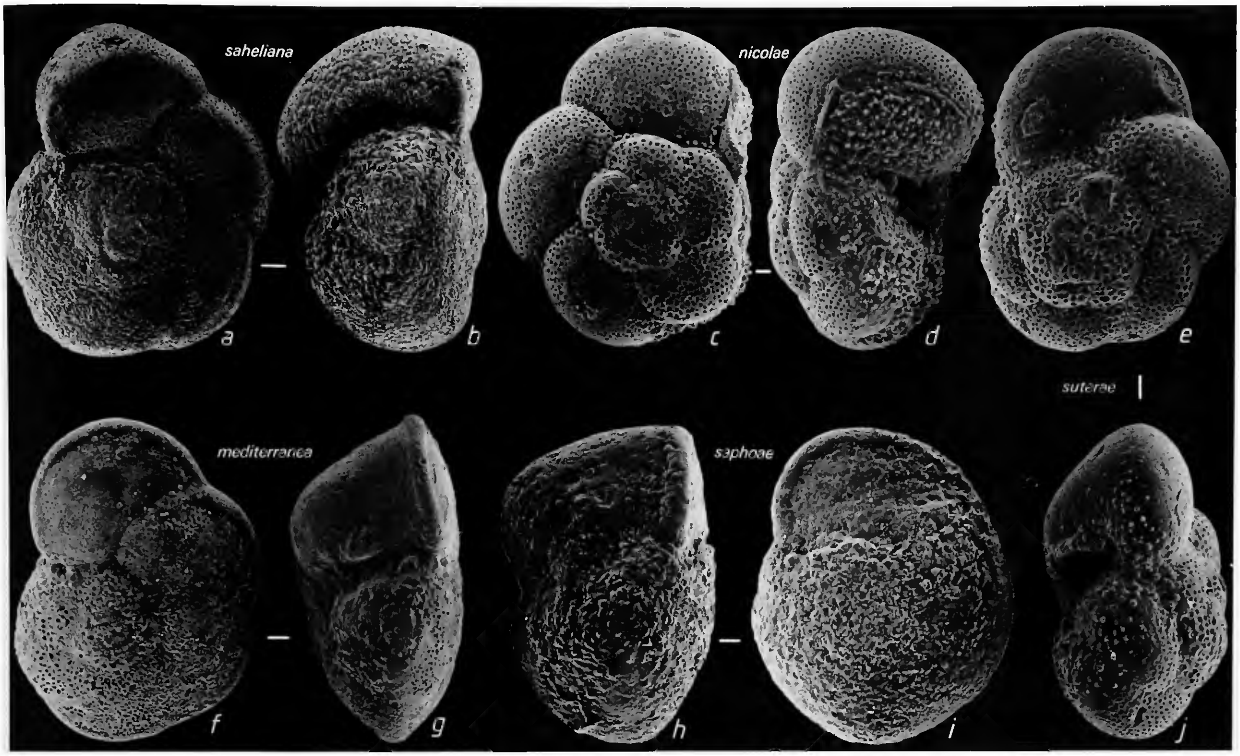


FIGURE 17.—*a,b, Globorotalia saheliana* Catalano and Sprovieri, Section Falconara, Sicily, upper Miocene (× 85); *c,d, Globorotalia nicolae* Catalano and Sprovieri, Section Monte S. Nicola, Sicily, upper Miocene (× 105); *e,j, Globorotalia suterae* Catalano and Sprovieri, Section Sutera, Sicily, upper Miocene (× 110); *f,g, Globorotalia mediterranea* Catalano and Sprovieri, Section Rossi, Sicily, upper Miocene (× 110); *h,i, Globorotalia saphoae* Bizon and Bizon, Strelia, Greece, upper Miocene (× 130).

Pliocene. The best documented connection is with the spiroconvex lineage leading to *G. hirsuta.* Several taxa that distinguish stages in the evolution of a keeled, spiroconical shell have been proposed. *Globorotalia praemargaritae* (Figure 16*s,t*) retains a ridged wall but chambers, spirally, are of the symmetrical A-type, elongated in the direction of coiling. There is only weak to moderate compression of the peripheral margin. The spiral surface of the shell is raised but matches the umbilical elevation of chambers so that shell shape remains biconvex at this stage. Chamber compression is more advanced in *G. martinezi,* and the periphery is subacute and tending to thicken (Perconig and others, 1980). This may correspond with rim formation in *G. miozea.* A very weak keel is developed on *G. andalusiana,* in which late-formed chambers form a high (radial direction) arch and the aperture is low, as in the succeeding *G. margaritae.* However, the umbilical surfaces of chambers remain raised, so that spiroconical form is still weak. The specimens identified here as *Globorotalia* aff. *margaritae* (Figure 12*m,o*) correspond with this evolutionary grade. In *G. margaritae* (Figure 12*i,j*) there is a distinct keel. Because the ventral surfaces of chambers are now depressed, the axial shape of the shell is more clearly spiroconical. Perconig and others (1980) considered that these transformations took place in the later Miocene (Zones N16–N17). On the evidence of chamber shape, we suggest that a form like *G. praemargaritae* offers a more direct ancestral connection than *G. juanai.* Several grades in the sequence may occur together as intrapopulation variants. Cita (1973:1352) proposed *G. margaritae primitiva* for small forms lacking the keel, which occurs in *G. margaritae* sensu stricto. This taxon corresponds in evolutionary grade with *G. martinezi* or *G. andalusiana*. Wernli (1977, pl. 6) illustrated the intergradation.

There are no further advances in the subsequent history of this lineage. Umbilical surfaces of chambers are less depressed in *Globorotalia praehirsuta*, and in some specimens of *G. hirsuta*, axial shape is quite similar to ancestors of *G. margaritae* (compare Figure 12*g* with Figure 12*o*). These later taxa retain the narrow, low keel of *G. margaritae* but have a larger umbilicus, signifying greater radial translation of the spiral side during ontogeny. Increase in shell size was reported by Parker (1967:179).

Globorotalia tumida Lineage

Banner and Blow (1965) regarded *Globorotalia merotumida*, *G. plesiotumida*, and *G. tumida* as a gradually evolving lineage and used these taxa as the principal criteria in recognizing the upper Miocene Zones N16–N18, particularly in tropical sequences. That they represent character transformations occurring during the late Miocene seems fairly clear but whether the transformations developed independently of the *G. menardii–G. cultrata* group remains uncertain (Bolli and Krasheninnikov, 1977:448).

Banner and Blow (1965) proposed that the lineage developed from *Globorotalia lenguaensis* (Figure 18*a,e*), a species that Bolli (1957) described from the *G. mayeri* and *G. menardii* zones (N13–N15) of Trinidad. *Globorotalia lenguaensis*

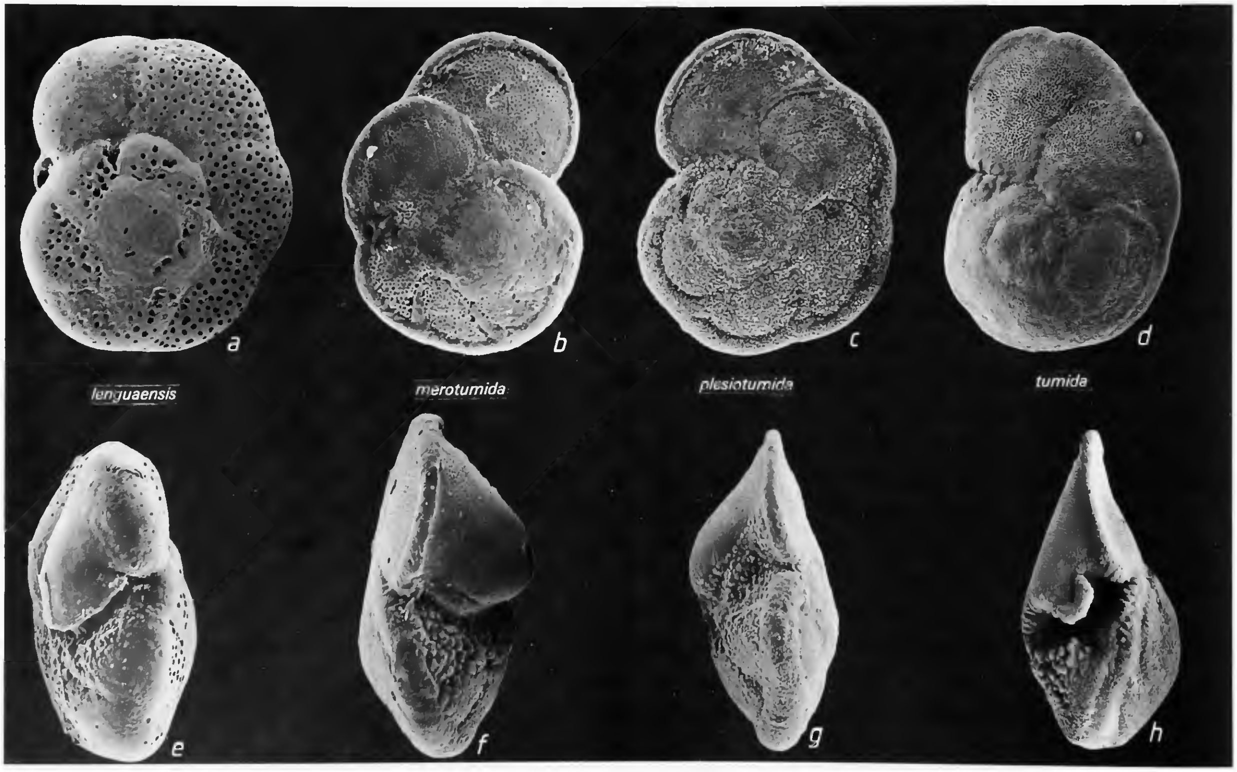


FIGURE 18.—*a,e*, *Globorotalia lenguaensis* Bolli, locality RM19507 (R. Muhlemann), Pozón Formation, Venezuela, middle Miocene (× 200); *b,f*, *Globorotalia merotumida* Banner and Blow, Well Cubagua-2, core 2700 ft (823.50 m), Venezuela, paratype (USNM 641928), upper Miocene (× 85); *c,g*, *Globorotalia pleisotumida* Banner and Blow, Well Cubagua-2, core 1400 ft (427.00 m), Venezuela, paratype (USNM 641929), upper Miocene (× 75); *d,h*, *Globorotalia tumida* (Brady), Atlantic Ocean, 22°07′N, 81°08′W, 270 fathoms, Recent (*d*, × 45; *h*, × 40).

is a small, circular form with a smooth wall, large pores, and a moderately compressed margin. Chambers are elongate in the direction of coiling and distinctly of the B-type throughout. This species is apparently rare and little is known about its variation spectrum. The figure of the holotype (Bolli, 1957, pl. 29: fig. 5) shows a slight keel or, more likely, a rim that bounds the entire peripheral margin. Blow (1969, pl. 34: figs. 10, 11) figured a near topotype that has only a partially formed rim around the periphery. *Globorotalia lenguaensis*, therefore, is of about the same evolutionary grade as *G. miozea* in terms of keel development. The origin of *G. lenguaensis* is cryptic.

Blow (1969:402) introduced *Globorotalia paralenguaensis* as a connection between *G. lenguaensis* and *G. merotumida*. An advance shown by *G. paralenguaensis* is the flaring, radially extended quasi-C-type chambers formed in later ontogeny (Blow, 1969, pl. 46: figs. 2,3). In other respects, however, this species shows little change. The periphery is little more compressed than in *G. lenguaensis* (Kennett and Srinivasan, 1983, pls. 36, 37). The carina shown by Blow (1969, pl. 46: figs. 4–6) is closer to a rim than a keel.

The shell of *Globorotalia merotumida* (Figure 18*b*,*f*) is much more compressed axially than either *G. lenguaensis* or *G. paralenguaensis*. Chambers are distinctly acute with all in the outer whorl bearing a strong keel. The keel is initiated at least by mid-ontogeny or, according to Banner and Blow (1965), extends throughout ontogeny. This indicates an advanced state of development since, by analogy with other groups, keels first develop in the last several chambers and then extend into the earlier ones. Forms with intermediate keel development, such as *G. praemenardii*, that provide a link between *G. miozea* and *G. menardii*, or *Fohsella praefohsi* that links *F. peripheroacuta* and *F. fohsi*, have not yet been found to connect *G. paralenguaensis* with *G. merotumida*. If *G. merotumida* did descend from *G. paralenguaensis* it represents a unique example of rapid, in toto, acquisition of a keel.

The principal architectural trend observed by Banner and Blow (1965) in the *Globorotalia merotumida*–*G. plesiotumida*–*G. tumida* series involves the spiral shape of chambers formed in later ontogeny. The C-type chamber is already well developed in *G. merotumida*, but this is followed by a progressive radial chamber extension in *G. plesiotumida* (Figure 18*c*,*g*) and *G. tumida* (Figure 18*d*,*h*), resulting in rapid increase of shell diameter and a characteristically flared appearance to the outer whorl. In *G. tumida*, late-formed chambers are extended to such an extent that they become virtually of the same design as the T-type chamber in *Fohsella*. Indeed, the resemblance between *G. tumida* and *F. fohsi* in spiral orientation is sometimes quite close (compare Figure 18*d* with Figure 8*a*). Note that Pliocene multichambered menardine forms, such as *G. multicamerata* and *G. pertenuis*, also are often characterized by radially extended chambers that are virtually the same as the T-type. The allometric change in chamber shape during ontogeny is considerable. As late as the middle whorl, chambers in *G. tumida* may retain a B-type design and then change to a normal C-type and finally to a radially elongate T-type. Trends in size increase, and perhaps also in strength of the keel noted by Banner and Blow (1965), are related to the late ontogenetic alteration in chamber shape.

The axial shape of the shell shows no progressive trend. *Globorotalia merotumida* has a thick, rather ventrally elevated profile. But it is succeeded by *G. plesiotumida*, which has an axial profile (Berggren and Poore, 1974, fig. 1) as compressed as that in *G. menardii*. In *G. tumida* there is a wide, biconvex profile that results, spirally, from the relatively high spiral of the inner whorls and, ventrally, by progressive elevation of chamber walls towards the umbilicus.

Biostratigraphically, the first appearances of *Globorotalia merotumida*, *G. plesiotumida*, and *G. tumida*, as originally proposed by Banner and Blow (1965), remain the primary criteria for the recognition of the upper Miocene zones in tropical sequences (Berggren and Poore, 1974; Vincent, 1977; Srinivasan and Kennett, 1981a). While this points to the reality of the character transformations, difficulties have been reported in distinguishing the taxa (Parker, 1967:180, 182; Fleischer, 1974:1027; Vincent, 1977:536). Jenkins and Orr (1972:1100) considered that *G. merotumida* might be a juvenile of *G. plesiotumida.* All three taxa are fully comparable to the *Globorotalia menardii–G. cultrata* group with which they coexisted in tropical habitats during the Miocene. However, a progressive convergence between the two groups during the later Miocene is not demonstrable. Axial shape fluctuated in development and, in this character, *G. plesiotumida* resembles *G. menardii* more closely than its successor, *G. tumida.*

The one distinctive character trend involves the radial extension of the final few chambers which became more pronounced between Zones N16–N18. If these flaring chambers are neglected, the resemblance with *Globorotalia menardii* is close, particularly when allowance is made for variation. Therefore, while there is good evidence for a chronoclinal development in the form of the terminal chambers, this change may have possibly occurred within populations closely related to *G. menardii.*

Later Developments

Whereas the dominant feature in the Miocene history of the globorotalid radiation was axial compression of the shell, substantially greater architectural diversity occurred in the later phase of the radiation. The menardine design continued to dominate in the tropical waters but other types of profiles, for which there were already precedents in the Miocene, were reintroduced and proved successful, especially in the subtropical, gyral waters. In the later part of the radiation we find a variety of profiles (Figure 7).

Ventroconical or Truncatuline: In the Miocene, this type of profile was introduced as variants among the later populations of *Globorotalia conoidea.* It was exploited afterwards to a much greater extent by *G. truncatulinoides.*

Spiroconical: *Globorotalia panda* utilized this profile successfully during the middle to late Miocene but never achieved a wide distribution. Its modern counterpart, *G. hirsuta,* is a more conspicuous element among subtropical assemblages.

Inflated Discoidal: *Globorotalia zealandica* introduced this profile in the early Miocene but became extinct. A modern version of the design is found in *G. crassaformis.*

Globose Profile: Reminiscent of the early paragloborotalids, this type of profile is now found in the quasiglobigerine *Globorotalia inflata,* a highly successful form.

These design changes may be related to climatic changes initiated in the late Miocene, which possibly led to better definition of extensive gyral watermasses. Subtropical gyral waters have become the domain of the nonmenardines. There has been encroachment into temperate regions, but the tropical waters have been the preserve of the menardines. The subpolar to polar waters, with important exceptions, have never been successfully colonized by globorotalids. We now survey several post-Miocene groups of architectural importance.

Globorotalia inflata Lineage

In the perspective of Neogene globorotalid evolution, in which keel development and chamber compression are major trends pursued by the important lineages, the Southwest Pacific history of the *Globorotalia inflata* lineage is remarkable. Reversionary trends have resulted in loss of the keel and inflation of chambers. These changes were initiated in uppermost Miocene populations of *G. conoidea* (close to the Epoch 5: Gilbert paleomagnetic boundary). Important features of *G. conoidea* shells at this time were the common occurrence of highly conical individuals (Figure 13*h*) and a strong preference for a 4-chambered arrangement in the outer whorl. The conical forms are commonly identified as *G. conomiozea,* but they are completely transitional to *G. conoidea* and are regarded as variants of the latter. The first evidence of modification is the loss of the keel on late-formed chambers of a few small specimens and its reduction in amplitude and

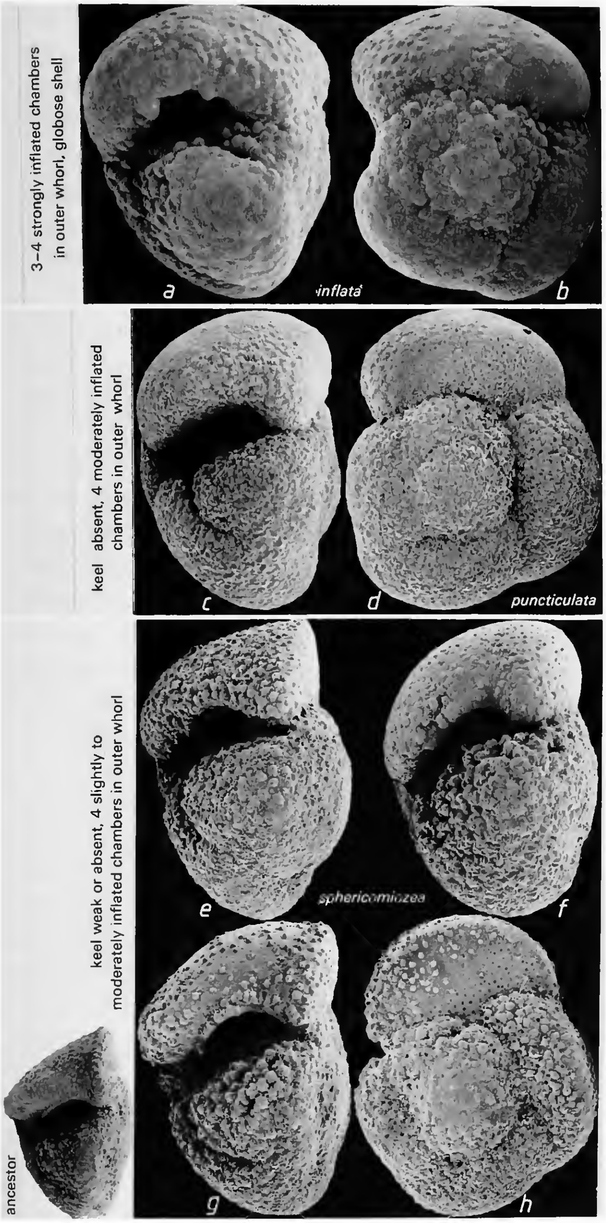


FIGURE 19.—*a,b, Globorotalia inflata* (d'Orbigny), DSDP Site 284, 9-1-100, Southwest Pacific, Pliocene (× 85); *c,d, Globorotalia puncticulata puncticulata* (Deshayes), DSDP Site 284, 11-2-20, Southwest Pacific, Pliocene (× 85); *e–h, Globorotalia puncticulata sphericomiozea* Walters (*e*, 15-6-20, × 95; *f*, 15-6-20, × 100; *g,h*, 14-6-20, × 85), DSDP Site 284, Southwest Pacific, Pliocene. "*ancestor*" *Globorotalia conoidea* Walters, DSDP Site 284, 16-3-20, Southwest Pacific, upper Miocene (× 45).

continuity in some others. The relative frequency of such individuals (Figure 39*b*) increases rapidly (Malmgren and Kennett, 1981; Scott, 1982). In the later stage of the trend, the keel is absent in most specimens and is vestigial in a few (where it appears in incident light as a dense zone around the periphery, perhaps analogous to the rim in a primitive *G. miozea*). Regressive changes in the keel, leading to its disappearance, are accompanied by decrease in the rate of curvature at the chamber periphery. The abrupt, angular junction between ventral and spiral surfaces in keeled specimens becomes rounded and there is also slight radial inflation of the ventral wall at the periphery. The spiral outline of chambers becomes symmetrically subquadrate rather than asymmetric as in *G. conoidea*. Populations in which these transformations occur are referred to *G. puncticulata sphericomiozea* (Figure 19*e–h*). They are polymorphic in terms of keel development. On a morphotype basis, totally unkeeled specimens could be identified as *G. puncticulata* sensu stricto (e.g., Figure 19*f*). However, continuity of variation in keel development and chamber shape suggest that a single taxon is represented. *Globorotalia puncticulata puncticulata* (Figure 19*c–d*) has been restricted to subsequent populations in which the keel is completely absent (Scott, 1980a).

The later history of the lineage in the Southwest Pacific is less dramatic. Further radial inflation of chambers occurred in *Globorotalia puncticulata puncticulata* and the number packed into the outer whorl declined to about 3.5 (Figure 39*a*). Shells with strongly inflated chambers (3–3.5 in the outer whorl) and resembling the modern form of *G. inflata*, appear as outliers in mid-Pliocene populations of *G. puncticulata puncticulata* and become dominant in the upper Pliocene (Figure 19*a,b*). There were no subsequent major innovations in design, and the morphotype with three chambers in the outer whorl represents the lower limit in chamber packing achieved anywhere in the radiation. The width of the morphologic spectrum developed in the radiation is indicated by a comparison of Figure 19*b* with

Figure 14*e* (*G. exilis*) or with other taxa (e.g., *G. multicamerata*, Lamb and Beard, 1972; pl. 12: fig. 5) in which chamber packing was raised to about 10. While outer chambers in *G. inflata* are characteristically inflated, giving a globose axial profile to the shell, this lessens in some populations, giving the shell a quasiventroconical axial profile. Theyer (1973) formally recognized such forms from the Southwest Pacific Pleistocene as *G. inflata triangula*. Comparable variants have also been recorded from Pleistocene horizons in the Gulf of Mexico (Lamb and Beard, 1972, pl. 27). The tendency for chamber envelopes to reduce their radial globosity increases the resemblance of axial profiles with those of the early representatives in the lineage. This resemblance can be seen by comparing the figures of *G. inflata triangula* given by Theyer (1973, pl. 1, fig. 6) and Lamb and Beard (1972, pl. 27: fig. 2) with Figure 19*g* of *G. puncticulata sphericomiozea*. However, while profiles became somewhat angular, reinitiation of a keel apparently has not occurred.

Records of the lineage from other regions are at variance with that from the Southwest Pacific. From a study of South Atlantic material (Rio Grande Rise, 30°S) Berggren (1977:306) concluded that *Globorotalia puncticulata* descended from a scituline form that he identified as *G. cibaoensis* and, in turn, evolved into *G. crassaformis*. The populations referred to *G. puncticulata* by Berggren (1977, pl. 4: figs. 4–16) have low, slit-like apertures, which are distinct from those in Southwest Pacific populations. Scott (1983) considered that they represent early stages in the evolution of *G. crassaformis* and were not connected with the *G. inflata* lineage.

Typical populations of *Globorotalia puncticulata puncticulata* occur in Mediterranean Pliocene sections but Gradstein (1974:94) held that they did not pass upward into *G. inflata*. He considered that the latter descended from *G. bononiensis*, a globose form with a particularly large, open aperture and less embracing chambers than *G. puncticulata*. However, Spaak (1981:213, 1983:39) interpreted populations of *G. bononiensis* as variants of *G. puncticulata* and a regional component of the *G. inflata* lineage. The origin of *G. puncticulata* does not seem to be recorded in Mediterranean sequences but the planktonic record there is interrupted by events of the Messinian salinity crisis.

In the Northwest Pacific, Maiya and others (1976:400) discussed an evolutionary lineage in which *Globorotalia inflata* descended from *G. orientalis* via *G. inflata praeinflata*. *Globorotalia orientalis* has four inflated chambers in the outer whorl. Spirally, chambers show greater radial inflation and less extension in the coiling direction than do those of the Southwest Pacific *G. puncticulata*. The aperture is relatively low arched. Maiya and others (1976:400) considered that chambers in the outer whorl increased in size more rapidly in *G. inflata praeinflata*, but this is an expression of the change in chamber packing that occurs between *G. puncticulata* and *G. inflata*. Thus, the Northwest Pacific populations are distinctive in some characters, although the gross architectural trends are similar to those in the Southwest Pacific.

Future work on synonymies and variation fields is likely to establish that *Globorotalia inflata* is preceded by widespread, but variable, populations of *G. puncticulata* in both hemispheres. More open, however, is the question of the distribution of the earliest populations of the latter (*G. puncticulata sphericomiozea*). Several workers (Poore and Berggren, 1974; Ujiié and Hariu, 1975; Oda, 1977; Keller, 1978;) have figured *G. puncticulata sphericomiozea* from the North Atlantic and North Pacific, but none have recorded the polymorphic populations that occur in the Southwest Pacific during keel regression. These are distinctive as they include specimens in which the keel is in various relic stages. Their apparent absence from the Northern Hemisphere may be related to the late Miocene variation in *G. conoidea*. In the Mediterranean and North Atlantic regions, at least, the 4-chambered form found in the south and from which G. *puncticulata sphericomiozea* seems to diverge never became dominant.

In review, the fullest record of the origin of the *Globorotalia inflata* lineage is found in Southern Hemisphere midlatitudes, the region in which modern *G. inflata* is now most abundant and widely distributed. We suggest that it originated in this region as branching populations from an advanced, keeled globorotalid. The primary architectural trend was the development of a globose shell. It was achieved by redesign of axial and spiral profiles of chambers and alteration in chamber packing and probably in coiling parameters. Although there was regression in keel development and loss of chamber compression, the resultant shell is distinct from those of the lower Miocene precursors of the keeled globorotalids. Chamber shape, spirally, retained the elongation of the *miozea* plexus. Axially, the ventrally vaulted chambers of the immediate ancestor of *G. puncticulata* were inflated to produce globose form. The extent of the evolutionary reversal in this lineage can be appreciated when it is recalled that d'Orbigny (1826:277) originally included *Globorotalia inflata* in *Globigerina*, a generic designation commonly followed until the last two decades.

Malmgrem and Kennett (1981) considered that the lineage evolved by gradual phyletic transformation. They mapped several long-term trends (reduction in number of chambers in the outer whorl, rounding of chamber periphery) that are consistent with this interpretation. But gradual phyletic transformation of *Globorotalia conoidea* into *G. puncticulata* is inconsistent with the continued presence in Southwest Pacific Pliocene strata of keeled populations (*G. mons*, *G. pliozea*) that retain the major characters of *G. conoidea*. Their occurrence indicates that *G. puncticulata* branched from the keeled stock. Keel regression was relatively rapid in early populations of *G. puncticulata* and probably identifies the period of divergence. Similarly, while *G. inflata* seems to arise by progressive transformation of *G. puncticulata* populations, there is wide variation in the latter and divergences may have occurred. The status of *G. bononiensis* and *G. praeoscitans*, found in the Northern Hemisphere, is relevant. In the Southwest Pacific, populations closely resembling *G. puncticulata* were recognized as a subspecies (*puncticuloides*) by Hornibrook (1981a:274) in the upper Pliocene-Pleistocene, contemporaneous with *G. inflata*. Their distribution also suggests that Malmgren and Kennett's (1981:236) model is too simple and that *G. inflata* possibly branched from *G. puncticulata*.

Globorotalia crassaformis Plexus

Since its origin near the base of the Pliocene, *Globorotalia crassaformis* has been a relatively minor component of most temperate to tropical assemblages and has never achieved the dominance of its contemporary, *G. inflata*, of grossly similar size and shell form. However, *G. crassaformis* and the plexus of taxa that are either its close relatives or descendants are significant in the history of the Neogene radiation both for their re-enactment of some of the principal Miocene trends and for their own peculiar course of architectural development. Whereas the lower Miocene globorotalid pioneers developed from the paragloborotalids by major redesigns, *G. crassaformis* possibly arose from a nonspecialized scituline globorotalid. Basic transformations were obviated and advanced characters (e.g., wall surface) were present at the outset. However, in contrast to the main course of early *Globorotalia* and *Fohsella* development, the main trend in the *G. crassaformis* plexus was not towards axial chamber compression but towards ventral extension or inflation. Some weakly discoidal variants arose in *G. crassula*, but this design was never fully adopted by the plexus. Minor ventral extension of chambers was initiated early in globorotalid evolution by *G. zealandica*, but that lineage occupied a minor position in the Miocene history of the radiation. In the Pliocene, the design was much more successful and culminated in *G. truncatulinoides*, the quintessential ventroconical form. There is close similarity here with the conical forms of *G. conoidea* and its Pliocene descendent, *G. mons*. Equally, there is an interesting difference. There was a long history of fully keeled shells in the plexus containing *G. conoidea* before ventroconical form developed. In the lineage leading to *G. truncatulinoides*, ventral extension, chamber compression, and keel development occurred almost concurrently.

We review some major aspects of the plexus: the origin of *G. crassaformis*, its relation with the *G. inflata* lineage, variation in keel development, features of *G. crassula*, and the history of the *G. truncatulinoides* lineage.

ORIGIN

The central taxon in the plexus, *Globorotalia crassaformis* (Figure 20*a,b,i,j*) appears early in Pliocene strata in midlatitude sequences, where the event provides a useful biostratigraphic datum in both hemispheres (Vincent, 1977; Keller, 1978, 1979a). These early populations are characterized by the smooth wall (often pustuled) of advanced globorotalids. Chambers have a quadrate spiral outline (four chambers in outer whorl) and a low slit-like aperture. The axial profile of outer chambers is moderately extended ventrally and is gently convex below the periphery. Generally, there is no keel. The axial shape of the shell is discoidal to weakly planoconvex.

Currently, there is little consensus on the origin of *Globorotalia crassaformis*, and there has been some nomenclatural confusion (e.g., Kennett, 1966). Cifelli (1976b) reviewed the history of usage. Commonly, *G. crassaformis* appears abruptly and gives no indication of its origin (Parker, 1967:176). A well-authenticated evolutionary sequence has yet to be documented, but there are several hypotheses (Figure 21). From a study of Italian populations, Colalongo and Sartoni (1967) suggested that *G. aemiliana* was the ancestor. This species is characterized by low crescen-

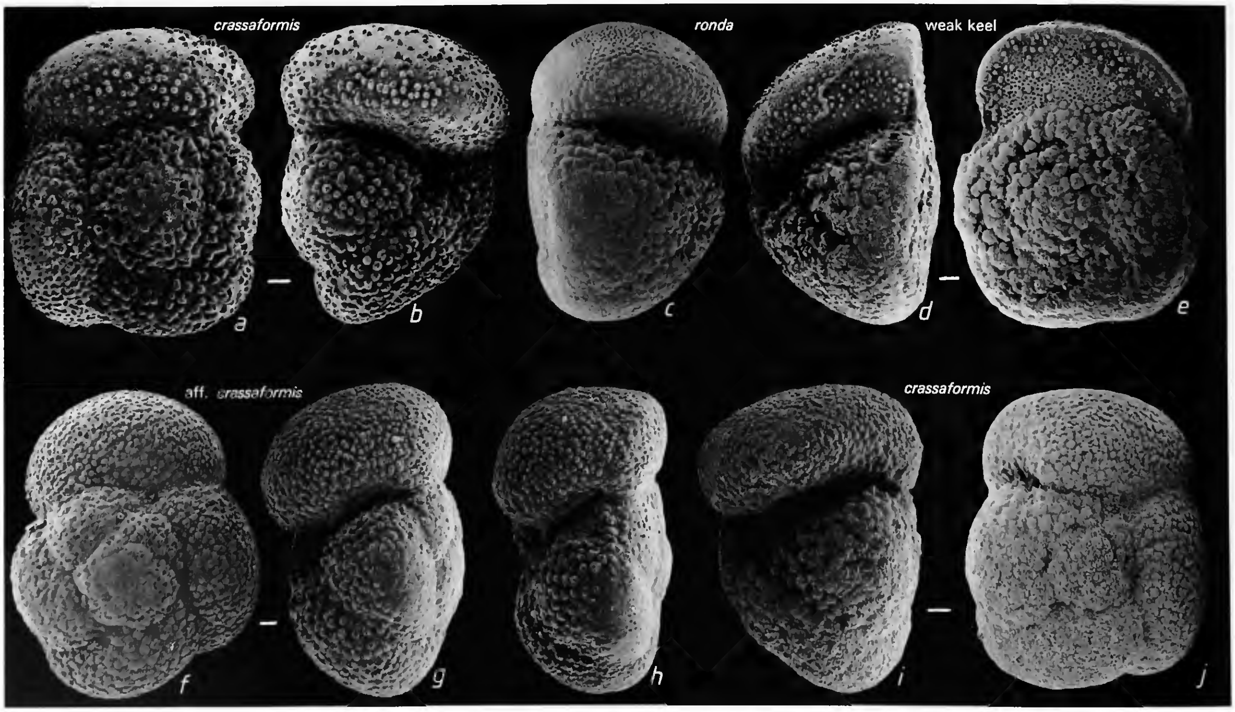


FIGURE 20.—*a–b,d–e,i–j, Globorotalia crassaformis* (Galloway and Wissler) (*a–b*, DSDP Site 284, 10-6-40, Southwest Pacific, Pliocene, (× 110); *d–e*, DSDP Site 284, 5-4-20, Southwest Pacific, Pleistocene (× 65); *i–j*, Chain Station, 115-6-67, 306 cm, South Atlantic, Pliocene (× 90)); *c, Globorotalia ronda* Blow, DSDP Site 200 1-cc, North Pacific, Pleistocene (× 70); *f–h, Globorotalia* aff. *crassaformis* (Galloway and Wissler), Chain Station, 115-6-67, 404 cm, South Atlantic, Pliocene (*f,g*, × 95; *h*, × 100).

tic to subquadrate chambers (spirally) and depressed to weakly elevated ventral surfaces. Lamb and Beard (1972:52, pl. 2) included *G. crassacrotonensis* as an intermediate, with greater ventral elevation of chambers. However, Gradstein (1974:91), from a biometric analysis of a wider range of Mediterranean populations, did not detect a consistent trend towards increased ventral elevation, and implied that the depressed primitive forms of the previous authors were intrapopulation variants. He considered that *G. crassaformis* appeared in Mediterranean sequences in the lower Pliocene, as in other oceans, whereas Colalongo and Sartoni (1967, table 1) and Lamb and Beard (1972, pl. 2) proposed that it evolved later in the Pliocene. Zachariasse (1975:112) noted that weakly elevated forms included in Colalongo and Sartoni's bioseries were common in the upper Pliocene of Crete and were preceded by typical *G. crassaformis*. Such data seem to invalidate the proposed bioseries. Indeed, these forms may belong to *G. crassula*.

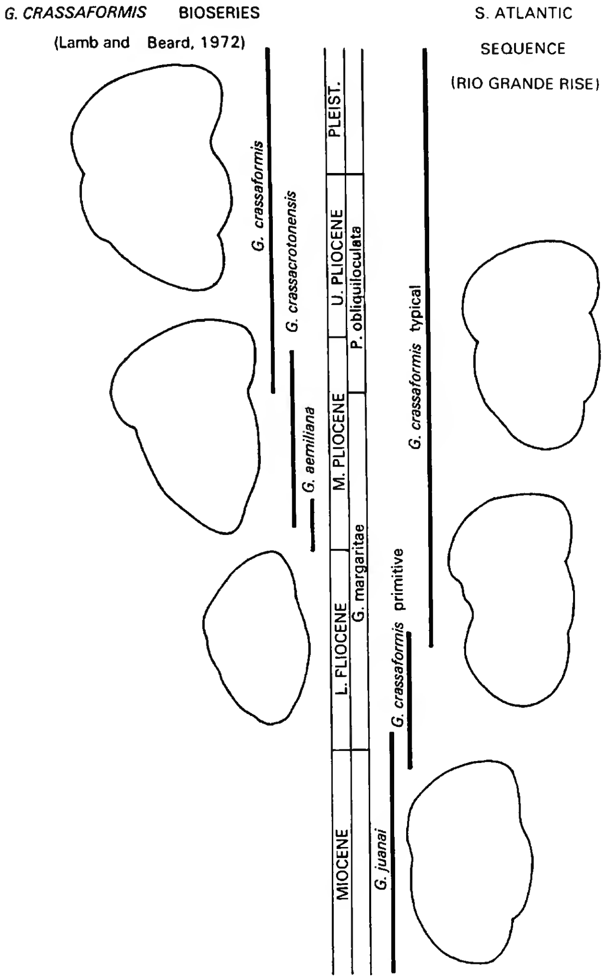


FIGURE 21.—*Left*, Origin of *Globorotalia crassaformis* from *G. aemiliana* in middle-upper Pliocene (after Lamb and Beard, 1972). *Right*, Origin of *G. crassaformis* from the scituline *G. juanai*, suggested by a South Atlantic sequence (Rio Grande Rise, Chain Station 115-6-67, Scott, 1983). Correlation of the South Atlantic sequence with Lamb and Beard (1972) zones is approximate. As yet, neither of the hypothesized lineages has been closely studied. The example shows that, even with a high resolution stratigraphic record of population histories, conflicts arise in phyletic interpretation.

Upper Miocene faunas contain small scituline forms with low apertures, crescentic chamber outlines (spiral side), and depressed ventral profiles that have been variously identified as *Globorotalia cibaoensis* (by Kennett and Vella, 1975, pl. 5: figs. 4–8; Berggren, 1977, pl. 4: figs. 1–3), *G. subscitula* (by Blow, 1969, pl. 3: figs. 1–3; Wernli, 1980, pl. 3: figs. 6,7) and *G. juanai* (by Stainforth and others, 1975, figs. 173, 174; Perconig and others, 1980, pl. 1: figs. 7, 8; Scott, 1983, pl. 2: figs. 21–25). Blow (1969, postscript) first suggested that *G. crassformis* may have descended from this group. Kaneps (1975) and Scott (1983) have concurred. Upper Miocene populations of *G. juanai* from Rio Grande Rise, South Atlantic, have the pustulose surface of *G. crassaformis* and a low aperture bordered by a prominent lip. They differ in that the axial outline of chambers is less elevated ventrally, the umbilicus is considerably wider, and spiral chamber shape is crescentic rather than subquadrate (Scott, 1983, pl. 2: figs. 21,22). Subsequent populations include individuals with axial chamber profiles somewhat more elevated ventrally and rather similar to those of *G. crassaformis*, although still retaining a relatively wide umbilicus (Figure 20*f–h*; Berggren, 1977, pl. 4: fig. 3,7,9). Such populations are succeeded by typical *G. crassaformis* in the lower Pliocene (Figure 20*i,j*).

With regard to the question of ancestry, the hypothesis of Blow (1969) reasonably fits the stratigraphic record of *Globorotalia crassaformis.*

If correct, it points to the diversity of architecture that arose from the later Miocene scitulines. One branch developed axially compressed, spiroconical shells leading to *G. hirsuta*; but in the *G. crassaformis* branch ventral elevation of chambers was the primary design feature.

RELATION TO *GLOBOROTALIA INFLATA* LINEAGE

Broad convergence in gross shell form between *Globorotalia crassaformis* and *G. inflata* lineage has been widely recognized and variously interpreted. Although Cifelli (1965, pl. 4: figs. 1–3) figured four-chambered variants of *G. inflata* from the western Atlantic that resemble *G. crassaformis*, and noted (1965:18) that end members were difficult to distinguish, it is significant that Pliocene populations commonly show closest resemblance to each other. Whereas *G. inflata* usually has 3–3.5 chambers in the outer whorl, the Pliocene *G. puncticulata* has four subquadrate chambers, which produce a spiral shell profile very similar to that of *G. crassaformis* (compare Figure 19*d* with Figure 20*j*). Axial outlines are also similar (Scott, 1980a). Gradstein (1974) biometrically characterized large Mediterranean Pliocene suites and established that variation in most chamber and shell dimensions overlapped. Among some samples there were real differences in relative height of the spire and in elongation of the last-formed chamber relative to shell diameter. While aperture shape is predominantly slit-like in *G. crassaformis* and arched in *G. puncticulata*, the variation fields marginally intersect.

Barbieri (1971), noting the presence of intermediates between typical *Globorotalia puncticulata* and *G. crassaformis*, suggested that the taxa were end members of an ecologically controlled morphoseries. To the contrary, Berggren (1977) considered that there was a phyletic relation, with "primitive" *G. puncticulata* being the ancestor of *G. crassaformis*. However, his "primitive" *G. puncticulata* probably refers to specimens intermediate between *G. juanai* and *G. crassaformis* (Scott, 1983). We suggest that gross resemblance in shell form arose in the Pliocene when the long term decline in number of chambers in the outer whorl in *G. inflata* lineage (Figure 39) reached the four-chambered stage and coincided with the mode in *G. crassaformis*. Subsequently, further reduction occurred in *G. inflata*, whereas there was no matching decline in *G. crassaformis* and resemblance between the taxa lessened. We see the resemblance between Pliocene representatives as due to convergence. However, even if stratigraphic evidence of separate ancestries for *G. crassaformis* and *G. puncticulata* is dismissed, it is notable that during their wide sympatry in the Pliocene they retained distinct modes in apertural shape, perhaps the best morphological discriminator. Such data suggest genetic isolation.

KEEL DEVELOPMENT

As in its presumed scituline forerunner, the junction between spiral and ventral walls of chambers in lower Pliocene *Globorotalia crassaformis* is typically rounded without a keel. Although this basic style is continued in many subsequent populations, including the large *G. ronda* (Figure 20*c*) and *G. oceanica* that appeared in the upper Pliocene in the tropics, there are forms with more compressed peripheries. In the Recent, some individuals have imperforate rims (Cifelli and Smith, 1970, pl. 6: fig. 3) and possibly even weak keels (Cifelli, 1965). Gradstein (1974) found that specimens with imperforate margins, or keels, comprised up to 85% of some Mediterranean Pliocene samples, but these structures were absent from others. In the temperate Southwest Pacific, Hornibrook (1982) found that the populations with rounded peripheries, like the lower Pliocene forms, disappeared prior to the entry of *G. truncatulinoides* and were replaced by populations with rims or weak keels (Figure 20*d,e*). Lidz (1972) observed in Atlantic and Caribbean populations that large, angular individuals with rims, or weak keels, predominated in Quaternary interglacials, while the smaller, inflated forms were dominant in low temperature periods. In terms of keel morphogenesis, the upper Pliocene-Recent history of *G. crassa-*

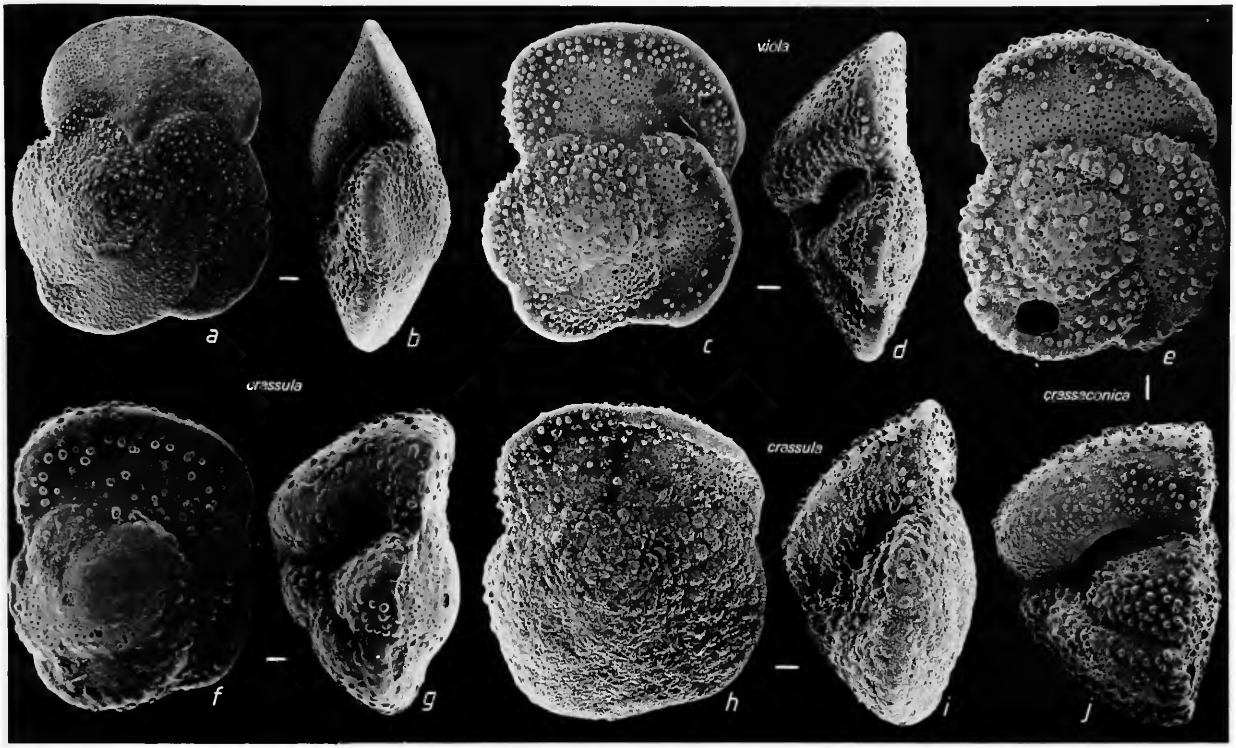


FIGURE 22.—*a–b,f–i, Globorotalia crassula crassula* Cushman and Stewart (*a,b*, DSDP Site 154, 2-6-120, Caribbean, Pliocene (× 55); *f,g*, S55/f937, Leader River, New Zealand, upper Pliocene-Pleistocene (× 105); *h,i*, DSDP Site 284, 6-3-20, Southwest Pacific, Pleistocene (× 100)); *c,d, Globorotalia crassula viola* Blow, type locality Canimar fauna (Palmer locality 1583), Cuba (× 105); *e,j, Globorotalia crassaconica* Hornibrook, DSDP Site 284, 10-6-40, Southwest Pacific, Pliocene (× 90).

formis is comparable with the *G. miozea* to *G. praemenardii* segment of the *G. praescitula* plexus in that specimens may develop rims or weak keels; however, strong folds, uniformly developed from midontogeny onwards throughout the population, are absent. *Globorotalia crassaformis*, in such a comparison, has not reached the stage of *G. menardii* and *G. conoidea*.

Weak, somewhat variable, keel development is also found in *G. crassaconica*, a Pliocene species (Figure 22*e,j*) found in the southern midlatitudes. It is probably a component of the *G. crassaformis* plexus. Its chambers are strongly elevated to produce a ventroconical shell, usually with an angular periphery; but the keel, while usually developed, does not form a strong fold, and only rims occur on some small specimens.

GLOBOROTALIA CRASSULA

This species, like *Globorotalia crassaconica*, has strong architectural similarities with *G. crassaformis*, but is widely distributed in the Pliocene and extends to the Recent. A major resemblance is in the subrectangular spiral shape of chambers in the outer whorl (typically formed by four chambers); but there is a subtle rectification of the leading and trailing edges to produce a shape well compared by Blow (1969:398) with the petal of the wood violet (Figure 22*c*). While the spiral outline of the shell is commonly also subquadrate, a more lobulate form with less compact arrangement of chambers occurs in some large, tropical populations (Scott, 1976). The major component of variation in *G. crassula* is in the axial profile. In tropical populations the ventral surfaces are usually strongly depressed and the axial shape of the shell is biconvex to compressed discoidal (Figure 22*b*). Biometric data (Scott, 1976) indicate that some ontogenetic change occurs, with larger shells tending to be more discoidal. Although axial form may broadly resemble that of *G. hirsuta* (Parker, 1962, pl. 5: figs. 10c,11c), spiral convexity is never strong. Discoidal shells are less common and less advanced in temperate regions. Here, the spiral surface of the shell is usually but slightly domed and the ventral region elevated. Scott (1976) studied an upper Pliocene South Pacific sample in which shell form was ventroconical (Figure 22*g*) and comparable with *conomiozea* variants of *G. conoidea.* Similar axial profiles were figured by Hornibrook (1981a, fig. 6i) also from New Zealand, and by Glaçon and others (1973, pl. 1: fig. 1e) from the Mediterranean. Generally, midlatitude populations display a spectrum of axial form ventrally, from low-domed to conical. *Globorotalia crotonensis, G. crassacrotonensis,* and *G. aemiliana,* originally described from the Mediterranean, fall within this range and may be variants of *G. crassula.*

Although Kennett and Srinivasan (1983, fig. 16) depicted *Globorotalia crassula* as the ancestor of *G. crassaformis,* we consider that the relation between these taxa is unresolved. There is general resemblance in chamber shape (both spiral and ventral), chamber packing, aperture shape, and in rather weak keel development (although the structure is much more prevalent in *G. crassula* than in *G. crassaformis*). There is also a general ontogenetic tendency for the spiral shape of chambers to be weakly crescentic in early whorls and more subrectangular in the outer whorl. Some populations of *G. crassula* are difficult to distinguish from sympatric representatives of *G. crassaformis* (Hornibrook, 1982), and the close similarity in morphology is reflected in interpretations of *G. crassula* as the ancestor of *G. crassaformis.* Differences are modest. The petaloid shape of chambers in *G. crassula* involves only a small alteration to the chamber envelope; moreover it is not an invariant feature, particularly in tropical populations. Discoidal form is uncharacteristic of *G. crassaformis* but develops in low-latitude populations of *G. crassula.* We suggest that *G. crassula* is a close relative of *G. crassaformis,* but we cannot resolve whether it is an upper Pliocene branch from the latter or a taxon that arose independently, perhaps from another scituline.

GLOBOROTALIA TRUNCATULINOIDES

Generally, morphoclines are ill-defined in the *Globorotalia crassaformis* plexus, which contributes largely to the problems in its sytematic treatment. The exception is the *G. truncatulinoides* lineage in which there are well-defined trends in architecture, analogous to those in Miocene taxa. Following Blow (1969), the stem species have been taken as *G. ronda* (Figure 23*k,l*) and *G. oceanica,* which are differentiated from *G. crassaformis* by their radially inflated chambers. In the *G. inflata* lineage this feature was retained and associated with reduction in the number of chambers in the outer whorl (compare Figure 19*c* with Figure 23*l*); in the *G. truncatulinoides* lineage the important early architectural changes were an increase in chambers in the outer whorl and a reduction of radial inflation. These reversals eventually resulted in a ventroconical shell (compare with *G. inflata,* Figure 7). Takayanagi and Saito (1962:81) described *G. tosaensis* with four chambers commonly in the outer whorl, but topotypes include specimens with five, and collections with up to five have been reported (Stainforth and others, 1975:413). Five chambers in the outer whorl could be simply obtained by halting the ontogenetic decline that occurs in *G. crassaformis.* In the *G. ronda* group, the alteration is associated with a decline in length of chambers and formation of a well-defined flattish apertural face. Late-formed chambers show less radial inflation and tend to extend ventrally, a feature also seen in keeled morphotypes of *G. crassaformis* and relatives like *G. crassaconica.* These changes result in a shell with a moderately angular periphery, which may have a thin rim, as is sometimes present in topotypes of *G. tosaensis*. The principal advances of *Globorotalia truncatulinoides* (Figure 23*a–d*) over *G. tosaensis* involve: (1) rectification, or straightening of the axial profile of chambers, (2) increased angularity of junctions between chamber surfaces, (3) development of a keel, (4) increased ventral extension of chambers. In addition, the umbilicus widened, signifying more evolute coiling than in *G. tosaensis*.

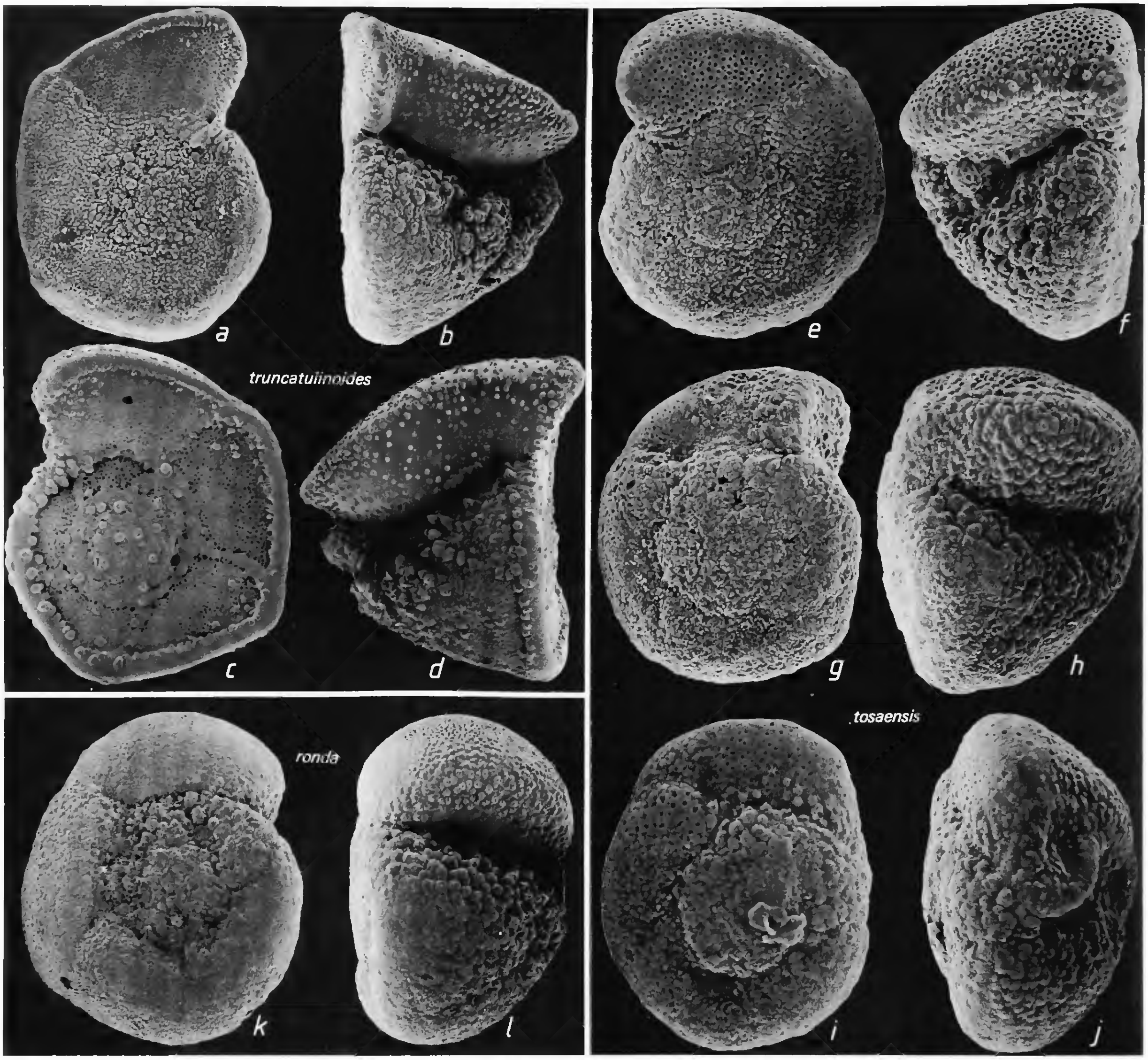
Globorotalia truncatulinoides is very distinctive in appearance. It has five to six chambers in the outer whorl and a profile that is linear or slightly convex (Figure 23*b,d*). At the periphery, there is a prominent keel which, in larger specimens, extends to the junction of the apertural face with the ventral wall. The ventral side may be highly conical, but this feature varies ontogenetically (Cifelli, 1965:21) and geographically (Kennett, 1968).

The onset of keel construction, the principal feature used in separating *Globorotalia truncatulinoides* from *G. tosaensis,* was rapid. From a magnetostratigraphically calibrated sequence, Berggren (1969) reported that keel development, once initiated on the last formed chamber, extended progressively around the outer whorl in 0.05 m.y. (Figure 39). This accelerating trend, (predisplacement of Alberch and others, 1979) has apparently continued since the Pleistocene. A section of a ?sub-Recent individual (Figure 24) shows that only the earliest chambers have rounded chambers as in *G. crassaformis*. A keel is present throughout the middle whorl.

While the architectural trends are well defined, the pattern of change remains obscure. In part, this is owing to the interpretation of Blow (1969:407) that crusted and crust-free morphotypes of *Globorotalia tosaensis* and *G. truncatulinoides* are members of separate lineages. Following this view, Rögl (1974) recognized four taxa branching from the crust-free form of *G. tosaensis* in a sequence from the Timor Sea. Rögl differentiated these sympatric taxa by small variations in profile, keel development, and encrustation. However, Berggren and others (1967), Phillips and others (1968), and Hornibrook (1976) have interpreted such forms as variants among intergrading morphotypes (Figure 24). There do not appear to be any consistent differences to uphold Blow's two-lineage interpretation.

In New Zealand sequences, Hornibrook (1976) found that the keeled morphotype gradually replaced the unkeeled morphotype (*Globorotalia tosaensis*) upward, but that the ratio between the two was highly variable. Kennett and Geitzenauer (1969) found in a Southeast Pacific core that the percentage of keeled specimens fluctuated widely (8%–98%) and the higher percentages of keeled specimens were associated with the more tropical type of assemblages. Also, the keeled specimens were noted to have a more acutely angular periphery, suggesting that keel formation was related to chamber compression. Therefore, it appears that while the keel developed by ontogenetic progression, there was not necessarily a uniform phyletic rate of development. The data of Kennett and Geitzenauer (1969) suggest that a regional, watermass factor may have been involved, with the tropical waters being more conducive to the spread of keeled forms.

Initially, a phase of rim formation only is indicated in tropical and subtropical populations (Rögl, 1974:748; Phillips and others, 1968), and also in the North Pacific (Japan, type population of *Globorotalia tosaensis*). This was succeeded by a period of expanded variation (reflected by Rögl's sympatric "taxa") as chamber compression increased and keels developed. This phase (about the base of the Pleistocene) possibly varied regionally, depending on watermass characteristics. A rapid morphocline in keel formation, after which *G. tosaensis* disappeared, was reported by Berggren and others (1967) from the subtropical Atlantic. But elsewhere the duration of this phase seems to have been extended as, for example, in the Gulf of Aden (Vincent and others, 1974) and variation was not clinal (e.g., as in the Southeast Pacific; Kennett and Geitzenauer, 1969). Contemporaneous populations at various stages of keel development may have existed, possibly with



AXIAL OUTLINES

SHAPE VARIATION OUTER WHORL

SHAPE CHANGE IN ONTOGENY

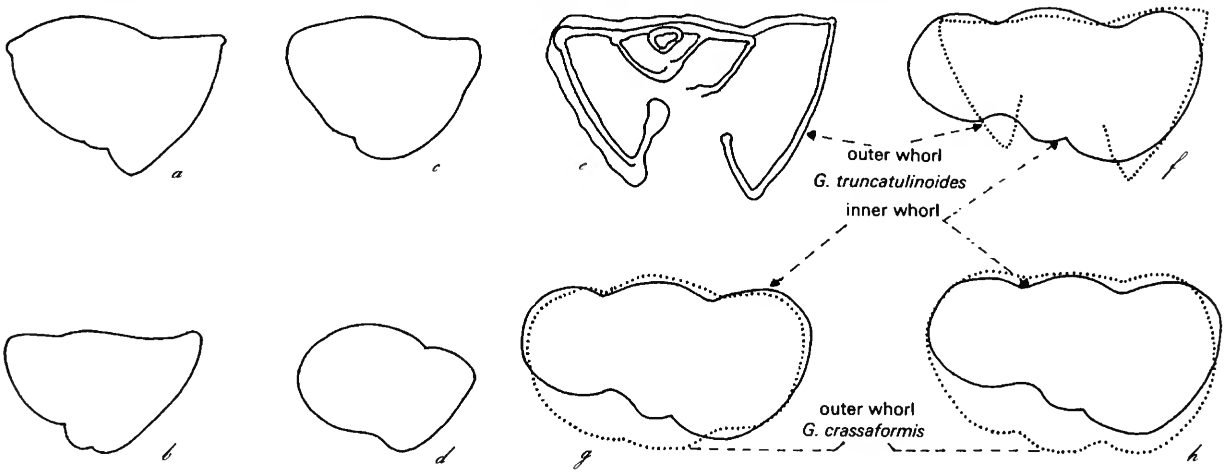


FIGURE 23.—*a–d*, *Globorotalia truncatulinoides* (d'Orbigny) (*a–b*, Chain Station 61-171, 397-402 cm, North Atlantic, Pleistocene (× 60); *c,d*, Challenger Station 166B, 39°03'S, 170°43'E, Southwest Pacific, Recent (× 90)); *e–j*, *Globorotalia tosaensis* Takayanagi and Saito (*e,f*, DSDP Site 200, 2-cc, North Pacific, Pliocene (× 105); *g,h*, Chain Station 61-171, 569-574 cm, North Atlantic, Pliocene (× 80); *i,j*, Nobori Formation, Japan, Pliocene (× 130)); *k,l*, *Globorotalia ronda* Blow, DSDP Site 200, 1-cc, North Pacific, Pleistocene (× 75).

the most advanced (in chamber compression and keel formation) occurring in the lower latitudes. This phase terminated with the spread of the advanced population (*G. truncatulinoides*) throughout the geographic range of the lineage. Apart from its potential stratigraphic value, the origin of *G. truncatulinoides* deserves attention as it promises unexcelled information on the morphogenesis of advanced characters in planktonic foraminifera and insights into their adaptive role and dispersal spatially.

In the Recent, regional variation in axial height of *Globorotalia truncatulinoides* was reported by Kennett (1968) and Takayanagi and others (1968:148). Kennett's data suggest a clinal relationship between the vertical extension of the ventral side of the test and sea surface temperature in the southern oceans. Highly conical forms are associated with warm, tropical waters while weakly conical, bioconvex forms are associated with the cold waters of the high latitudes. More recently, Lohmann and Malmgren (1983) studied regional differences in axial shape by means of image digitization and eigen analysis. Lohmann and Malmgren also found that there are two morphotypes of *G. truncatulinoides* in the southern ocean with the weakly conical form occupying the higher latitudes. However, in this study the relationship between shape and temperature was poorly defined, since there was little shape change associated with a strong temperature gradient. The weakly conical morphotype was designated as *G. truncatulinoides malvinensis* by Boltovskoy and Watanabe (1981:112).

FIGURE 24.—Axial outlines: *Left*, Intergradation in axial shape within one sample between shells (*a,b,*) in which late-formed chambers have keels (*Globorotalia truncatulinoides* morphotypes) and those without keels (*c,d*, *G. tosaensis* morphotypes). Chambers tend to be less compressed at the periphery in the latter (specimens from 711 ft (216:86 m), Wairoa Drillhole, New Zealand, after Hornibrook, 1976; text-fig. 5). *Right*, Change in axial shape of chambers between inner and outer whorls of *G. truncatulinoides* and comparison with *G. crassaformis* (*e*, section of *G. truncatulinoides* from core MSN-536, Indian Ocean (after Takayanagi and others, 1968, figure 3); *f*, inner and outer whorls of *e* superimposed (the inner whorl has been reflected); *g,h*, inner whorl of *e,f* superimposed on outer whorl of Pliocene specimens of *G. crassaformis* (Chain Station 115-6-67, South Atlantic, *g* from 306 cm, *h* from 404 cm). The inflated, discoidal axial profile of juvenile *G. truncatulinoides* resembles the late ontogenetic shape of the ancestral *G. crassaformis*).

In the North Atlantic the occurrence of two distinct morphotypes is not immediately evident, as populations of weakly conical forms have not been recorded. This absence may be partially explained by the fact that, in the North Atlantic, *Globorotalia truncatulinoides* is confined to tropical and subtropical waters while in the southern oceans it extends into subantarctic waters (Cifelli, 1971). However, North Atlantic populations do show an ontogenetic change in shape. Immature forms are weakly conical while the adults are vertically extended on the ventral side and distinctly conical (Cifelli, 1965:21). Therefore, the morphotype found in the high latitudes of the southern oceans might be viewed as a case of arrested ontogenetic development.

There are several analogies with the evolution of *Globorotalia menardii*. Both developed marked compression of chambers. The obvious contrast in the form of chambers is due primarily to axial compression in menardines and radial compression in *G. truncatulinoides*. But in both, surface area is increased relative to volume. The angular apertural face in *G. truncatulinoides* also serves to expand surface area and is a design feature not explored by the ventroconical forms of *G. conoidea*. In both lineages rim development precedes formation of keels. Further, both originated in the tropics or subtropics.

Apart from the striking architectural contrast (which may be of lesser significance hydrodynamically), there are contrasts in evolutionary tempo, in taxonomic diversity and in biogeography. *Globorotalia tosaensis* represents the rim to incipient keel stage of development; it existed for about 1 m.y. In the comparable stage leading to *G. menardii*, *G. archeomenardii* and *G. praemenardii* had a history of over 3 m.y. (Ryan and others, 1974, table 7). But *G. menardii* has led to a plexus of multichambered, discoidal variants, particularly in the post-Miocene. This has not been duplicated by *G. truncatulinoides*. In part, this may be due to the recency of its origin. Moreover, the biogeography of *G. truncatulinoides* indicates that it occupies a wider watermass spectrum than menardine taxa. The latter have seldom extended beyond the subtropics. *Globorotalia truncatulinoides* is now a major midlatitude species that extends both towards the tropics and poleward beyond the transitional zone (Bé, 1977:58). Modal axial shapes differ in populations occupying contiguous watermasses (Figure 40), but speciation has not occurred.

Analysis of the Succession

Globorotalid Radiations

OVERVIEW

While we have repeatedly commented on the repetitive patterns of architectural design within the radiation, Neogene species also show striking resemblances to globorotalid forms of the earlier Cretaceous and Paleogene radiations (Cifelli, 1969). The resemblances are all the more remarkable because the stratigraphic record suggests that there is no phyletic connection between the three globorotalid groups. Severe reductions among the planktonics occurred at the close of the Cretaceous and the Paleogene radiations, and the new globorotalid stocks developed from residual planktonic populations composed entirely of simple phenotypes.

This scenario provides the opportunity for "outgroup" comparisons of the Neogene radiation with groups of independent origin that have developed comparable architecture. Such comparisons are potentially useful in identifying adaptive characters and in revealing the influence of founding taxa on subsequent developments.

All three radiations clearly began with quasiglobigerine ancestors (Brönnimann and Brown, 1956:513; Walters, 1965:112, Blow, 1979(1):253) and showed important phyletic trends in common (chamber compression, reduction in surface relief leading to a flat topography, and formation of a keel at the chamber periphery). In the Neogene radiation, these developments are closely correlated and, in the lower to middle Miocene, remarkably unidirectional. A keel was achieved only after the wall had become fully flattened and the axial profile acutely angular. The same trend occurred in *Fohsella* and in the *Globorotalia praescitula* plexus. In the later Cenozoic, when the axial profile became inflated during the development of *G. puncticulata* from *G. conoidea*, the keel was lost. This further suggests close structural linkage between these characters.

The Cretaceous development was more complex and probably less unidirectional than that of the Neogene. Brönnimann and Brown (1956, fig. 21) recognized two principal Cretaceous lineages in which compressed, keeled forms developed. Both were derived from coarse walled, quasiglobigerine ancestors which, unlike the mid-Cenozoic paragloborotalids, were not honeycombed, but may have been spinose. Honeycombed textural patterns seldom developed in the Cretaceous: *Hedbergella washitensis* (Masters, 1977, pl. 26) is a notable example. The wall became progressively flattened in one lineage, culminating in the smooth-walled *Globotruncana*. The excellent SEM micrographs in Smith and Pessagno (1973) of *Globotruncana* from the Maestrichtian Corsicana Formation of Texas show a texture fully comparable to that of Neogene

Globorotalia, except that the Cretaceous forms have an ornate arrangement of pustules or muricae. In the lineage leading to *Rugotruncana* the texture assumes a pattern of meridionally aligned costellae, a peculiarly Cretaceous feature that is totally unknown from the Cenozoic. Not only does it occur in *Rugoglobigerina* and *Rugotruncana,* but it is also seen in the Heterohelicidae. The costellae appear to develop from a coalescence of spine bases (Petters, El Nakhal, and Cifelli, 1983). However, in more highly developed forms, costellae became fused into well-formed ridges that rise from a smooth wall (e.g., Smith and Pessagno, 1973. pl. 25: figs. 1–3;8–10). The end member of the rugoglobigerine series, *Rugotruncana,* is closely isomorphous with *Globotruncana* as it has a well-developed single or double keel. The latter feature is peculiar to the Cretaceous. In both *Rugotruncana* and *Globotruncana* the keel may develop prior to the development of an acute profile (e.g., *R. tiveli* and *G. saratogaensis*). In later radiations the keel always developed as the periphery became more acute, a relation that is consistent with a structural function. The inversion in the Cretaceous development pattern suggests that topographic ridges on the periphery of inflated, globigerine-like chambers may have originally had another function and were preadapted to the structural role that emerged as chamber compression developed.

Like the Cretaceous, the Paleogene radiation developed in several directions from coarse walled, quasiglobigerine ancestor(s) (McGowran, 1968). One type includes *Morozovella,* which has a flat wall punctuated by dense concentrations of spike-like muricae. The shell is highly compressed (often into a ventroconical form), with a keel at the periphery that consists of fused muricae (Blow, 1979(1):401). *Morozovella* was by far the most successful globorotalid in the Paleogene. *Acarinina,* and possibly *Truncorotaloides,* which show various degrees of chamber compression but lack keels, may represent stages in the development of *Morozovella.* The other Paleogene globorotalid, *Planorotalites,* has a smooth wall, over which isolated pustules are sparsely distributed. It has a compressed axial profile with a rim, or weakly formed keel. Although much less successful than *Morozovella, Planorotalites* is closely isomorphous with Neogene *Globorotalia.* Indeed, Blow (1979) in his typological classification ignored the genus and placed its species in *Globorotalia.*

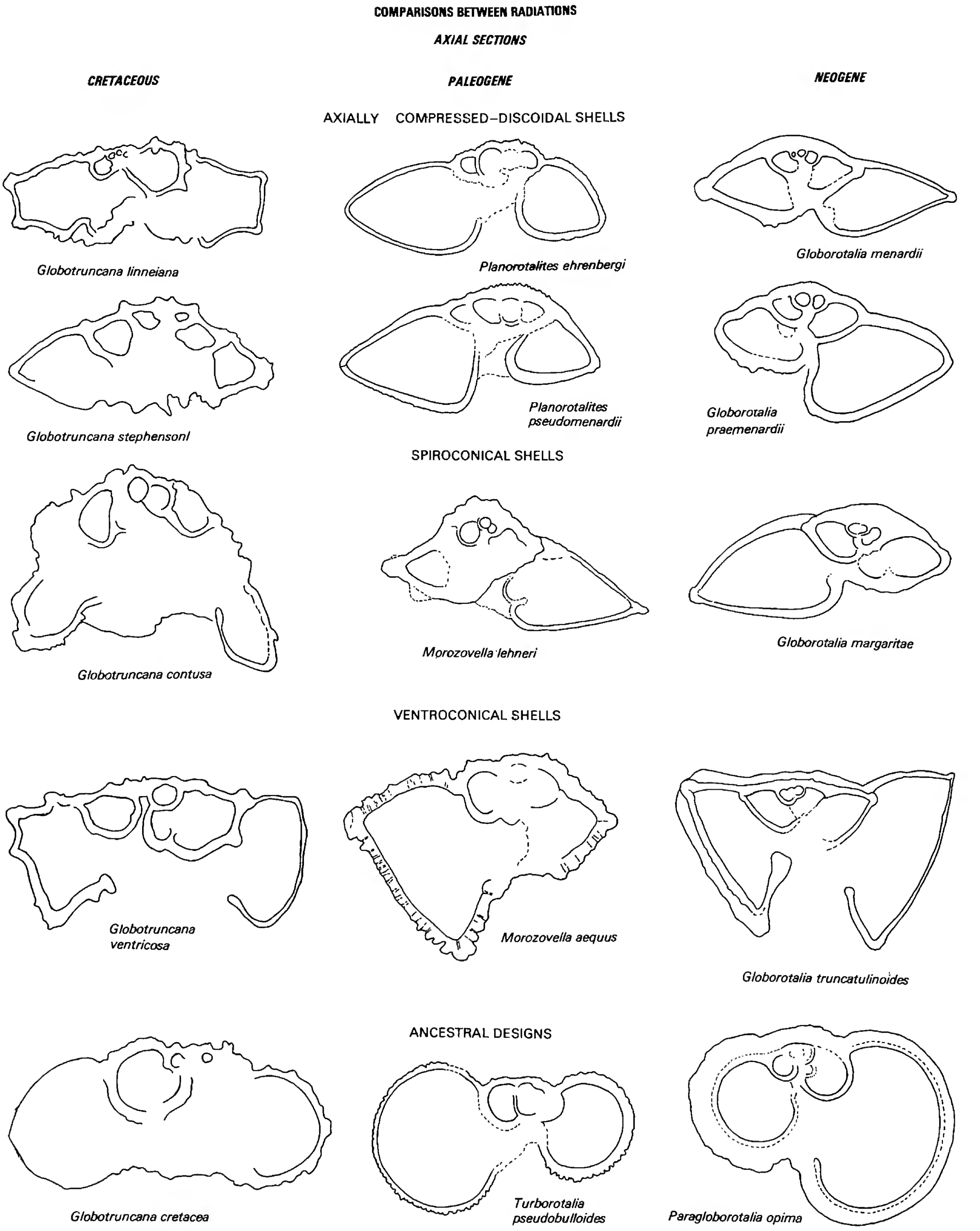
We compare several major features of shell architecture in the three radiations in greater detail.

AXIAL SHAPE OF SHELL.—Neogene taxa utilized three principal designs in shell construction with direction of chamber compression and rate of whorl translation along the coiling axis as major variables. Compression in the direction of the coiling axis, with low rate of translation, produced disk-shaped shells, and, with higher rates of translation, spiroconical shells. Radial compression of chambers (approximately normal to the direction of the coiling axis) coupled with a low rate of whorl translation produced ventroconical forms. Excellent examples of these three designs occur in the Cretaceous and Paleogene radiations, with some close replicas (Figure 25).

Well-known Cretaceous examples of disk-like shells include *Rotalipora appenninica, Globotruncana fornicata, G. mayaroensis,* and *G. renzi.* Forms with a single keel at the periphery or closely spaced twin keels (e.g., *G. stephensoni*) resemble Neogene examples more closely than those like *G. linneiana* (Figure 25) and *G. mayaroensis.* In these, the wide spacing of keels creates a disk form of uniform thickness right to the periphery. This form is not encountered in Neogene taxa.

Paleogene *Planorotalites* includes several species (*P. pseudomenardii, P. ehrenbergi,* Figure 25) that closely resemble the Neogene menardine taxa (Figure 26), although shells are usually less than half the diameter of advanced Neogene forms.

As in the Neogene, spiroconical shells are relatively rare in earlier radiations. However, the Cretaceous *Globotruncana contusa* (Figure 25) has a particularly high rate of whorl translation and,


COMPARISONS BETWEEN RADIATIONS
AXIAL SECTIONS
CRETACEOUS
PALEOGENE
NEOGENE
AXIALLY COMPRESSED–DISCOIDAL SHELLS
Globotruncana linneiana
Planorotalites ehrenbergi
Globorotalia menardii
Globotruncana stephensoni
Planorotalites pseudomenardii
Globorotalia praemenardii
SPIROCONICAL SHELLS
Globotruncana contusa
Morozovella lehneri
Globorotalia margaritae
VENTROCONICAL SHELLS
Globotruncana ventricosa
Morozovella aequus
Globorotalia truncatulinoides
ANCESTRAL DESIGNS
Globotruncana cretacea
Turborotalia pseudobulloides
Paragloborotalia opima

in terms of spire height, is a more advanced spiroconical shell than the Neogene examples (*Globorotalia panda, G. margaritae, G. hirsuta,* Figure 12). Although some specimens of *Morozovella lehneri* (Figure 25) have a moderately high spire, there seem to be no distinctively spiroconical taxa in the Paleogene radiation.

Ventroconical designs, rare in the Neogene, are common in earlier radiations. *Globotruncana ventricosa* (Figure 25), *G. canaliculata* (Figure 27*c*), and *G. elevata* are Cretaceous examples. However, in all Cretaceous ventroconical taxa there is only minor extension of chambers ventrally and the high ventroconical form of the Neogene *Globorotalia truncatulinoides* is not developed (Figure 26). Conversely, only the Quaternary *G. cavernula* approaches the low ventroconical form that typifies the Cretaceous radition. The Paleogene development is closer to the Neogene. In forms like *Morozovella velascoensis, M. aequus* (Figures 25, 27*b*), *M. angulata,* and *M. crater* there is substantial extension of chambers ventrally, and shell architecture resembles that of *Globorotalia truncatulinoides.*

FIGURE 25.—Axial sections of major shell designs from Cretaceous, Paleogene, and Neogene radiations redrawn from micrographs. Widely separated dual keels as in *Globotruncana linneiana* (after Pessagno, 1967, pl. 97: fig. 13) inhibit tapering of chambers towards the periphery and a disk-like shell of rather uniform thickness is produced. Single, or very closely spaced dual keeled designs from the Cretaceous (e.g., *Globotruncana stephensoni,* after Pessagno, 1967, pl. 96: fig. 5) have axial profiles that are more comparable with Paleogene and Neogene taxa. Note that raised ridges are developed on sutures only in Cretaceous designs. In *Planorotalites pseudomenardii* and *P. ehrenbergi* (after McGowran, 1968, pl. 4: figs. 7, 12) the degree of chamber compression compares with the Neogene *Globorotalia praemenardii.* Keels are very weak on all 3 taxa. On *Globorotalia menardii* there is greater compression and inflational folding (Figure 28) produces a strong keel. Early whorls form a much higher spiral in the Cretaceous *Globotruncana contusa* (after Pessagno, 1967, pl. 96: fig. 16) than in a Paleogene example (*Morozovella lehneri,* after McGowran, 1968, pl. 2: fig. 5). In comparison, *Globorotalia margaritae* (after Postuma, 1971:331) is a weaker spiroconical design. Ventral extension in *Globotruncana ventricosa* (after Pessagno, 1967, pl. 95: fig. 11) is less than in the last chamber of the Paleogene *Morozovella aequus* (after McGowran, 1968, pl. 1: fig. 4). However, still greater ventral extension is seen in *Globorotalia truncatulinoides* (after Takayanagi and others, 1968, fig. 3). Ancestral taxa in each radiation have inflated discoidal, or globular, shells with little change in chamber shape throughout ontogeny (*Globotruncana cretacea,* after Pessagno, 1967, pl. 94: fig. 4; *Turborotalia pseudobulloides,* after McGowan, 1968, pl. 3: fig. 18; *Paragloborotalia opima,* after Postuma, 1971:345). Chamber compression in more advanced shells is always strongest in the outer whorl. There is close similarity in the ontogenetic strategy followed by taxa from each radiation. Note the wide umbilical area of Cretaceous taxa relative to Neogene forms. (*Globorotalia truncatulinoides* excepted).

KEEL CONSTRUCTION.—Structurally, the common denominator of the Neogene radiation is the development of keels at angular junctions of chambers. Similar structures are a feature of the Cretaceous and Paleogene assemblages. Although critical rates of curvature for keel morphogenesis have not been worked out, inspection suggests that, for a particular type of profile, keels originated in each radiation at comparable states of compression. This may simply indicate that mechanical properties of walls in the three radiations were comparable. In Neogene and Paleogene taxa, keels occur only at angular junctions and are thus confined to advanced species. However, some Cretaceous species developed keel-like structures before a distinct angular profile was attained (*G. saratogaensis, R. tiveli*).

While keel locations are often identical in taxa from the three radiations, there are differences in constructional detail, notably in the method used to obtain a large cross-section. In Neogene taxa, additional lamellae are added to the folded wall (Figure 28). They taper rapidly in thickness away from the fold (Hemleben and others 1977; pl. 11: fig. 3). The extent to which this technique was utilized in taxa from previous radiations seems to have been minor. *Planorotalites pseudomenardii* (Paleogene, Figure 29*c*) shows some thickening at the site of the keel (McGowran, 1968, pl. 4: fig. 7). However, lamellar inflation of keels in Neogene taxa is strongest in large, compressed chambers and the small size of chambers in *P. pseudomenardii* and other Paleogene disk-like forms probably explains the weak infla-

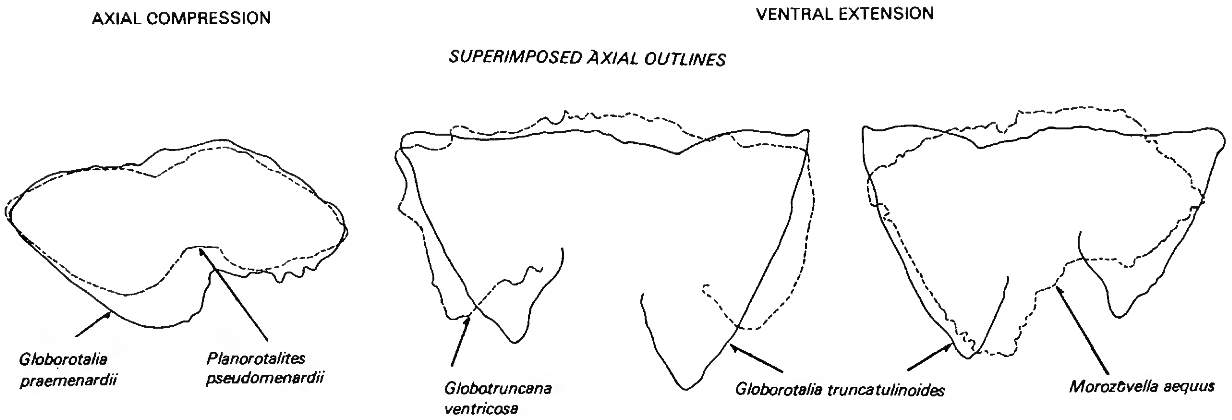


FIGURE 26.—Shell outlines (axial orientation) of taxa with similar designs from the 3 radiations, enlarged to common diameters and superimposed. In *Globorotalia praemenardii* (after Scott, 1973a, pl. 2: fig. 6) and *Planorotalites pseudomenardii* (after McGowran, 1968, pl. 4: fig. 9) the degree of axial compression of the last-formed chambers is comparable. Neither taxon has fully developed keels. *Globotruncana ventricosa* (after Pessagno, 1967, pl. 95: fig. 11) illustrates the low ventroconical design of many Cretaceous taxa. *Morozovella aequus* (after McGowan, 1968, pl. 1: fig. 4) is a Paleogene ventroconical shell with greater ventral extension of the last-formed chamber than in *Globotruncana ventricosa*, but junctions between chamber surfaces are less angular than in the Neogene *Globorotalia truncatulinoides*. Early chambers of the outer whorl are also less compressed than in the latter.

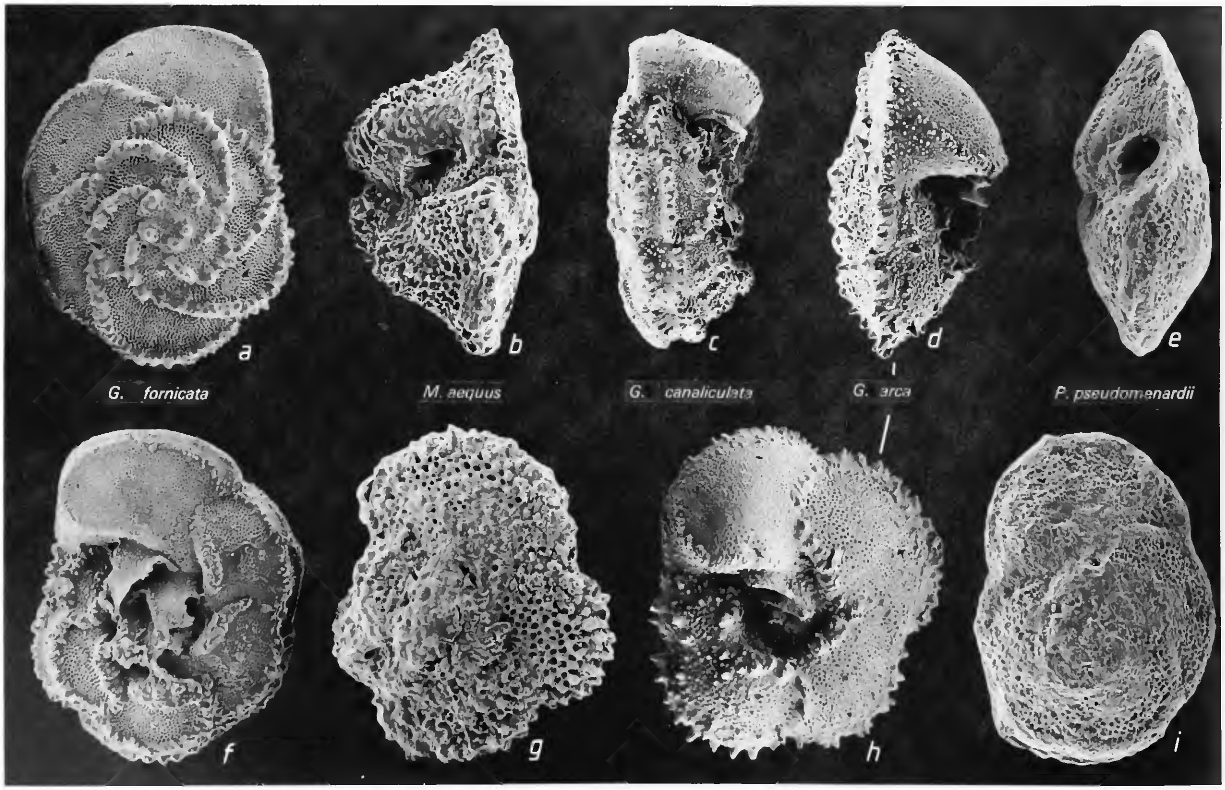


FIGURE 27.—*a,f Globotruncana fornicata* (Plummer), Upper Taylor Formation, Mustang Creek Valley, Texas, Campanian (× 90); *b,g Morozovella aequus* (Cushman and Renz) sensu lato, Well L.G. Hammond No 1, Maryland (Cushman Collection No. 61873), Paleocene (× 130); *c, Globotruncana canaliculata* (Reuss), Upper Taylor Formation, Mustang Creek Valley, Texas, Campanian (× 75); *d,h Globotruncana arca* (Cushman), Upper Taylor Formation, Mustang Creek Valley, Texas, Campanian (× 105); *e,i Planorotalites pseudomenardii* (Bolli), type locality *P. pseudomenardii* Zone, Pointe-a-Pierre, Trinidad, Paleocene (× 170).

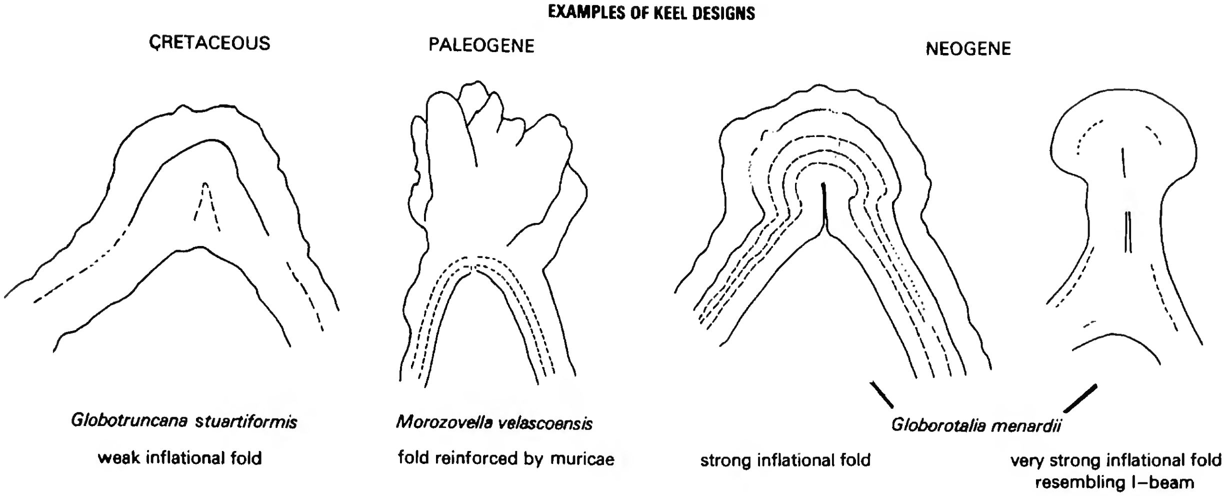


FIGURE 28.—Sections through keels of late-formed chambers (*Globotruncana stuartiformis*, after Banner and Blow, 1959, pl. 2: fig. 4; *Morozovella velascoensis*, after Blow, 1979, pl. 216: fig. 6, boundaries between wall laminae (dotted) are diagrammatic to show Blow's interpretation (e.g., 1979, pl. 206: figs. 5,6) that muricae develop from the outer lamina; *Globorotalia menardii*, (*left*) after Scott, 1973a, pl. 2: fig. 2; (*right*) after Hemleben and others, 1977, pl. 11: fig. 4).

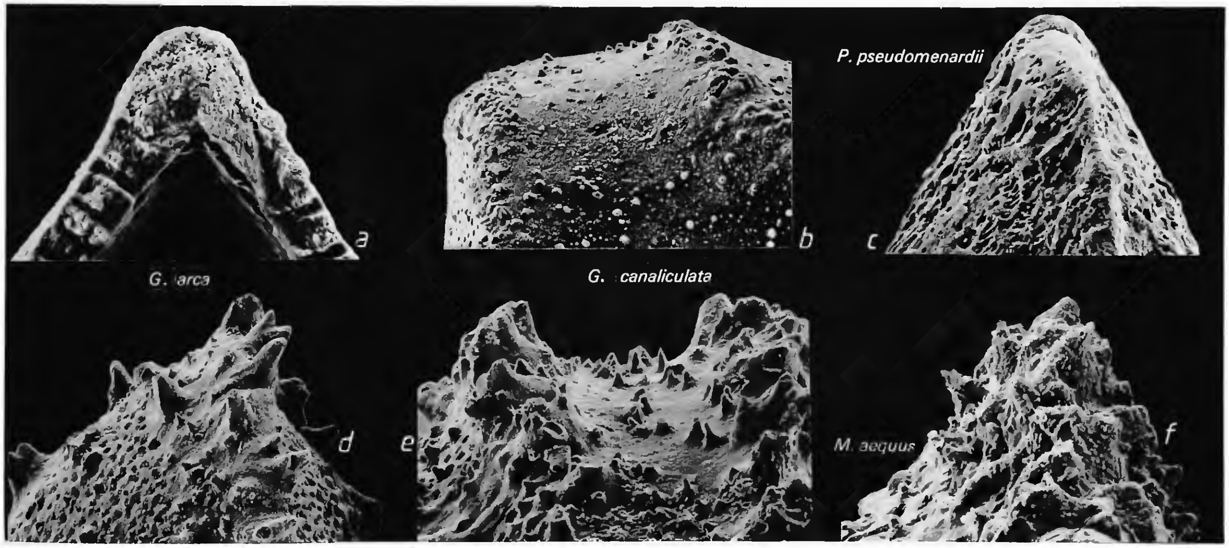


FIGURE 29.—*a,d*, *Globotruncana arca* (Cushman), Upper Taylor Formation, Mustang Creek Valley, Texas, Campanian (*a*, × 690; *d*, × 300); *b,e*, *Globotruncana canaliculata* (Reuss), Upper Taylor Formation, Mustang Creek Valley, Texas, Campanian (*b*, × 350; *e*, × 495); *c*, *Planorotalites pseudomenardii* (Bolli), type locality *P. pseudomenardii* Zone, Pointe-a-Pierre, Trinidad, Paleocene (× 455); *f*, *Morozovella aequus* (Cushman and Renz) sensu lato, Well L.G. Hammond No. 1, Maryland (Cushman Collection No. 61873), Paleocene (× 580).

tion. Possibly, there are more advanced examples of lamellar inflation in the Cretaceous (Figure 28; Banner and Blow, 1959, pl. 2: figs. 2*c*, 4*b*). However, cross-sections of keels in many Cretaceous and Paleogene taxa were enlarged (somewhat irregularly) by aggregation of pustules (muricae of Blow, 1979) on the external surface of the fold (Figures 27*a,h*; 29*e*). "Beaded" keels in some Cretaceous taxa result from alignment of single (sometimes elongate) pustules, which are in close proximity but not necessarily fused. Coarse, masonry-like aggregations are particularly characteristic of the Paleogene morozovellids and, in some taxa, occur at all angular junctions. No member of the Neogene globorotalid radiation utilized this aggregative technique and, like the double keels of the Cretaceous, it is a good example of nontransference of characters from one radiation to the next.

UMBILICUS.—The umbilicus in Neogene taxa is usually a poorly defined depression in the ventral surface of the shell in the vicinity of the coiling axis. Generally, there are no calcified structures in the depression. However, Cretaceous taxa, especially the more advanced ones, have a large, open umbilicus with elaborate structures (portici, tegillae) that extend partially into, or completely cover the umbilicus (Figure 27*f,h*). Brönnimann and Brown (1956:508) suggested that these structures are best developed on forms with the widest umbilical depression. Portici and tegillae, therefore, may have developed as protective structures. Minor extensions of the aperture were observed by Blow (1979(2);1047) on *Turborotalia pseudobulloides*, a founder of the Paleogene radiation, but conspicuous umbilical plates did not develop in later taxa. Possibly this may be significant to functional interpretation because the umbilicus in some morozovellids, especially some variants of *Morozovella velascoensis* (Blow, 1979, pl. 99: fig. 1), is as wide as in some globotruncanids. Umbilici are generally small, even closed, on many Neogene species. Significantly, only in *Globorotalia pertenuis*, which has a wide umbilicus, are there plate-like extensions into the umbilicus analogous to those of the Cretaceous.

SURFACE TOPOGRAPHY.—The wall of advanced taxa in the Neogene radiation is of a single type, consisting of a flat surface with relatively few pustules concentrated around the apertural area. There is no conspicuous coalescence or fusion of pustules to form ridge, or node-like structures, nor do the pustules have any role in the formation of reinforcement of the keel. In the Cretaceous, a flat wall also developed, but it occurs in two different forms. One is very much like the Neogene wall with a smooth surface. However, the pustules do coalesce, especially in sutural areas and around the periphery (Figure 27*a,c,h*). In the other (rugoglobigerine) the surface is overlain by costellae that are arranged meridionally, although the pattern is highly variable. In primitive taxa the costellae appear to form by coalescence of spine bases. In more advanced taxa the costellae form more regularly developed ridges.

The smooth, featureless wall is again achieved by the Paleogene *Planorotalites*, which is even more Neogene-like (figure 27*e,i*). Pustules are relatively minor and, unlike Cretaceous taxa, they do not coalesce to form bead-like structures in sutural areas or around the periphery. In contrast, *Morozovella*, by far the most prominent globorotalid in the Paleogene, had a wall studded with spike-like muricae (Figure 27). These are concentrated in the sutural areas and around the periphery, where they make up most of the keel. Thus, while the planorotalids resemble the Neogene globorotalids, the contemporary morozovellids show much closer resemblance with the preceding globotruncanids.

SHAPE OF CHAMBERS, SPIRAL SIDE.—We have emphasized the importance of chamber shape, in spiral orientation, for identifying some Neogene lineages. However, few novelties were actually introduced in the Neogene. Crescent shapes (A, B types, Figure 5) are as common in the globotruncanids, morozovellids, and acarinids as the Neogene lineages. Designs resembling the T-forms of *Fohsella* occur in the Cretaceous *Rotalipora appenninica* and *R. greenhornensis* (Pessagno, 1967, pl. 51: figs. 10, 15). Chamber forms in the Paleogene *Acarinina praecursoria roedermanni* and *A. carinata anapetes* (Blow, 1979, pl. 86: fig. 3) compare with the primitive T form of *Fohsella kugleri.* Although subquadrate chamber outlines do not feature in the Cretaceous, they are as well represented in the Paleogene (e.g., *Acarinina bulbrooki, A. pseudotopilensis, Truncorotaloides topilensis*) as in the Neogene *Globorotalia crassaformis* plexus.

EVALUATION

The outstanding similarities among the radiations are in chamber compression, keel location, and shell shapes. Axial and radial styles of chamber compression, together with spiroconical, ventroconical, and disk-like shell designs all arose in the Cretaceous and reappeared in later radiations. The Neogene record shows no major novelties in these designs. However, globose forms, which appeared late in the Paleogene and Neogene radiations, did not occur at all in the Cretaceous. Convergences in form between the radiations are associated with similar phyletic and ontogenetic strategies. All founding taxa had globigerinid, quasispherical chambers (Figure 25) and, in the course of each radiation, compressed architecture was always introduced late in ontogeny. Such canalization of form and ontogenetic and phyletic histories suggest that common adaptations were made in the three radiations.

Each radiation has distinctive features. The weak ventroconical architecture of the Cretaceous is the major example involving shell shape. Many distinctive characters, however, do not involve gross form of chambers or shell but occur in smaller structures. Surface topography, umbilical apparatus, and keel structure are examples, and it is at this scale that the influence of ancestry seems to be most obvious. That convergence primarily relates to gross shell form again points to its apparent adaptive importance.

Although stratigraphic data and character analyses suggest that the Neogene globorotalid radiation was unrelated to its predecessors, it is interesting to review the data from the perspective of improvements in design. Architecturally and structurally (but neglecting functionality), the Neogene radiation shows the following five leads in design.

Discoidal shells: largest and most compressed forms (menardine taxa).

Ventroconical shells: greatest ventral extension and strongest radial compression throughout outer whorl (*G. truncatulinoides*).

Keel design: strongest development of inflational folds (in larger menardine species).

Surface topography: greatest development of flat surfaces (practically all middle Miocene and later *Globorotalia*, as well as later *Fohsella*).

Apertural area: closed umbilicus, mostly unmodified.

All of these traits were anticipated in earlier radiations, and comparisons are peculiarly constrained by lack of data on function. However, several can be interpreted as simplifications or as advances in design. Earlier radiations produced smooth, flat walls, but surfaces were often supplemented with costellae, fused pustules, or muricae. There was no single trend towards a completely flat, open surface as in the Neogene. Neogene-Recent *Globorotalia* still retain pustules, especially in the *G. crassaformis* plexus, but they do not fuse into discernible structures. Yet the architectural simplicity of the advanced globorotalid wall should be weighed against the success (e.g., species diversity, duration) of the spiky morozovellids. Selection appeared to favor the enhancement of muricae and it might be conjectured that they were functionally important. There is isotopic evidence (Boersma and others, 1979) that some morozovellids occupied the epipelagic niche which, in modern oceans, is the preferred location of spinose species (Figure 36). In contrast, as we mention later, Recent representatives of the Neogene radiation often occupy bathypelagic environments.

The double keels of the Cretaceous, although elegant in appearance, might be viewed as redundant relative to the single support of Neogene taxa. However, the influence of ancestry may be seen here if double keels were due to the conversion of pre-existing features to a new structural role. The single keel of the Paleogene morozovellids was constructed by concentration and piling of muricae along the periphery. It is essentially a masonry type of construction that tends to be bulky. The simple, inflational keel utilized during the Neogene is analogous to the man-made laminate type of construction, which is an efficient structural support. Nevertheless, the morozovellids constructed ventroconical shells about as large as *G. truncatulinoides* and were a successful group. There is no evidence that the masonry technique of keel construction was inadequate. The minor development of lamellar folds in *Planorotalites* might be taken to indicate that they were less advanced than those in *Globorotalia.* But scale is important here. Planorotalids were small taxa and only in large menardine shells of the Neogene are strong folds found.

Apertural and umbilical apparatus, so highly developed in evolutely coiled Cretaceous taxa, yet so conspicuously absent in the Neogene, may also be size-related if its function was protective. This argument is supported particularly by the development of analogous structures in *G. pertenuis*, which, in Cretaceous style, developed a large, evolutely coiled shell.

Relative to earlier globorotalid radiations, Neogene to Recent taxa are characterized by simple design and features lost rather than features gained. We cannot judge whether design was improved. Indeed, with presumed independence of ancestry, there is no reason to expect improvement. The distinctive characters of Neogene taxa can be characterized as modulating the strong (adaptive?) signal of shell shape that unites the radiations. The modulating information is derived from founders and trends, such as size that developed within the radiation.

Biogeography

SOME PRECEPTS

Probably the single most difficult concept to grasp of the biogeography of planktonic organisms is that it is dynamic. The difficulty arises because of a natural tendency to reduce all phenomena to simple, static terms and thus assign particular physical or geographic boundaries to species distributions. Yet, the ocean is in constant motion and the movement of the water causes faunal displacement; planktonic species, therefore, must be adapted to a mobile existence and they are not easily compartmentalized. We should also realize that the parallels of latitude are man-made constructs and not, in themselves, natural phenomena. In the North Atlantic (Cifelli and Beniér, 1976; Cifelli, 1979), it was found that the distribution of planktonic foraminifera makes a sensible pattern if the factors of ocean climate, dispersal routes dictated by watermass circulation, and boundary conditions are taken into account. Pteropods show a strikingly similar pattern in distribution (Cifelli and McCloy, 1983). The pattern of neither planktonic group makes much sense if species are grouped according to specific temperature or latitudinal ranges. Of course, the North Atlantic is not typical of all oceans, because it is a small basin, has an unusually strong boundary current (Gulf Stream), and a climate markedly skewed with respect to latitude. Moreover, the North Atlantic studies deal only with the advective processes that affect distribution and take no account of the convective processes that also must be of some importance, particularly in areas of upwelling. Also, there are poorly understood biologic factors involved (Cifelli and McCloy, 1983), so that too literal a reading of the North Atlantic record for interpretations elswhere, or in the past, is ill-advised. Nevertheless, there are certain aspects of distributional relationships that should apply to all oceans, present or past. In fact, there is an ordering of foraminifera that seems to be general throughout the world oceans (Bradshaw, 1959; Boltovskoy, 1969; Parker, 1960), indicating a commonality of certain dynamic processes. In the North Atlantic, as elsewhere, planktonic foraminifera are divisible into cold water and warm water faunas, with the cold water fauna being characterized by low diversity and the warm water fauna by high diversity. The boundary between these faunas is always associated with the boundary that separates the cold temperature waters from the warm gyral waters. In the North Atlantic this boundary is sharply marked by the Gulf Stream, a fast set of moving currents, across which there is a strong temperature gradient. It is important to recognize that the Gulf Stream is the boundary of a very large body of warm, gyral water and not a river of warm water flowing through a cold ocean (Stommel, 1965:174). In other oceans, which are much larger, temperature gradients between temperate and warm, gyral waters are less steep and the boundary is more diffuse. Nevertheless, as a general principle, one would always expect to find, when proceeding from temperate to gyral waters, a low diversity fauna eventually replaced by a high diversity fauna of a different species composition.

The warm water fauna is divisible into subtropical and tropical subfaunas, or assemblages, but the distinction between them is not strongly marked, since a number of species characterize both assemblages. The subtropical assembly can be thought of as occupying the gyral waters, and the tropical assemblage the bounding equatorial current system. While diversity is somewhat higher, overall, in the tropical assemblage, the difference is not appreciable. In turn, the cold water fauna is divisible into temperate, subpolar, and polar assemblages. Diversity is very low in all assemblages and is lowest in the polar assemblage, which is monospecific. In the North Atlantic, the temperate assemblages occupy the slope waters and are separated from the subpolar assemblage by the Labrador Current. The polar assemblage occupies the high arctic regions and is limited in distribution.

The above breakdown of faunal divisions, which is paralleled by the pteropods, must be a reflection of the climatic constraints on the distribution of plankton. However, these faunal divisions reflect only the static aspects of distribution and should not be taken to reflect the total pattern of distribution as it actually exists in the water column or on the ocean bottom. The gyres, rotating in a roughly circular fashion, cause displacement and expatriation of species beyond their preferred habitats, so that large parts of the ocean may contain assemblages of mixed composition and origin. In the North Atlantic, rotation is clockwise, so that displacement is towards the north on the western side of the ocean and towards the south on the eastern side. Most of the mixing occurs around the gyral margins, which negates the latitudinally compartmentalized faunal provinces implicit in the methods of stratigraphers. There is, of course, a latitudinal component in plankton distribution but, as noted before, latitude is not in itself a fact of nature. Stratigraphers are increasingly inclined to recognize high latitude and tropical zonations (Srinivasan and Kennett, 1981a, fig. 13). A two-fold scheme of this sort may carry certain practical advantages, but it should also be realized that it has totally artificial implications. Nowhere could a line be drawn between the areas of applicability of the zonations since mixed associations of temperate-subtropical, subtropical-tropical, and even temperate-subtropical-tropical forms occur in various parts of the ocean along gyral margins. Moreover, the latitudinal displacement of species may be considerable, as can be seen from a comparison of assemblages from the western and eastern side of the North Atlantic (Figure 30). On the western side, in the temperate waters adjacent to the western boundary current (Gulf Stream) at about latitudes 40°–42°N, the temperate *Globigerina bulloides*, *G. incompta*, *G. egelida*, and *Globorotalia inflata* occur in association with a diverse group of subtropical forms that include species of *Globigerinoides* and *Globigerinella aequilateralis*, as well as tropical forms such as *Globorotalia cultrata*. The tropical forms are rarely abundant, but their presence is conspicuous. The temperate and subtropical forms are brought into association by the mixing that occurs in the vicinity of the boundary current, while the tropical elements are expatriates that are introduced by the northward movement of the gyre. On the eastern side of the ocean, essentially the same types of mixed assemblage are found, but at latitudes between about 10°–20°N. The principal difference is that in the eastern assemblage, the temperate forms are minor components, carried southward by the eastern arm of the gyre. This type of latitudinal displacement is not unique to the North Atlantic. In the South Pacific, where the circulation is counterclockwise, *G. cultrata* is limited to the equatorial region on the eastern side (Parker, 1960) but may extend to latitude 35°S or higher on the western side (Eade, 1973). Displacement of tropical forms such as the menardines can afford a clue to past patterns of circulation.

The Neogene assemblages do not lend themselves to a high versus low latitude categorization

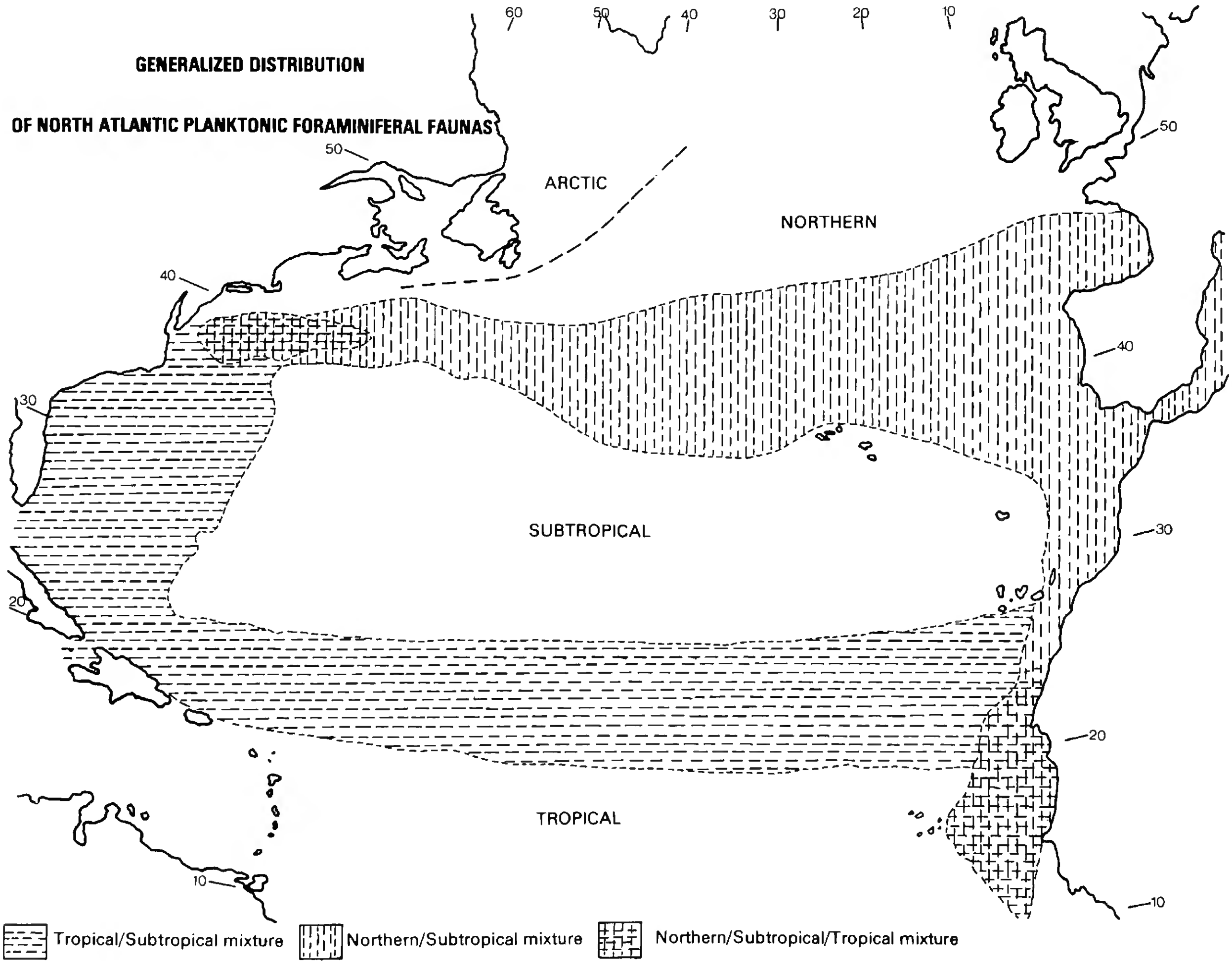


FIGURE 30.—Generalized distribution of major planktonic foraminiferal assemblages in the North Atlantic showing broad zones of mixing (after Cifelli and Beniér, 1976).

any more than do the Recent assemblages. This is amply demonstrated by the important discovery by Poore and Berggren (1974) of an early Pliocene mixed assemblage in a DSDP core located in the Labrador Current at about latitude 50°N. The assemblage contained not only temperate globigerine and typical subtropical forms but also some characteristic tropical elements, such as *Globorotalia tumida*, *G. menardii*, and *Sphaeroidinella dehiscens*. Such an association, in fact, is typical of the kind found in the Gulf Stream, as noted by Poore and Berggren. Its occurrence some 10° or more north of the present Gulf Stream therefore has a special significance. It cannot be viewed as an indication of a wayward path of the Gulf Stream during the Pliocene, since the Gulf Stream cannot flow independently of adjacent waters. The best assumption is that the mixed Pliocene assemblage is indicative of a boundary current, like the modern Gulf Stream and that the tropical elements were introduced via the clockwise motion of the gyre. From this, it would appear that warm gyral water was expanded far north of its present limits in the western part of the North Atlantic during the early Pliocene (Cifelli, 1976a).

The ocean is very much a closed system in which no part, theoretically, becomes completely isolated. Even a well-defined boundary, such as the Gulf Stream, does not serve as a complete barrier, as evidenced by the mixed assemblages found in its vicinity. Isolated bodies, such as the detached eddies of the Gulf Stream, are ephemeral entities that lose their identity after a month or so. The Mediterranean has the appearance of an isolated portion of the North Atlantic, but it is not. Water is renewed from the Atlantic, about every hundred years and the Mediterranean planktonic fauna shows no sign of endemism (Cifelli, 1974). If planktonic organisms were like plastic drift cards and immune to the environment, they probably would inhabit every part of the ocean, as suggested by the experiments of Shannon and others (1973). Indeed, the generally uniform ordering of planktonic species with respect to watermasses throughout the world suggests that the ocean is a kind of huge "mixing bowl," although the actual routes and times of dispersal from one ocean basin to another remain a mystery. Yet, lines of communication are not always completely maintained. The temperate-subpolar *Globorotalia truncatulinoides* variant, characteristic of the southern ocean, but absent in the north, is an example of interregional differences in population structure. Therefore, oceanic circulation does not completely negate the possibility of some genetic isolation, and there is no reason to expect that fossil planktonic species will be totally lacking in interregional variation.

ADAPTIVE STRATEGY

The gross pattern of Neogene globorotalid development, showing a strong unidirectional trend at its beginning and a more varied development after the middle Miocene, suggests that the shell modifications occurred as adaptive responses to a changing environment. This will be reviewed in the following section; here we deal with general aspects of adaptive strategy.

There is a generally symmetrical relationship between the distribution of planktonic foraminifera and watermasses at the present time. That is, species tend to be cosmopolitan, but at the same time they tend to have preferred habitats. The symmetry is not, by any means, perfect. There are a few species that show a preference for a particular ocean, and there are two species of *Globorotalia* that are inconsistent in their habitat preferences. Nevertheless, in a given set of hydrographic circumstances, it is usually possible to predict the overall composition of an assemblage with a reasonable degree of confidence. Circulation and seasonality are factors that strongly affect the composition of planktonic assemblages.

The modern menardines have made the tropical waters their special domain (Figure 31) and are associated with water bounded by the North and South equatorial currents. They are not confined to these waters, since they are expatriated by currents and may be found in subtropical and even temperate waters along gyral margins. Nevertheless, they maintain a good stable relationship with watermasses throughout the oceans. In all, there are perhaps five menardine species of which the disk-like *G. cultrata* is the most common. The menardines appear to be more diverse in the Indian Ocean than elsewhere.

The principal domain of the remaining, nonmenardine, *Globorotalia* is the subtropical water of the central gyres. Modern *Globorotalia* that are endemic, or at least partially endemic, to subtropical water are *Globorotalia inflata* (globose chambers, no keel); *G. truncatulinoides* (ventroconical, keeled); *G. crassaformis* (inflated discoidal to globose, mostly non-keeled); *G. hirsuta* (spiroconical, keeled); *G. crassula* (discoidal, sometimes compressed, usually keeled); *G. scitula* (discoidal, weakly compressed, no keel). In general, these species have maintained a less stable relationship with their habitat than the menardines. At the present time they may extend into the tropics but tend to avoid the equatorial domain of the menardines. Their exclusion from this region is a relatively new phenomenon, since they are found fairly commonly in Pleistocene sediments.

Of the nonmenardine *Globorotalia*, *G. inflata* and *G. truncatulinoides* have proven the most successful. However, both of the species are highly inconsistent in their habitat preference. *Globorotalia inflata* is a characteristic temperate species in the North Atlantic and only rarely is it found in abundance in the Central Gyre (Cifelli and McCloy, 1983). In the North Pacific, this species is characteristic of the Central Gyre (Bradshaw, 1959). In the South Atlantic it is mostly temperate, as in the North Atlantic (Bé, 1969). *Globorotalia truncatulinoides* is a typical member of winter assemblages in the North Atlantic and North Pacific gyres. However, in the Southern Ocean, this species flourishes in the subantarctic waters and is scarce in the Central

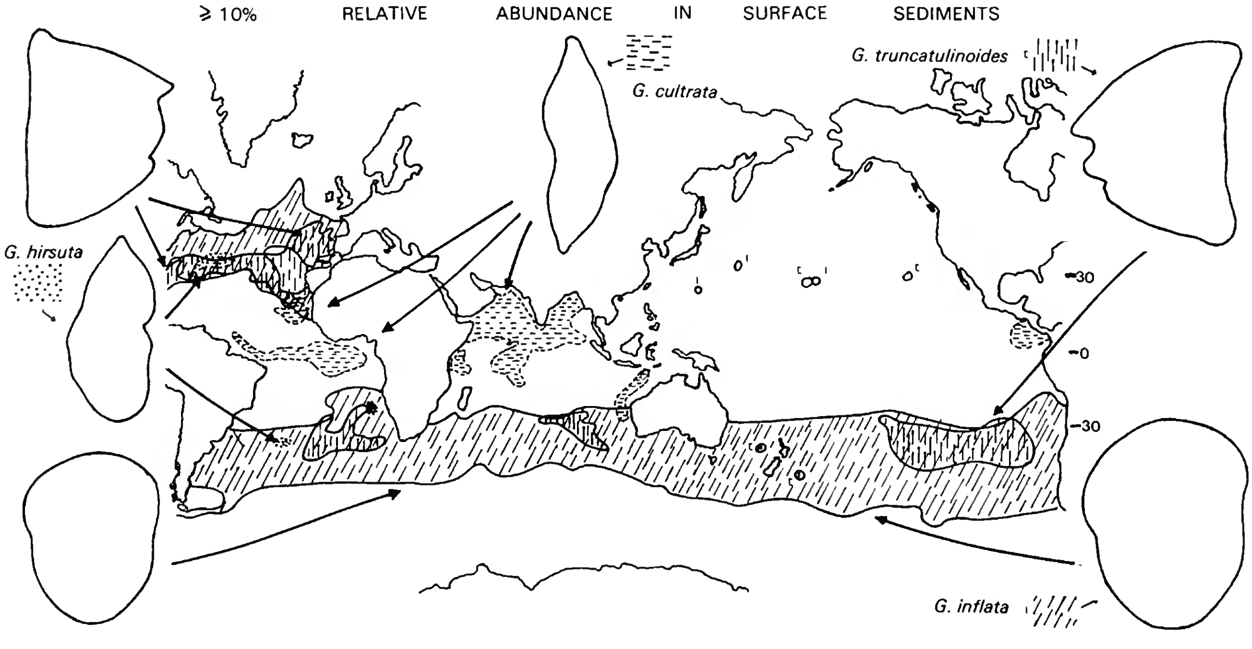


FIGURE 31.—Relative abundance (frequencies ≥ 10% are shaded) of taxa representing the major globorotalid architectures (after Bé, 1977).

Gyre (Bé, 1969). Except for *G. hirsuta*, the remaining nonmenardine *Globorotalia* generally do not occur commonly in the modern ocean. The reason for the general lack of a stable relationship with habitat preference is not clear but is reminiscent of a similar lack of stability on the part of the pteropods in the North Atlantic (Cifelli and McCloy, 1983).

AN HISTORIC PERSPECTIVE ON THE EVOLUTION OF FORM

A principal feature of the Neogene radiation is the sequential appearance of the various shell designs found in the Recent. The main early Miocene lineages developed axially compressed chambers. Spiroconical populations expanded after the early acme of the latter and were succeeded in order by ventroconical and globose forms. About 15 m.y. elapsed between the initiation of the early lineages and the completion of the modern range of shell architectures. What is the significance of this pattern? Does it indicate that new niches became available during the Neogene?

To provide further insight into the evolution of form we examine the distribution of new architectures and the timing of their arrival in relation to the history of marine temperatures. We select this watermass parameter because its history through the Neogene has been quantified by oxygen isotope studies and because of its likely influence on life processes and population histories of plankton. Climatic history provides a broad guide to the evolution of planktonic environments. Although paleotemperature data from a high latitude site (Figure 32) and from a tropical and high latitude synthesis (Figure 33) are considered in relation to events in the globorotalid radiation, there are major fluctuations in some sequences (e.g., at DSDP Site 357, South Atlantic; Boersma and Shackleton, 1977) that are not obvious in Figures 32 and 33. Further, fluctuations of comparable magnitude to those reported by Boersma and Shackleton in the lower Miocene, have been recorded with a periodicity of about 0.3 m.y. in a New Zealand lower Miocene sequence (Nelson and Burns, 1982). Thus the temperature data, like that on geographic distributions of taxa, should certainly be regarded as provisional, and generalized.

The upper Oligocene planktonic assemblage was dominated by globigerines and paragloborotalids. Such taxa used quasispherical chambers throughout ontogeny. About this time, *Globoquadrina* was the most notable taxon (nonspinose) in which compressed chambers were formed in later ontogeny. The predominant upper Oligocene architectures correspond with those of modern, high-latitude taxa (e.g., *Globigerina bulloides, Neogloboquadrina pachyderma*). There was considerably less architectural diversity than in the modern planktonic assemblage. Architectures characteristic of modern subtropical and tropical assemblages such as globigerines with supplementary apertures, planispiral taxa, and compressed globorotalids were absent (Keller, 1983, fig. 2).

Lower Miocene globorotalids appeared in a period when surface water temperatures were rising. Perhaps significantly, there was a parallel expansion of *Globigerinoides* at this time. Tropical temperatures (Figure 33) rose progressively and gradually in the lower Miocene, leading to a maximum in the interval of Zones N9–N13. However, Boersma and Shackleton (1977) reported an earlier temperature peak in Zones N5–N6 in a South Atlantic sequence (30°S). This event may be related to the appearance of *Globorotalia praescitula* in the temperate Southwest Pacific about the base of Zone N6. Its entry there coincides approximately with a marked increase in the abundance and distribution of the *Globigerinoides trilobus* group, which, like its recent relatives, was probably a warm water form. Populations of the *Globorotalia zealandica* lineage also expanded about N6 in the Southwest Pacific.

In the founding period of the radiation (Zones N5–N7) regional differences in architecture

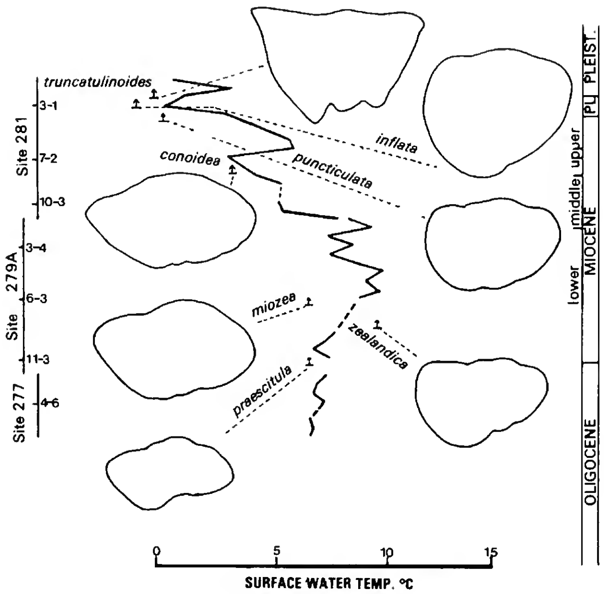


FIGURE 32.—Relation between history of surface water temperatures at high latitude Southwest Pacific sites and the appearance of some major globorotalid architectures. Temperatures estimated from oxygen isotope analyses of planktonic foraminifera from DSDP Sites 277, 279A, 281, latitudes 48°–52°S (afer Shackleton and Kennett, 1975, fig. 2; biostratigraphic data after Jenkins, 1975).

were minor, suggesting good communication between well-dispersed, but relatively small, populations. However, differences in the biogeographies of the two principal lineages are apparent. *Globorotalia praescitula* established a wide extratropical distribution in this interval, and extended poleward to at least 50°S in the Pacific (Jenkins, 1975; DSDP Site 279) and to 63°N in the Atlantic (Poore, 1979, fig. 3; DSDP Site 408). *Fohsella peripheroronda* did not extend as far poleward. It was not recorded from the North Atlantic site in this interval, while in the Southern Hemisphere it did not reach northeastern New Zealand (38°S). Subsequently, however, as marine temperatures rose further in Zones N8–N12, *F peripheroronda* expanded poleward and occurs at both Sites 279 and 408.

The mid-Miocene thermal maximum, as depicted by Savin and others (1975), coincided with the culmination of the early phase of the Neogene radiation (Figure 33). Axial compression of chambers was the principal architectural trend in this phase and the only lineage (*Globorotalia zealandica*) not to pursue this trend was the least

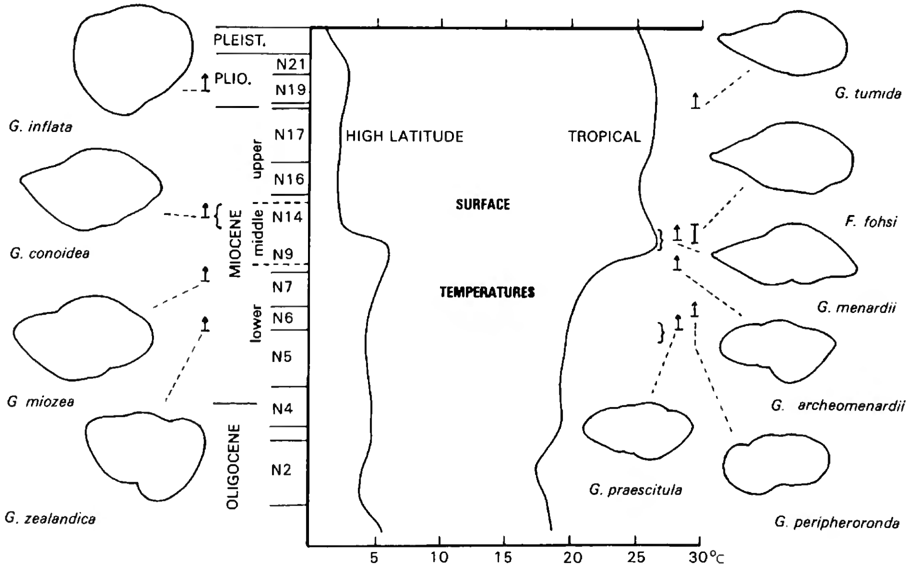


FIGURE 33.—Synthesis of tropical and high latitude temperature regimes (Oligocene–Quaternary), after Savin, and others, (1975, figs. 6–7a). Events in the tropical records (at right) of *Globorotalia* and *Fohsella* are positioned after Blow (1969). Events at left are located by their record in the temperate Southwest Pacific. Some detailed high latitude data are given in Figure 32.

successful (in population sizes and distribution). However, *Fohsella* and the *Globorotalia praescitula* plexus recorded significantly different histories during the build up to the temperature maximum. In *Fohsella*, the branch leading to *F. robusta* originated about Zones N9–N10 but there was no comparable divergence in the *G. praescitula* plexus during this period. Further, the distribution of the innovative populations of the *Fohsella robusta* branch began to progressively contract and to become confined to warm waters in the Pacific (Figure 34). In this ocean the distribution of *F. robusta*, the most advanced member, lies close to the modern tropics, whereas contemporary populations of *G. praemenardii* maintained the wide distribution that the *G. praescitula* plexus had previously established. Data from the western North Atlantic do not conform to this simple pattern, as there are records (Bartlett, 1968) from 46°N that probably reflect the operation of a Miocene Gulf Stream that introduced tropical planktonic assemblages to a region that now supports subarctic taxa (Cifelli and McCloy, 1983).

The middle Miocene temperature maximum was followed by a minor decrease in the tropics but a major decline in the temperature of high southern latitude water (Figure 32). As we have noted, it is quite uncertain whether the change in temperature regime was a factor in the extinction of *Fohsella robusta*. However, it is likely to have led to greater differentiation of water-masses between the poles and the tropics. Savin and others (1975) attributed the thermal decoupling to the development of the modern circum-Antarctic circulation and thermal isolation of Antarctica, which resulted in a redistribution of solar energy. Berger and others (1981) further analyzed the change. Loutit and others (1983) showed that in the South Pacific oceanic thermal structure substantially changed (vertically and horizontally) and considered that the warm South Pacific subtropical gyres became decoupled from the Southern Ocean as zonal circulation developed. Such a new regime may have had an important effect on the biogeography of the *Globorotalia praescitula* plexus. When temperatures were rising, *G. praemenardii* ranged very widely. Subsequently, populations were partitioned into *G. conoidea* and *G. menardii*. *Globorotalia conoidea*, architecturally a fully keeled version of *G. praemenardii*, maintained the latter's broad latitudinal distribution. In contrast, the disk-like *G. menardii* became centered in the tropics (Figure 35). Again, however, there is an exceptional distribution in the North Atlantic where it extended to at least 57°N (Poore and Berggren, 1975), as well as into the Mediterranean. On this basis, Cifelli (1976a) and Cifelli and Glaçon (1979) proposed that there was a highly expanded mass of warm gyral water in the Atlantic during the upper Miocene, with the western boundary of the gyre in the vicinity of Newfoundland. This expansion persisted into the lower Pliocene in the western Atlantic. Retraction occurred in the east, however, as suggested by the absence of the menardine group in the Mediterranean and adjacent Atlantic. There is no suggestion of similar poleward expansion in the Southwest Pacific. In the latitudes of New Zealand (34°–47°S) *G. menardii* appeared about Zone N15, significantly after its origin in the tropics. Specimens are small and are rarely found beyond 40°S.

The major feature of the later phase of the radiation is that novel architectures developed beyond the tropics during the upper Miocene. Although there are earlier prototypes associated with *Globorotalia praemenardii*, distinct spiroconical populations of *G. panda* did not develop until about Zone N14 in the New Zealand region of the Southwest Pacific, and the strongest spiral convexity occurred still later (about Zone N16). The largest populations occur north of 40°S. *Globorotalia panda* occurs northward to about 30°S in the Southern Hemisphere (DSDP Site 206, South Pacific; Rio Grande Rise, South Atlantic), and Poore (1979, table 5) recorded it from DSDP Site 410 in the North Atlantic (45°N). The absence of records from the tropics possibly indicates that, like its modern counterpart (*G. hirsuta*), it inhabited the subtropical to transitional zones. The distribution of *G. panda* possibly correlates well with the upper Miocene

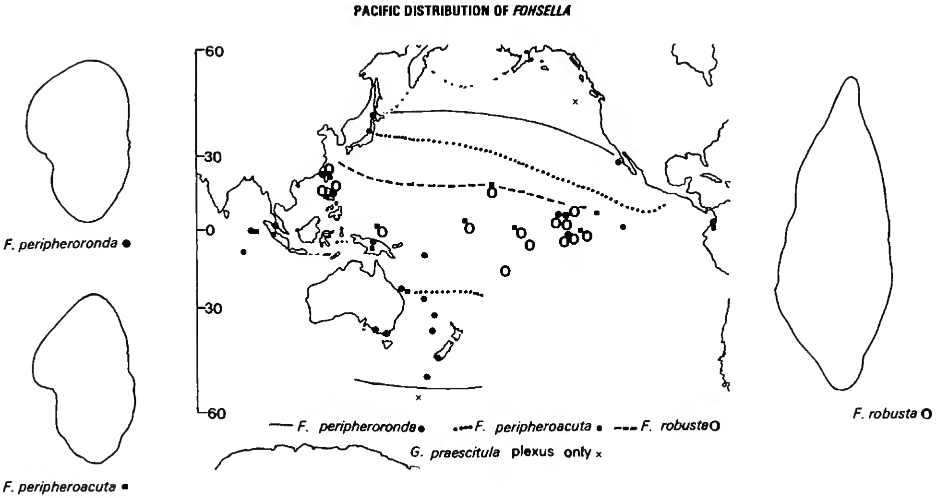


FIGURE 34.—Paleobiogeography of *Fohsella* in the Pacific (modified from Saito, 1977). Development of a large, axially compressed shell (culminating in *F. robusta*) occurred as populations contracted towards the Central Pacific. However, the smaller, more primitive *F. peripheroronda* continued to occupy southern temperate water. Saito's records of *F. lobata* have been amalgamated with those of *F. robusta*. Axial outlines of topotypes of *F. peripheroronda* and *F. peripheroacuta*, and of the holotype of *F. lobata* (here regarded as a synonym of *F. robusta*) are from Blow and Banner (1966, pl. 2: figs. 3–4, text-fig. 4–1*b*) and are redrawn to a common scale.

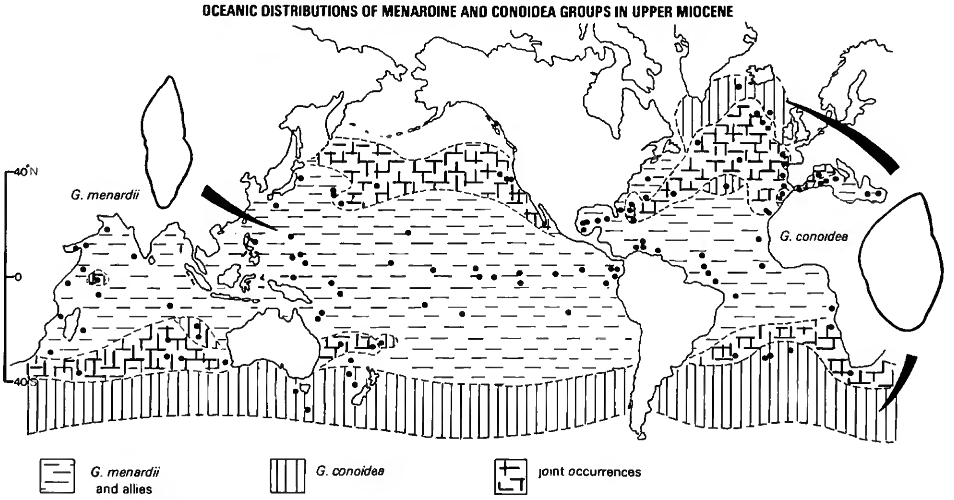


FIGURE 35.—Major partitioning in the biogeography of the *Globorotalia praescitula* plexus developed in the upper Miocene. Axially compressed, menardine taxa beame centered on the tropics whereas the more ventrally vaulted *G. conoidea* group (architecturally similar to the ancestral *G. praemenardii*) occupied temperate watermasses. However, there are broad zones of mixed assemblages at the interface of the menardine and *conoidea* provinces. In the North Atlantic the northward extension of tropical taxa in the upper Miocene was greater than in modern seas (Figure 30). (Data from DSDP sites after Berggren, 1984, fig. 2); menardine records include *G. menardii*, *G. limbata*, *G. plesiotumida*, and *G. merotumida*.)

emergence of the subtropical gyres in the Pacific.

The earliest ventroconical shells appeared still later in the upper Miocene thermal decline. As with the spiroconical *Globorotalia panda*, the evidence is primarily from the Southern Hemisphere midlatitudes. Throughout their history, southern populations of *G. conoidea* included individuals in which chambers extended ventrally. This feature developed strongly in the uppermost Miocene (about Zone N17) and particularly in crust-free individuals. In some, the extension is as pronounced as in *G. truncatulinoides*. Northern Hemisphere relatives of *G. conoidea* do not show marked ventroconical form (Figure 13*q*,*r*). A further indication that southern populations were relatively isolated from northern ones in the upper Miocene is the reduction in the number of chambers in the outer whorl to about four in the former, while the latter retain five chambers. The ventroconical development in southern populations of *G. conoidea* continued into the basal Pliocene (as *G. mons*) and then ceased. It was much less successful (in terms of geographic distribution) than was achieved subsequently by *G. truncatulinoides*.

The most dramatic architectural development in the second phase of the radiation probably originated in the southern midlatitudes near the base of the Pliocene. Onset of chamber inflation (and shell globosity) in *Globorotalia puncticulata* reversed the primary architectural trend of the first phase of the radiation. Eventually *G. inflata* became one of the principal extratropical foraminifers, demonstrating the high degree of plasticity in shell design and adaptive potential of the *G. praescitula* plexus.

By mid-Pliocene all major shell designs found in the Recent had been implemented at least once. Repetitions of forms characterize the late history of the radiation. Speciation occurred in the tropical menardines, but the basic, axially compressed architecture was always retained. Another spiroconical form, *Globorotalia margaritae*, developed near the base of the Pliocene, probably from a scituline. Globose forms of *G. crassaformis* (*G. ronda*) appeared in the upper Pliocene in subtropics and tropics. The development of the strongly ventroconical *G. truncatulinoides* lineage is best recorded in subtropical and tropical sequences, although a variant form now shows a preference for subpolar waters in the Southern Ocean.

Are there correlations between Neogene and Recent distributions of taxa with similar shell designs and does the order of appearance of designs correlate with watermass history? The paleogeography of taxa with axially compressed, menardine shells most closely corresponds with the Recent distribution. This design evolved during a period of rising marine temperatures and has since been associated with tropical and subtropical watermasses. The distribution of fossil spiroconical taxa may correspond quite closely with that of their modern counterpart, *Globorotalia hirsuta*. Their paleobiogeography may be related to the differentiation of subtropical to transitional watermasses after the middle Miocene.

Ventroconical and globose designs show less consistent biogeographic patterns. *Globorotalia mons* and *G. conomiozea* morphotypes of *G. conoidea* preferred southern temperate water, whereas *G. truncatulinoides* probably arose in warmer water and subsequently spread into cooler environments. The globose *G. inflata* maintains largest populations in southern temperate water (its ancestors may have originated there), whereas a similar globose design in the *G. crassaformis* plexus (*G. ronda*) occupied subtropical to tropical environments. Such examples suggest that there is not a close correlation between watermass type and certain shell designs. Indeed, the history of *G. truncatulinoides* shows that a taxon may develop an advanced design in low latitudes and then expand poleward. These considerations possibly call into question the extent to which the warm water preference of the menardine design is due to architecture per se. Nevertheless, the history of design developments indicates clearly that diversification occurred in a relatively short period in the upper Miocene and Pliocene. It seems unlikely that this is simply coincidental. It occurred at a time when temperatures of high southern latitude water were very low, but with short-term oscillations (Blank and Margolis, 1975; Kennett and others, 1979), while those of tropical water were high (Figure 33). Keller (1979b) produced evidence of oscillatory temperature regimes in the midlatitudes of the North Pacific at this time, as did Zachariasse and Spaak (1983) from the Mediterranean. Such regimes imply greater differentiation of watermasses, an expanded range of potential habitats, and possibly improved isolation of populations undergoing architectural transformations (allowing founders a greater chance of survival). This scenario contrasts with that of the lower and middle Miocene, when the thermal gradient between poles and equator was considerably reduced. The very broad distribution of such taxa as *Fohsella peripheroronda*, *Globorotalia miozea*, and *G. praemenardii* and the limited amount of architectural diversity may indirectly reflect much weaker differentiation of watermasses.

BATHYMETRY AND ARCHITECTURE

As planktonic foraminifera occupy the upper few hundred meters of the modern oceans, their biogeographic domain has a significant third dimension. Hart (1980) and Caron and Homewood (1983) have stressed the biogeographic importance of the vertical distribution of planktonic taxa and have proposed that the repeated adaptive radiations that characterize their history represent successive attempts to colonize bathypelagic environments. Analogous with Bé's (1977) classification of modern depth habitats, "bathypelagic" loosely signifies the zone from 100 m down to about 1000 m. Primarily from Cretaceous evidence, these authors have argued that colonization of deep water and development of advanced architectures (including globorotalid styles) occurred when upper levels of oceans were well stratified, currents sluggish, and upwelling was reduced. These conditions are correlated with periods of warm, stable climate in which sea level was rising and nutrient supply diminishing. Planktonic radiations into bathypelagic habitats terminated when these conditions led to anoxic events that caused ecosystem "crashes." In addition, Caron and Homewood (1983) considered that bathypelagic taxa, characterized by advanced architectures like those of the globorotalids, tended to be K-strategists, with longer lifecycles, larger individuals, and smaller populations than the epipelagic r-strategist globigerine taxa, which retained conservative shell designs. MacArthur and Wilson (1967:147–180) discuss K- and r-selection.

To what extent does the evolution of architecture in the Neogene globorotalid radiation fit this model? An important perspective is provided by the bathymetric distribution of modern globorotalids.

Because the vertical distribution of many taxa is wide and highly variable, Bé (1977:28) cautioned that their depth classification is valid only in a statistical sense. The depth at which maximum concentration of specimens occurs can shift very rapidly. Sampling by Fairbanks and others (1982) in the Panama Basin showed that *G. theyeri* (a compressed variant of *G. crassula*) moved about 170 m per day over a vertical distance of 600 m. Various factors, including stage in ontogeny, reproduction, watermass location, and position of trophic resources (Hemleben and Spindler, 1983) influence the daily and seasonal distribution of populations.

Although the constraints just noted prejudice generalizations, data from plankton tows (summarized by Berger, 1969) support isotopic data (Lidz and others, 1968; Oba, 1969; Hecht and Savin, 1972) that globorotalids are the predominant taxa in the deepest habitats occupied by planktonic foraminifera (Figure 36). These are generally below the photic zone and the tropical thermocline.

Axially compressed menardine shells tend to maintain higher positions in the water column than the ventroconical *G. truncatulinoides*. As discoidal architecture evolved well before ventroconical, it might be argued from premises of a bathymetric radiation, that ventroconical shells represent a further penetration of deep planktonic environments. However, this conclusion is at variance with the evidence of *G. scitula*, for example. The architecture of this taxon resembles that of *G. praescitula*, which was one of the founders of the radiation and, in terms of the bathymetric theory, probably epipelagic. In neither is chamber compression advanced. Yet modern populations of *G. scitula* occupy particularly deep sites (500–1000 m) in the Antarctic (Bé, 1977:26).

Settling rates of shells are possibly relevant to colonization of bathypelagic environments. As well as size, and the relative densities of (shell + organism) and ocean, the rate of passive sinking is affected by shell shape (Hutchinson, 1967:260–270; Smayda, 1970:357). On a water depth model of globorotalid evolution, advanced architectures might provide hydromechanical advantages relevant to maintaining particular positions in the water column. Empirical data (Figure 36) on shell settling rates is flawed for evaluating this question because it is based on empty shells and entirely neglects effects of spine loss (on globigerines) and of life processes (e.g., vacuole formation and lipid concentration; Anderson and Bé, 1976:17) that considerably influence buoyancy. However, the data show that spinose globigerine taxa have the slowest rates of descent; this is consistent with their preference for the photic zone. Globorotalids have a wide spectrum of rates and there is no simple relation between their shape and settling velocity. Size probably accounts for the rapid sinking rate of *G. tumida* (Figure 36). Menardine shells are the largest in the Neogene planktonic assemblage, and a phyletic trend for size increase occurred early in their history as axial compression of chambers developed. Discoidal shape offers improved form resistance (Hutchinson, 1967:265; Scott, 1973b:145) and it may have developed in the *G. praescitula* plexus and *Fohsella* as a technique for reducing the sinking rate of large shells. With all other factors held constant, discoidal shape will reduce settling velocity and its evolution relates more simply with size increase than with occupancy of a deep position in the water column. However, the globose shape of *G. inflata* should, theoretically, have poorer form resistance than discoidal shells (its experimental velocity is high, Figure 36), and such a design might facilitate depth migration.

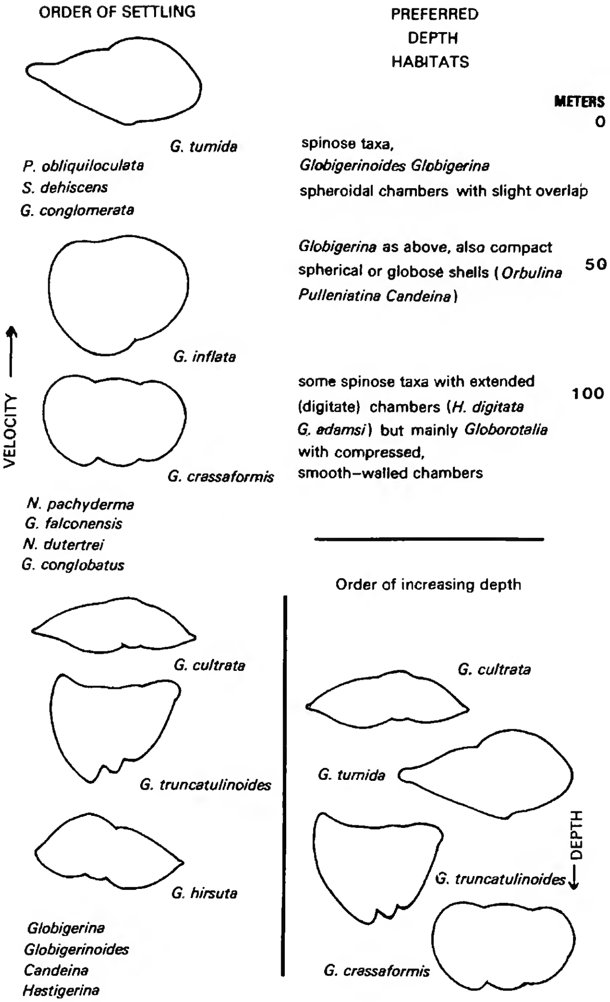


FIGURE 36.—*Right*, Summary of data on depth stratification of Recent planktonic taxa (Bé, 1977). The globorotalid order is an average of the ranked data compiled from several studies by Douglas and Savin (1978). Note that *Globorotalia scitula* (not shown) occupies deep sites (500–1000 m) in the sub-Antarctic (Bé, 1977:26). *Left*, Order of settling velocities (after Berger and Piper, 1972).

While there is no firm evidence that the founders of the Neogene globorotalid radiation were epipelagic, the onset of encrustation in southern populations of the *G. praescitula* plexus within Zone N7 may indicate occupancy of deep water quite early in the phylogeny of that group. Douglas and Savin (1978:179) gave isotopic evidence that *Fohsella* was deep dwelling by Zone N12.

Further, the early history of the radiation matches some features of the Cretaceous scenario depicted by Caron and Homewood (1983). Seas were transgressive (Berger and others, 1981), ocean temperatures were rising, and variation patterns and the biogeography of the major lineages suggests that watermass differentiation was weak. Bathypelagic populations developed, at least in the southern oceans. But environmental changes during the upper Miocene and Pliocene (regressive seas, oscillating but generally cooler ocean climate at high latitudes, intensified ocean circulation and perhaps weaker stratification) match those which Caron and Homewood regard as unfavorable to deep water colonizers. Their model predicts habitat contraction in such conditions, with conservative, globigerine architectures predominating. In fact, the record in this period was of architectural diversification in the globorotalids, particularly beyond the tropics. There is no indication of habitat contraction.

There is insufficient information on life processes and trophic patterns of modern globorotalids (Bé and others, 1977) to allow confident assessment of their relation with shell design. Whether globorotalids are K-strategists with long life cycles, and whether this also has a bearing on architectural specialization are unknown.

We conclude that, while there is evidence that the habitat of Neogene-Recent globorotalids extended over a considerably greater bathymetric range than that of the spinose globigerines, no close relation between architecture and preferred depth habitat is apparent. Architectural innovation seems to be more closely correlated with climatic and ocean histories than with invasion of deep oceanic environments, although this occurred. Recall that some Paleogene morozovellids, counterparts of the Neogene ventroconical design, seem to have occupied epipelagic rather than bathypelagic environments.

Evolutionary Patterns

We have traced the history of Neogene globorotalids over a period of about 20 m.y. While the review has pointed to various biostratigraphic and taxonomic problems, there are nevertheless some aspects relevant to current issues in evolutionary biology. The review is made at three levels: Firstly, we briefly summarize the shape of the phyletic tree, the macroscopic record of globorotalid evolution. Turning to the lowest level of analysis, we note some features of ontogeny that influenced the history of lineages. However, most of the discussion concerns the intermediate level and deals with relationships of populations and taxa that form the elements of the phyletic tree.

Shape of the Phyletic Tree

The tree shown in Figure 2 combines hypotheses about relationships with more factual data on taxonomic ranges. There are several principal features.

The radiation has multiple roots and represents a set of lineages or plexi that followed common morphological pathways. Berggren (1966) and McGowran (1968) postulated a single founder taxon (*Turborotalia pseudobulloides*) for the Paleogene radiation. Neogene globorotalids, in contrast, did not develop after a plankton crisis like that at the Cretaceous-Tertiary boundary and a wider range of potential founders existed in the Oligocene than in the lower Paleocene. In this respect the Neogene radiation may be more comparable with the Cretaceous.

The number of separate roots in the tree is uncertain. We show five, but this rises if the *Globorotalia scitula* plexus had a separate origin. Conversely, there may have been as few as three roots if the *G. tumida* lineage belongs to the menardine group (probable), and the *G. crassaformis* plexus arose from the scitulines (possible). Kennett and Srinivasan (1983) postulated three roots for the groups we have studied, but their tree structure is substantially different.

Diversifications occurred particularly between Zones N9–N13 and between Zones N17–N19. The earlier, in a period of ameliorating climate, saw the rise of axially compressed taxa. The later occurred after marked deterioration in high latitude climate and involved an expansion of architectural designs.

Because of its longevity, and diversity of species and architectures, the *Globorotalia praescitula* plexus stands out as the central element of the tree. The radiation would have been substantially limited after the middle Miocene had this plexus gone the way of *Fohsella.*

PATTERN IN INDIVIDUALS

Evolutionary advance has to be implemented via individuals and the ontogenetic pattern greatly influences the macroscopic evolutionary pattern. There are several important common factors in the ontogeny of many taxa in the radiation.

The outstanding feature is that increments in chamber compression invariably occur initially in the last few chambers of the outer whorl (Figure 37).

Relatively gradually, compression of chambers is implemented progressively earlier in ontogeny. Within an individual it is generally weaker in the middle than in the outer whorl, and chambers of the inner whorl (close to the proloculus) are usually unaffected (Figures 24, 37). Similar patterns occur in shells from earlier radiations (Figure 25).

Increase in size of adults occurs generally within lineages. Because the number of chambers formed during ontogeny does not vary greatly (about 15±3) in the history of several lineages, increment in growth rate is likely to have been a general strategy for size increase (Figure 38). However, in axially compressed designs, rate of expansion of the radial diameter of shells is also assisted by changes in chamber shape. C-type chambers in menardine taxa, and advanced T-type chambers in *G. tumida* and in the later fohsellids are examples of this technique. As with changes in axial profiles, these are most prominent in late ontogeny (outer whorl).

Coiling parameters (rates of vertical and horizontal translation of whorls) are fairly uniform in ontogeny. However, the number of chambers per whorl (packing) is varied in several lineages in late ontogeny (decline in *Globorotalia inflata* lineage, increase in some menardine taxa). As with chamber compression, this is a strategy of late ontogeny.

While the effect of earlier onset of chamber compression in successive populations established a recapitulatory pattern in phylogeny, this does not clarify the significance of the strategy in contemporary populations. Functionally, the onset and strongest development of chamber compression at the latest stages of ontogeny suggests

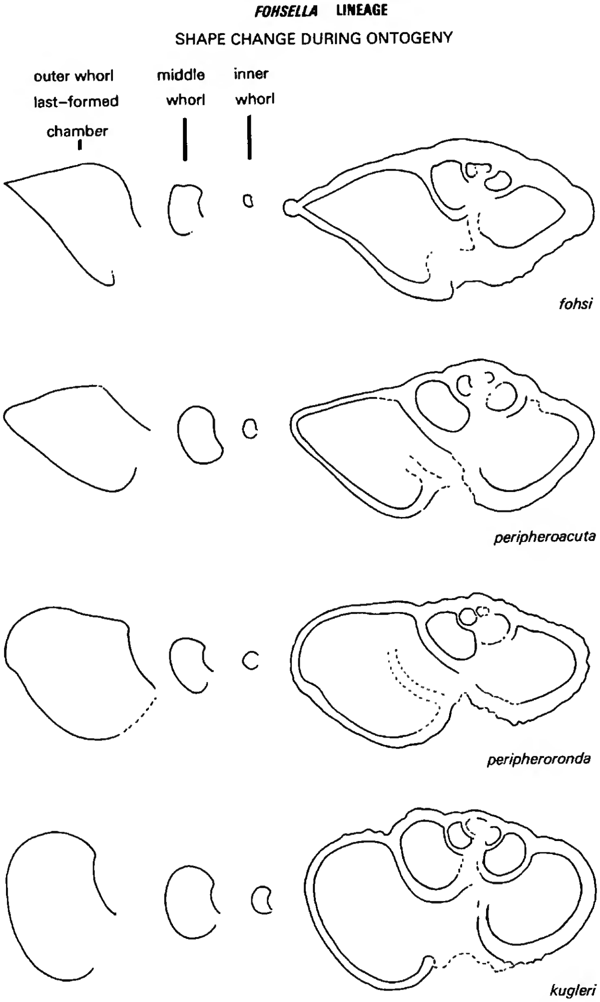


FIGURE 37.—Axial shape of chambers in *Fohsella* (sections redrawn from Postuma, 1971:323, 325, 347, 349). In the early taxon (*F. kugleri*), little change in shape occurs during ontogeny. In succeeding taxa, compression increases progressively in late-formed chambers (outer whorl). Chambers in the middle whorl show weaker and less clearly progressive change.

that it was an architectural response related to shell size. Although still poorly documented (and unfortunately minimized in our SEM illustrations), size increase was a feature of axially compressed *Fohsella* and *Globorotalia* in the early Miocene. Chamber compression was superimposed on this trend. Compression of chambers increases surface area, and probably form resistance. Disk-like shells, theoretically, will sink more slowly than spherical (Lipps, 1979:73; Scott, 1973b). While the organism has other systems that affect buoyancy, it is plausible that the "cost" of a large shell in late ontogeny was diminished by chamber compression. Further, once the compressed design was established, the hydromechanical advantage may have led to its being selected for progressively earlier in ontogeny. A suitable scenario for the initiation of these ontogenetic changes may have been provided by the lower Miocene climatic amelioration, which would have reduced the density of tropical water. In axially compressed shells there may have been two complementary trends in late ontogeny. Modifications to the spiral profile of chambers promoted the development of large shells; compression of the axial profile of chambers reduced the hydrodynamic penalties of size.

If globorotalid innovations had resulted from abrupt developmental changes in early or mid-ontogeny, taxonomic distinctions and phyletic patterns in the radiation would have been more discernible. Instead, during episodes of morphological transformation, innovation late in ontogeny produced a "noisy" signal. There is often a spectrum of adult specimens in a sample, in various stages of advance, depending partly on the proximity of a particular ontogeny to completion and partly on the amount of transformation being achieved in that ontogeny. Variation between populations from different regions compounds the latter influence, with individuals from low latitudes commonly proceeding further with compressive transformations than their higher latitude counterparts.

On the other hand, pattern in late ontogeny is more stable in taxa in which the initiation of major shape transformations have migrated back to mid-ontogeny. A picture of phyletic stasis is affected by long sequences of populations in which adult morphology is relatively static because transformations have occurred earlier in ontogeny.

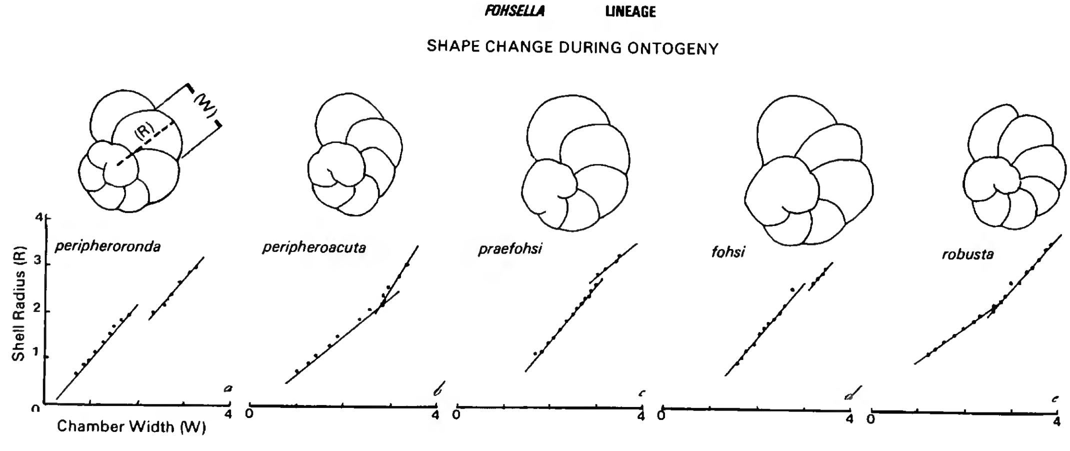


FIGURE 38.—Plots of shell radius and chamber width (logarithmic data) in the ontogenies of specimens of *Fohsella* (after Olsson, 1972, figs. 6–10). Commonly, shape change occurs about mid-ontogeny. Chamber width increases in *a* and *d*; shell radius increases in *b* and *e*. Increments in shell radius (by extension of chambers) is an important technique to achieve larger shell size in late ontogeny. Olsson (1972:174) noted an increase in the number of chambers in specimen *e*. This occurred partly by a decline in rate of width expansion (allowing more chambers per whorl) and partly by modest extension in total degrees of whorl in ontogeny.

PATTERN WITHIN THE TREE

MODELS.—Eldredge and Gould (1972) profoundly altered thinking about evolutionary development when they challenged the traditional view of phyletic gradualism and argued that the fossil record indicated patterns of punctuated equilibria. Following Darwin, paleontologists had traditionally envisaged evolution as primarily phyletic and involving gradual, progressive transformations of entire ancestral populations. Long continued, unidirectional character trends were interpreted, adaptively, as functional improvements to a static, or gradually changing environment. According to the new view, species do not change in a continuous, progressive fashion, but undergo long periods of stasis during which morphological change is either nondirectional or of little consequence. Actual speciation occurs in small, peripherally isolated populations and is associated with rapid modification of morphology. Once the transformation is achieved, the new species expands, and another period of stasis follows under the new adaptive equilibrium that has been forged. An extension to the argument is that selection within lineages occurs at the species level (Stanley, 1979:186–195) and that the process of speciation is decoupled from population dynamics.

Punctuational evolution should leave a distinctive stratigraphic record. The theory postulates that founder populations are so small and the morphological transformation so rapid that no trace of the change is likely to be preserved. Effectively a "revolution on a bedding plane" is hypothesized and recovery of connecting links between ancestors and descendants is improbable. Morphological discontinuities are to be expected and the stratigraphic record will provide a poor guide to ancestry.

The models are of particular interest to paleobiologists because of the contrasting stratigraphic records that they should generate. Potentially, evolutionary mode may be identified from fossils. Note, however, that the models are not strictly alternatives. The punctuational model focuses on speciation and lineage divergence. In contrast, the gradualist model focuses on transformations within lineages. In the following we review relevant features of Neogene globorotalid history and, after consideration of population structure, try to assess their evolutionary mode.

GRADATIONAL VARIATION.—Commonly, there is evidence of intergradation between successive globorotalid taxa. Examples can be cited from all lineages and often relate to extent of chamber compression and keel formation (*Globorotalia miozea–G. praemenardii*; *G. tosaensis–G. truncatulinoides*; *G. martinezi–G. margaritae*; *Fohsella peripheroacuta–F. praefohsi*). But there is also intergradation in taxonomic transitions based on introduction of other features (e.g., C-type chambers, *G.praemenardii–G. menardii*) and on changes in number of chambers per whorl (*G. miocenica–G. pertenuis*; *G. puncticulata–G. inflata*).

Further, globorotalid histories are not characterized by sudden appearances of novel architectures. Indeed, the lack of design discontinuities has led biostratigraphers to base taxonomic concepts on particular morphotypes. This is well demonstrated by Blow and Banner's (1966) revision of *Fohsella* in which taxa were defined using stages in keel development around the last whorl (rounded periphery throughout, *F. peripheroronda*; acutely angled periphery on last three chambers, *F. peripheroacuta*; keel on last three chambers, *F. praefohsi*; keel on all chambers of outer whorl, *F. fohsi*). Several of these taxa were shown as contemporaries. Biostratigraphic information was extracted by carefully defining variants that appeared successively in an intergrading continuum. The example is important. The pattern (Figure 2) is depicted as step-like and might be viewed as punctuational. Only when the nature of the "taxa" is considered is it obvious that the pattern is not that of a set of discrete species. Architectural change in *Fohsella* is a typical example of globorotalid chamber compression and keel construction. It took place over a period of 1–1.5 m.y. and apparently involved continuous transformations and a spectrum of morphotypes like those in *Globorotalia miozea–G. praemenardii*, and in *G. ronda—G.*

truncatulinoides. Still longer trends, some extending over a period of about 8 m.y., have been mapped by Malmgren and Kennett (1981) in a study of the origin of *G. inflata*.

While some globorotalid taxa are certainly "vehicles of biostratigraphic convenience," far removed from the biological species concept, continuity of variation between ancestor and descendant is characteristic of most lineages. The problems it has presented to biostratigraphers are apparent when the high resolution data of Malmgren and Kennett (1981) are considered. We contend that the variation pattern (vertically) in globorotalid lineages is much closer to the gradualist model than to the punctuational.

TEMPO OF CHANGE.—Phyletic evolution is usually represented as involving long-term trends, whereas the punctuational model envisages rapid transformations, certainly on geological scales (thousands of years at most; Gould, 1980). Much recent attention has therefore been focused on tempo. As expected, there is a wide spectrum of rates, and no simple demarcation between the models on this basis is available. Transformations in speciation events of up to 50,000 years have been accepted as punctuational (Williamson, 1981). Nevertheless, even this duration appears to be about the lower limit of the globorotalid data. This is represented by an estimate of 50,000 years for the spread of the keel around the chambers of the outer whorl of *Globorotalia truncatulinoides* (Berggren, 1969; Figure 39*c*). However, this is a partial estimate of the time taken for keel development as it neglects evolution of the earliest stages of the structure. Loss of the keel during the origin of *G. puncticulata* also seems to have occurred relatively rapidly (estimated as 0.09–0.27 m.y. by Scott, 1982, and as 0.48 m.y. by Malmgren and Kennett, 1981). The inception of the keel in the *G. praescitula* plexus represents a much longer period. In the Southwest Pacific the first weak folds appeared with Zone N8. It was not until upper N12 or N13 (over 3 m.y. later) that the structure was fully developed and fixed in the phenotype. Comparable transformations in *Fohsella* occupied over 1 m.y. These latter examples relate to rates of major architectural transformation within lineages. While they are unacceptably slow in terms of the punctuational model, they do not directly confront it.

Yet the scene, generally, is not one of continued redesign throughout the history of a lineage. Chamber compression and keel development were finite, delimitable episodes and were usually followed by extended periods of relative stasis without further developments in the form of adult shells. Variations among *Globorotalia conoidea* populations arose in its 8 m.y. history, but architectural innovations comparable with those of chamber compression and keel formation did not develop. The *G. menardii–G. cultrata* lineage has an even longer history (15 m.y.) in which the basic discoidal shell form did not alter. Note that ontogenetic strategy influences the pattern of variation perceived. Predisplacement of keel development to progressively earlier stages results in stable "adult" morphology, although earlier formed chambers may still be undergoing transformation. Further, morphological stasis was not confined to lineages that followed the chamber compression–keel formation trend to its conclusion. *Globorotalia scitula* is a good example. It never progressed to the keeled stage and has retained its moderately compressed architecture for about 12 m.y.

The data on rates of change and on duration of particular architectures illustrate well the view that globorotalids pursued strategies that seldom conform closely to either model. There are extended episodes of transformation far exceeding the durations envisaged in the punctuational model. There are also some long, gradual clines. Yet, there are taxa that retained a basic design for extended periods. The most significant generalizations are that bedding-plane revolutions in morphology are absent and that rates of evolution were sluggish.

POPULATION STRUCTURE AND VARIATION.—The distribution, size, and number of constituent populations representing a taxon and their degree of intercommunication are likely to signifi-

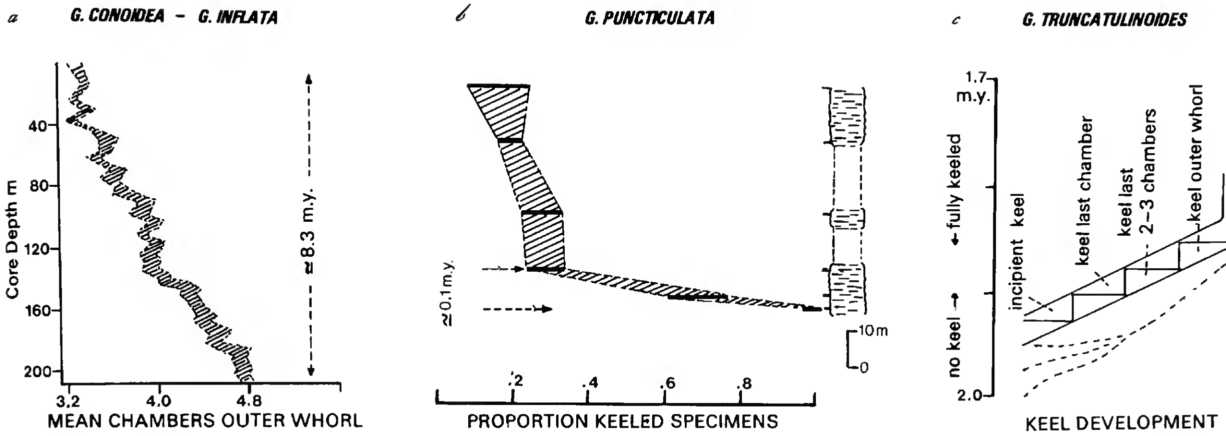


FIGURE 39.—Rates of morphological transformation in globorotalids: *a*, Long-term (upper Miocene-Quarternary) decline in number of chambers in the outer whorl of *Globorotalia conoidea* and a descendant lineage (*G. inflata*) at DSDP Site 284 (after Malmgren and Kennett, 1981, fig. 2; the envelope includes 95% confidence limits). This trend probably occurred throughout temperate watermasses in the Southern Hemisphere. The upper Miocene segment has not been identified in Northern Hemisphere populations. *b*, Relatively rapid regression of the keel during the divergence of the *G. inflata* lineage from *G. conoidea* (after Scott, 1982, fig. 9). Polymorphic populations (*G. puncticulata sphericomiozea*), with the keel in various stages of reduction, progressively became dominated by completely nonkeeled individuals (*G. puncticulata puncticulata*) in the lower Pliocene. The decline in keeled specimens (including those in which the keel has lost its topographic expression and is reduced to a moderate thickening of the wall at the periphery, Scott, 1982, fig. 8e–f) is shown as a proportion (envelope includes 95% confidence limits). The data are from a shallow, landward sequence at Kapitea Creek, New Zealand. In the oceanic sequence to the west at DSDP Site 284, Malmgren and Kennett (1981, fig. 2) recorded an oscillatory decline. *c*, Development of the keel in the evolution of *G. truncatulinoides* (after Berggren, 1969, text-fig. 3; data from Chain Station 61-171, subtropical North Atlantic, further data in Berggren and others, 1967). The typical globorotalid phyletic pattern is followed in which the keel originates on chambers formed at the conclusion of ontogeny and, subsequently, appears progressively earlier in the ontogenetic sequence. Figure 24 shows a specimen (sub-Recent) in which the keel occurs in the middle whorl. Predisplacement of the keel in *G. truncatulinoides* occurred more rapidly than in the *G. praescitula* plexus where several million years elapsed before the keel became established around the other whorl in all individuals.

cantly influence evolutionary patterns.

Recent taxa provide the best guide to the nature of globorotalid populations. Most are very widely distributed (Figure 31) but exhibit significant regional variation, especially in the equatorial-polar direction. Is there evidence that species are partitioned into populations? As a first approximation, watermasses may impose a population structure on globorotalid taxa. Planktonic foraminifera are involuntary travellers and circulation is more regular and better defined within, rather than between, watermasses. In common with other members of the plankton (McGowan, 1971; Zeitzschel, 1978), some planktonic foraminiferal distributions are related to watermass boundaries (Berger, 1969), although there is considerable expatriation of individuals.

If watermass boundaries are significant in defining the limits of species distributions, they might be expected to partition widely distributed taxa. The existence of such a population structure might be revealed in patterns of shell variation. Studies of variation in *Globorotalia truncatulinoides* are relevant because of its wide latitudinal distribution. Kennett (1968) did not consider watermass distributions directly, but the clinal relation he envisaged between shell form and temperature suggests that population structure is indistinct. Similarly, Lohmann and Malmgren (1983) did not discover shape changes about a watermass boundary. However, in a detailed study of a latitudinal transect (Figure 40), Healy-Williams (1983) recognized two shape families whose distributions were related to watermass patterns. A third family occurred in a wide zone of mixing adjacent to an intervening boundary (subtropical convergence).

For a widely distributed species, watermass divisions would create geographically extensive populations. A hypothetical taxon distributed between about 50°N to about 50°S in the Pacific might be divided into 7 populations on the basis of present day watermass divisions (Bradshaw, 1959, fig. 4). Potentially, population sizes might be very large. Abundances of one globorotalid per cubic meter occur in surface water (Tolderlund and Bé, 1971, table 4). At this density, a small watermass dimensioned 1200 km by 500 km would carry 10^{12} individuals. Certainly, this estimate is very crude. It neglects the vertical distribution of species (likely to be significant in deep dwelling globorotalids), age structure, seasonality, and patchiness (Phleger, 1951:31; Hemleben and Spindler, 1983:144). Nevertheless, it provides an indication of magnitudes.

While the watermass hypothesis suggests that globorotalid populations are likely to have been very large, an important question is whether small isolates could form. This is especially relevant to the punctuational model as it is part of the modus operandi of rapid evolutionary advance. Eddies often become detached from the major gyres for several months and would provide the opportunity for several generations of a small subpopulation of a planktonic taxon to be expatriated and for architectural transformations to be initiated. Within watermasses, patchiness and seasonal fluctuations might lead to the isolation of small subpopulations. However, the very temporary existence of such entities is stressed. There is a high probability of reincorporation. When this occurs the subpopulation loses its shelter and is likely to be submerged by the large parent population. McGowan (1971:54) noted that isolates in the Kuroshio and California currents are rather quickly extinguished. There is no suggestion in the foraminiferal literature of the formation of very small subpopulations that might be effective in evolutionary processes.

In review, although data on the structure of globorotalid populations are woefully inadequate, the following features possibly apply: (1) Taxa are probably composed on a few, large, populations weakly defined by watermass distributions (intrapopulational structure and actual deme sizes are quite unknown). (2) Populations are usually contiguous; population boundaries are dynamic and partial (Figure 40), so that interpopulation communication can occur. (3) Isolation of very small subpopulations, either on the margins, or within watermasses due to patchiness, seasonal fluctuations, or physical factors, is for limited periods (several months at most, perhaps for no more than 5 globorotalid generations) and is likely to be followed by their reincorporation into the parent population.

Evaluation

Several aspects of globorotalid history must be taken into account in an evaluation of their evolutionary mode: (1) Within lineages, episodes of chamber and shell redesign were usually protracted (sometimes over 1 m.y.) and left a good record of gradationally changing populations. (2) While there were large transformations, phyletically, within lineages, major branching occurred in most; divergences were not abrupt. (3) Architectural stasis developed, notably in taxa that developed out of episodes of chamber compression.

The structure, size, and extent of intercommunication between globorotalid populations were possibly major determinants of their evolutionary pattern. Consider the tempo of change. The design revolutions of the punctuational

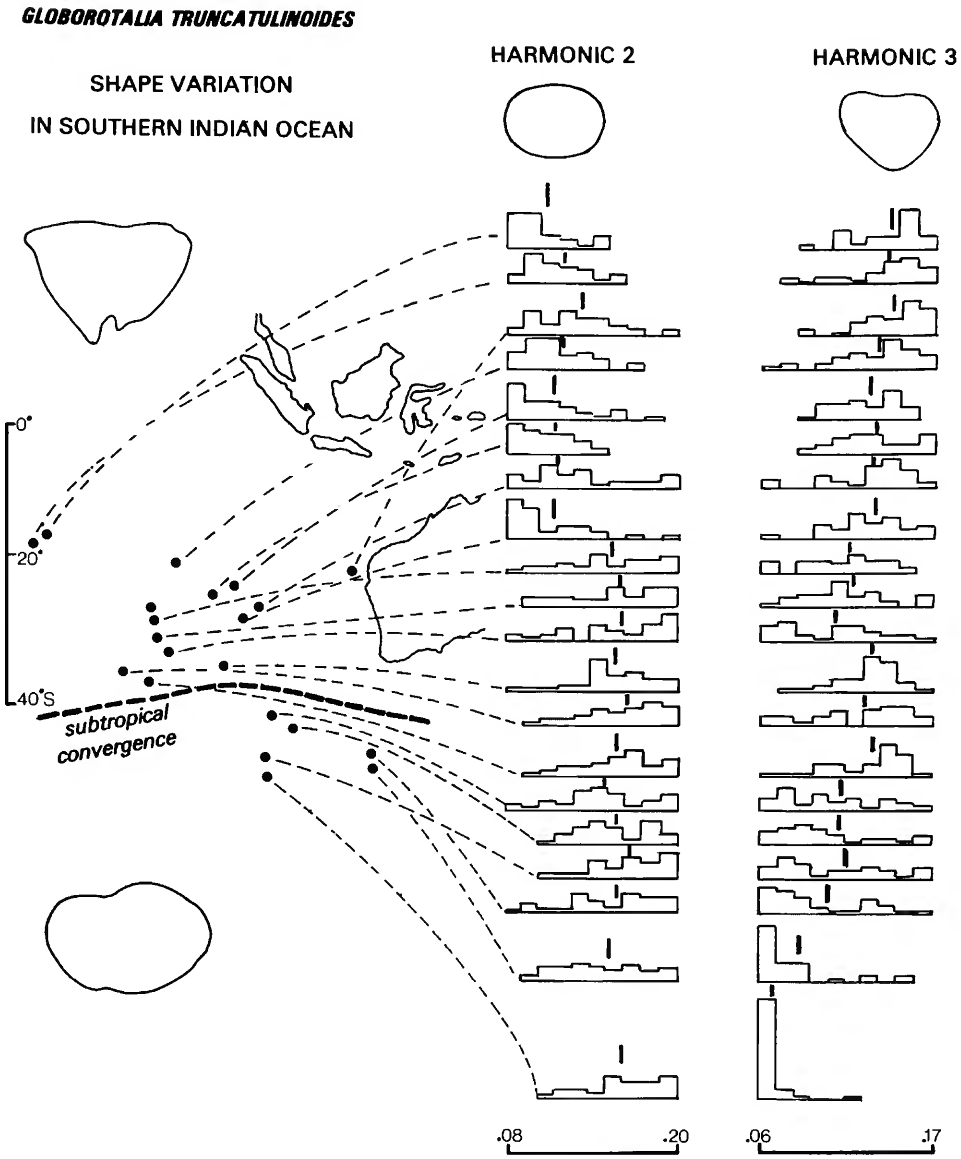


FIGURE 40.—Shape analysis of axial outlines of *Globorotalia truncatulinoides* in core top samples from the southern Indian Ocean (after Healy-Williams, 1983, figs. 1, 3). Distributions and means (vertical markers) of normalized amplitudes are shown. Harmonic 2 represents elongation of the outline. Harmonic 3 represents a trefoil which, in *G. truncatulinoides*, is influenced by the ventral elongation of the shell. Reconstructions of a particular outline generated by harmonics 1-2 and 1-3 (Healy-Williams and Williams, 1981, fig. 2) are shown at the head of the histograms. Southernmost samples from the subpolar watermass are elongated and very weakly conical. Adjacent to the subtropical convergence there is still marked elongation, but conical shape is stronger. North of the subtropical convergence shells maintain or increase their conical shape, but elongation diminishes (this is related to change in coiling direction). The watermass boundary is within a broad zone of shape transformation between the typical central watermass morphotype and the subpolar morphotype. A conical specimen (upper left), typical of the central watermass, and the holotype (lower left), of *G. truncatulinoides malvinensis* (56°S, South Atlantic; Boltovskoy and Watanabe (1981, pl. 3: fig. 1c) are illustrated.

model require small, fully isolated subpopulations (Figure 41). Although Lande (1980) discounted the effectiveness of Mayr's founder principle, he still suggested that, under selection intensities of a few percent, only a few hundred to a few thousand generations might be required for the origin of a new phenotype in small, isolated populations. Perhaps about 1000 years might be required for 10,000 generations of a planktonic foraminiferal species. Small, local populations are also an important component in Wright's (1932, 1982) shifting balance theory. This is a model for phyletic evolution. The taxon is divided into small, partially isolated populations (Figure 42), which are envisaged as probing the adaptive landscape for higher optima. A local population that has been moved off its present peak by random drift in gene frequencies may find its way to higher adaptive territory, for example, via the introduction of a novel feature that improves functionality. If this occurs, and there is sufficient diffusion to its neighbours, all populations will eventually follow the leader towards the new adaptive peak. The effectiveness of the process is controlled by the amount of genetic drift, selective pressures, population size, and intercommunication. Templeton (1982) gives an excellent physical analogy of the interplay between drift and selection in this process.

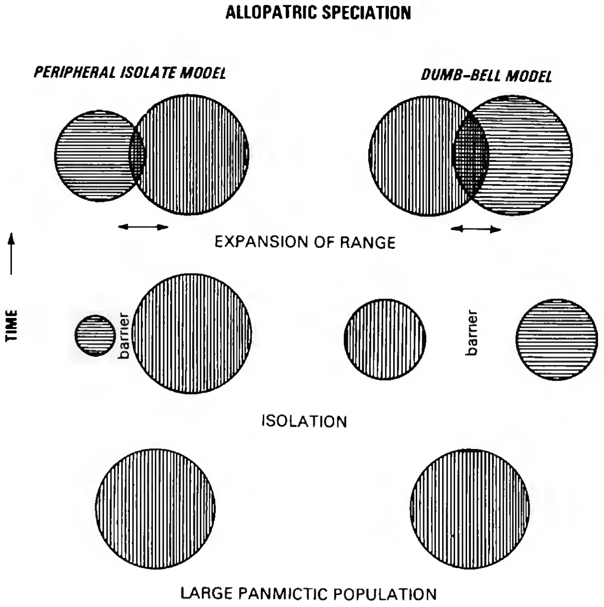


FIGURE 41.—Allopatric speciation models (after Bush, 1975, figure 1). *Right,* Dumb-bell model; a widespread species is divided into two relatively large populations by an extrinsic barrier. Gene flow is interrupted and the populations accumulate genetic differences as they respond to differing selective pressures. Differences in genotype so built up may result in hybrids being selected against should the populations re-establish contact. Eventually, reproductive isolation may occur. *Left,* Peripheral Isolate model: A few individuals, perhaps remnants of a population "flush" that has penetrated beyond the normal environment of the species, attempt to exploit a new habitat, isolated from the parent population. Individuals from semi-isolated peripheral populations are best suited to be preadapted as colonists and also may tend towards inbreeding. Speciation may occur rapidly.

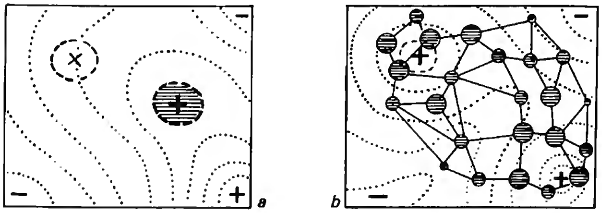


FIGURE 42.—Evolutionary mechanisms in which multidimensional genotypes are represented by two dimensions and the adaptive topography for gene frequencies is portrayed by fitness contours: *a*, a large panmictic population is shown responding to changing conditions (after Wright, 1932, fig. 4c). The selective peak has moved to (+). The readapting population (shaded) is shown moving from the old location (X) towards the new peak. *b*, a species is divided into many small, partially isolated, populations (after Wright, 1932, fig. 4f). There is trial and error exploration of the adaptive topography. The variability of the species is magnified by differentiation of populations and the influence of selection is aided by diffusion from the superior populations. Some populations have moved (by genetic drift) from one adaptive peak (+ upper left) and have crossed a saddle to a higher peak (+ lower right). Eventually, others should follow.

Globorotalid populations do not appear to have the structure required by these models. Neither the extent of isolation required by the punctuational model nor the fine partitioning of the shifting balance model is indicated by present knowledge of modern populations. The very large population sizes of modern taxa, perhaps with panmixus over large regions, suggests that models based on changes in small populations are unlikely to have operated in globorotalid evolution. The distinctly sluggish rates of evolution we have noted thus seem to support the inferences about population characteristics. In short, the population structure to allow rapid evolution was not available. A similar argument was advanced by Brinton (1962:244) concerning the evolution of crustacean zooplankton.

Stasis in morphology for the greater part of species histories is an important prediction of the punctuational model. Stasis is also an important feature of the globorotalid pattern. Mayr (1963:542) and Eldredge and Gould (1972:114) attributed phenotypic stability to genetic homostasis (the tendency for a population to return to its original state following perturbations). In this view, genetic structure acquired by the peripheral isolate is retained thereafter. But does stasis uniquely identify the operation of the punctuational model? Lande (1980) questioned the significance of homostasis and argued that phenotypic stasis is primarily maintained by stabilizing selection. In one of Wright's models (1932) stasis is shown to develop in a panmictic, populous taxon (occupying a relatively stable habitat), which, having climbed an adaptive peak, is kept there by selection. The *Globorotalia menardii–G. cultrata* group may be an example of this condition. It is widespread, populous, and of considerable longevity (nearly 15 m.y.) The tropical environment in which it lives has probably had the most stable climatic history of those occupied by globorotalids.

Gradual evolution in large populations via mass selection can be envisaged as a tracking process. Environmental changes effectively alter the selective topography of a taxon (Figure 42). If these changes are directional even populous taxa will tend to track the movement of the adaptive peak they previously occupied. The early to middle Miocene increase in surface temperatures was prolonged and directional (Figure 33) and altered important physical parameters (e.g., density of surface water). This scenario may have been responsible for the evolutionary pattern in the *Globorotalia praescitula* plexus and *Fohsella*, which culminated in the axially compressed design. Possibly rates of evolution, which would be necessarily slow in very large populations (rate of genetic change tends to be inversely proportional to population size), followed the progress of the environmental trend. The trend reducing the number of chambers in the outer whorl of *G. conoidea–G. inflata* (Figure 39*a*) may be a comparable upper Miocene-Pliocene example of a long, environment-driven morphocline.

While both stasis and long term transformations in globorotalid histories may have resulted from selection variously acting on large populations, mechanisms of branching require a different perspective. Cessation of gene flow is a prerequisite for divergence, yet the ocean is an efficient mixer; globorotalid populations were probably large, contiguous, and only weakly isolated. How could they become disjunct? We must exclude from consideration purely genetic mechanisms (Templeton, 1980), because of the absence of data.

Geographic separation of populations can be brought about by the emergence of barriers between oceans. This allows the dumb-bell model (Figure 41) to operate. Some menardine taxa (Figure 15) that evolved in the Pliocene are largely confined to the Caribbean and tropical Atlantic (Parker, 1973:267; Bolli and Krasheninnikov, 1977). The truncated history of *Globorotalia pertenuis* in a Pacific sequence adjacent to Central America was considered by Keigwin (1982) to be due to the increasing effectiveness of the emerging Panama Isthmus as a barrier. However, the role of this barrier in the Pliocene menardine speciations is yet to be established clearly. All of these taxa seem to have arisen in the Caribbean–tropical Atlantic and, although *G. menardii* (a probable ancestor) was largely excluded, Bolli and Krasheninnikov (1977) recorded its continued presence in one sequence in that region. Probably, the emerging isthmus served only to partially isolate the Caribbean–tropical Atlantic populations from those of the Indo-Pacific.

Watermass movements in response to temperature oscillations might also isolate populations (Brinton, 1962:246; McGowan, 1971:54). In the Southern Hemisphere, northward expansion of cool temperate watermasses would isolate Pacific and Atlantic populations of warm temperate taxa. Expansion of the area of warm temperate water would re-establish contact. This scenario might allow operation of the dumb-bell model, particularly after the Miocene, when the mid-latitude climatic regime was oscillatory. Although various speciations are recorded from this period in the Southern Hemisphere (e.g., *Globorotalia puncticulata*; Scott, 1982), there are still insufficient biogeographic data to judge the importance of this mechanism.

While full allopatry would arise only in special circumstances, parapatric speciation develops from partial isolation of populations particularly those varying clinally, and thus aligns with a major feature of globorotalid distributions. It can be implemented by divergent selective pressures operating on populations in different habitats. While the previous discussion of variation in *Globorotalia truncatulinoides* (Figure 40) focused on the significance of a watermass boundary, the broad geographic pattern in the data is one in which morphological separation increases with distance. The same feature shows in an analysis of axial shape in *G. conoidea* and relatives (Figure 43). Morphometrically, the closest neighbors to Mediterranean samples are from the South Atlantic; in turn, these are closest to New Zealand samples.

Several data favor the operation of parapatric speciation in globorotalids. Polytypic taxa are common and their variation often has a significant clinal component. As judged from morphology (Figure 40) populations in contiguous watermasses appear to be locally adapted and might serve as possible blueprints for future species (Pierrot-Bults and van der Spoel, 1979:166). Further, some divergences (e.g., *Globorotalia menardii, G. puncticulata, G. truncatulinoides*) are regionally represented by widely varying populations, which include innovative as well as ancestral architectures. They may indicate broad zones of contact between populations responding to different selection pressures. The seemingly slow tempo of divergence (as in *G. menardii*) would be compatible with the large populations involved.

Analysis of speciation from biostratigraphic data is highly constrained by the degree of stratigraphic resolution and the availability only of broad geographic and stratigraphic patterns. Bush (1982:128) observed that even the current models "are little more than speculation based on the subjective interpretation of equivocal data." Carefully contrived sampling of the record might point to the operation of differential selection pressures, which are an important component of the parapatric model. It might also detect extrinsic factors (e.g., oceanographic) that facilitate reproductive isolation. But intrinsic genetic factors are also significant in parapatric speciation (Endler, 1977:142–151; Barton, 1980), and, as yet, their operation in globorotalid populations is quite unknown. In review, allopatric speciation might occur in globorotalids when special geographic or oceanographic patterns arose. We have not identified good examples. This is also true of parapatric speciation, but there are certainly factors in globorotalid population structure and distributions (modern and fossil) that favor its operation.

Retrospect

There has been considerable research on Neogene globorotalids but as this survey suggests very significant gaps remain in our knowledge about their history, biogeography, and evolutionary strategies, as well as about the functional significance of shell form. Some of these problems and possible lines of research into their solutions, are emphasized below.

The origins of several lineages are still quite obscure. This applies not only to the lower Miocene founders but also to later plexi, such as *Globorotalia crassaformis* and *G. scitula*. Population sequences (comparable to those within the radiation) to show transformation series between paragloborotalids and primitive globorotalids have not been documented. Earliest populations

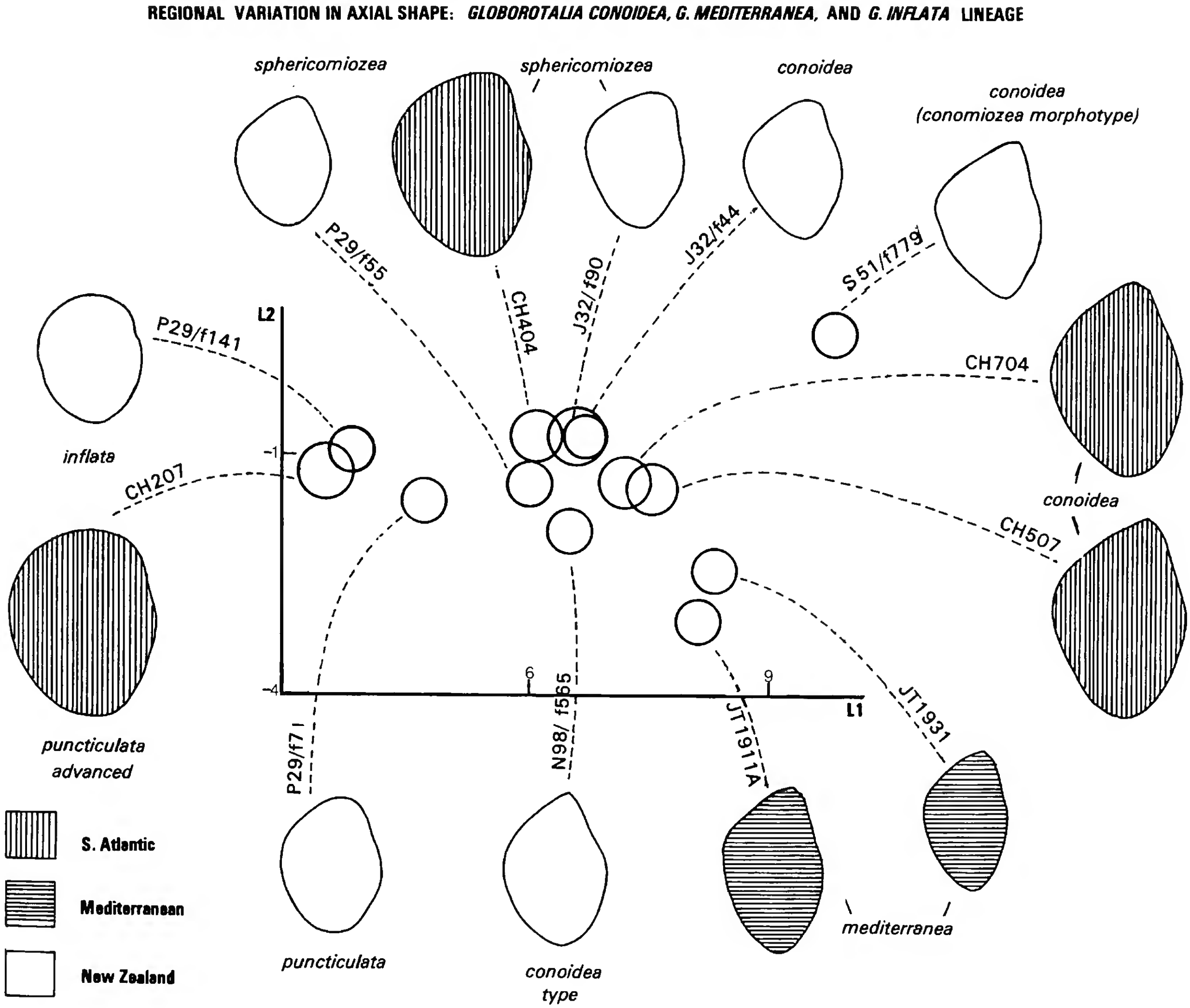


FIGURE 43.—Regional variation in axial shape of *Globorotalia conoidea*, *G. mediterranea*, and *G. inflata* lineage (mean axial outlines, plotted to a common scale, are derived from digitized samples of 27 to 52 specimens). Specimens in which the last-formed chamber was smaller than the penultimate were excluded. The graph shows the disposition of samples in a canonical analysis of 15 normalized Fourier harmonic amplitudes. L1, L2 account for 81% of total variation; circles give approximate 95% confidence limits for means. Upper Miocene samples from the South Atlantic (CH507, CH704) occupy an intermediate position between a New Zealand (J32/f44) and Mediterranean collections (JT1911A, JT1931). Morphometric distances among these samples reflect the amount of geographic separation. N98/f565 is from an older (middle Miocene) horizon, near the entry of *G. conoidea*. S51/f779 represents a population in which the Southwest Pacific ventroconical *conomiozea* morphotypes are common. In contrast, Pliocene samples of *G. puncticulata sphericomiozea* (CH404, J32/f90, P29/f55), *G. puncticulata puncticulata* (CH207, P29/f71), and *G. inflata* (P29/f141) from the South Atlantic and New Zealand show a common trend towards increasing globosity, and regional differences are not obvious. (Sample details are given in Scott, 1983.)

may have been small and localized. However, from present data it is premature to conclude that globorotalid origins are beyond the resolution of the stratigraphic record. Like *G. incognita*, some founders may have closely resembled ancestral paragloborotalids. As yet, neither has the record been adequately searched nor has variation in primitive globorotalids and paragloborotalids been sufficiently mapped.

Our assessment, mainly from comparative morphology but supplemented from stratigraphic distributions, is that Neogene globorotalids are polyphyletic. This applies both to lower Miocene founders and later plexi originating in the upper Miocene and Pliocene. The implications of such a history for classification have yet to be satisfactorily resolved. Biostratigraphers (Jenkins, 1971; Kennett and Srinivasan, 1983) have used *Globorotalia* as a form genus and identified lineages by subgenera. This procedure is an uneasy amalgam of horizontal and vertical classifications. For the globorotalids it suggests that they are a group of closely related lineages. We consider that many similarities among lineages are the result of repetitive trends and do not indicate phyletic relationship. As a unit of phyletic classification, *Globorotalia* possibly should refer only to the *Globorotalia praescitula* plexus with subgenera identifying its branches (e.g., Pliocene menardines, *G. inflata* lineage).

Once established, the major lineages left extensive, high resolution records. We argue that, in piecemeal fashion from section to section, most of their histories can be traced from the preserved populations. If these are sampled at sufficient density they are likely to provide a sequence of overlapping variation fields. The primary example of quantitative documentation of lineage history is by Malmgren and Kennett (1981). We suspect that the record they portrayed is representative of the radiation and exceptional only in its continuity at one site. More documentation of this sort is required to better establish relationships.

A phyletic tree derived from biostatigraphic evidence is decried by those who advocate reliance on morphological relationships. We think that the density of much of the record of lineages, the relatively slow rate of character evolution, and the absence of very rapid speciation events permits the biostratigraphic approach. Furthermore, the stratigraphic position of some taxa have been subject to considerable testing because of their use in biostratigraphic zonal classifications. Phyletically, these provide historical reference points. The order of taxa in lineages, established from biostratigraphy, corresponds excellently with observed character trends. No instance of the alleged *bête noire* of phyletic reconstruction from biostratigraphy (ancestors, as judged from comparative morphology, appearing in the record subsequent to descendants) was found. Advanced taxa (in terms of chamber compression and keel development) in a lineage are always preceded in the record by less advanced populations. In Fortey and Jefferies (1982) term, the globorotalids have a "high" record. It is likely that many taxa are preserved for much of their real ranges and that the stratigraphic tree will eventually be a good approximation to the correct phyletic tree.

While we argue for a biostratigraphic approach to the assessment of phylogeny, there are a number of specific problems of lineage membership and relations to be resolved from closer sampling of the record and studies of population variation: (1) Is *Globorotalia zealandica* part of the *G. praescitula* plexus? (2) There are various problems with the *Globorotalia tumida* lineage: discrimination from coeval menardine taxa at various stages of ontogeny; discrimination of *G. merotumida* from *G. plesiotumida*; interpretation of the morphological hiatus between these taxa and supposed ancestors (*G. lenguaensis* and *G. paralenguaensis*). (3) Connection between *Globorotalia gigantea* and *G. scitula* and their relation with *G. praescitula* plexus. (4) Relationships among upper Miocene scituline taxa; are there several lineages? (5) Origin of the *Globorotalia crassaformis* plexus; relationship of *G. crassula* to the plexus.

The outstanding feature of the radiation is that a few, simple architectural trends were pursued in common by separate lineages. To cladists the latter assertion will seem to be weakly supported. But the likelihood of strong convergence within the radiation is certainly strengthened by the impressive resemblances with earlier radiations that lacked direct connections with the Neogene. Some similarities between taxa from different radiations (e.g., compressed discoidal shells of Paleogene and Neogene) are as close as those within a single Neogene lineage. However, while biostratigraphy echoes convergence, it is much more difficult to decode explanations of architectural form from this source. Of the major designs only the menardine shows a distinctive paleobiogeographic pattern to which shell form can be related. We have found few clues from paleobiogeography about the functionality of other shell designs. Input from studies on living globorotalids is required. "Cost benefit" analyses of various shell shapes are but one approach. A broad spectrum of data is needed, ranging from feeding patterns, through the role of the smooth globorotalid wall in life processes, to the significance of vertical migrations and occupancy of bathypelagic environments. Ontogenetic data are likely to be very important: recall the size (age) related changes in chamber form that are so prominent during growth of globorotalid shells.

In evolutionary studies the biostratigraphic literature may be misleading because some taxa are arbitrarily defined intrapopulational morphotypes and range charts suggest abrupt taxic transitions. However, inspection of character transformations indicates that the tempo of phyletic change within lineages was slow and represented by long sequences of intergrading populations. Studies of shell variation integrated with paleobiogeographic and paleoenvironmental data should help to resolve the relation between clines in morphology and environmental trends. The evolution of ocean climate and structure was possibly the engine of Neogene globorotalid evolution, but the connection has been surmized rather than established. A potential for circular reasoning exists, however, because paleoceanographic inferences partially rest on interpretations of evolutionary innovations.

Despite the current vogue of the punctuational model, mechanisms of speciation and divergence are still poorly understood. Abrupt appearances of new globorotalids are not typical. Divergences are represented by gradational transformations, which particularly involve modifications to chambers formed late in ontogeny. The question remains as to how population disjunction, life history, and environment are interrelated. The biogeographic patterns of bifurcating populations and the way in which genetic isolation was established are unknown. The very nature of the planktonic environment poses severe difficulties for allopatric speciation through small, isolated populations. Some indirect evidence favors parapatric rather than allopatric speciation, but we lack good examples of either process. The fossil record lacks sufficient temporal resolution for highly refined analyses of speciation. Further, it is biased towards the successful and provides only some of the clues about speciation mechanisms. Understanding of variation, structure, distribution, and communication of modern populations will provide others. Are there short-term experiments? Are most submerged by the parent population? How do they achieve isolation initially? If some of these questions can be resolved, interpretation of patterns in the fossil record will be advanced.

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