

ORIGIN, PHYLOGENETIC DEVELOPMENT AND SYSTEMATIC TAXONOMY OF THE *TENUITELLA* PLEXUS (GLOBIGERINITIDAE, GLOBIGERINININA)

LI QIANYU

Postgraduate Unit of Micropalaeontology, Department of Geology, University College London, Gower Street,
London WC1E 6BT, England¹

ABSTRACT

Detailed systematic work on the genus *Tenuitella* Fleisher, 1974, and related taxa reveals that this group contains species with a small maximum test size, a microperforate (perforation diameter $<1\ \mu\text{m}$) wall and pustular wall surface. The subfamilies Tenuitellinae Banner and Globigerinitinae Bermúdez possess similar walls and hence are phylogenetically closely related. The only differences between them are apertural details: intraextraumbilical apertures in the Tenuitellinae and anterointraumbilical to axiointraumbilical ones characterizing the Globigerinitinae. Three genera, *Praetenuitella* n. gen., *Tenuitella* and *Tenuitellita* n. gen., with 14 species (including n. spp.: *P. impariapertura*, *P. patefacta*, *P. praegemma*, *T. fleisheri*, *T. neobrevispira*, *T. neoclemenciae*) are proposed for the Tenuitellinae (late Eocene to Holocene). One new genus, *Tenuitellinata*, having 3 species, is added to the Globigerinitinae (Oligocene to Holocene).

Some test morphocharacters vary widely, but the microperforate, pustulate wall structure seems to have changed little in the forms ascribed to the Globigerinitidae. Evidence suggests, however, that all of the microperforate globigerinitids were derived from a finely macroperforate (approximately $1.5\ \mu\text{m}$) to microperforate ancestor, *Praetenuitella*, which evolved from some planispiral *Pseudohastigerina* in the late Eocene. This exemplifies a “morphological reversal” (rather than, commonly, “unidirectional”) trend in the evolution of planktonic foraminifera.

INTRODUCTION

Many, if not all, small, non-keeled, globorotaliiform foraminifera (diameters commonly $<200\ \mu\text{m}$), or so-called “microglobigerinids” of post-Danian age, have been neglected for years in both biostratigraphic and taxonomic studies. Workers tend to group them, often for simplicity, as “planktonic juveniles” or “undetermined planktonics,” even if they contain described forms of potential biostratigraphic significance. On the screen of an SEM, however, these small planktonic specimens exhibit various morphocharacters that distinguish them into consistently different form-groups. Some may be juveniles of larger, known species (Huang, 1981; Brummer and others, 1986), but others are distinct species with small adult tests. *Tenuitella*, a genus proposed by Fleisher (1974), comprises a group of such

small species, having a microperforate ($0.5\text{--}0.8\ \mu\text{m}$) wall. The species range from late Eocene to Holocene, but characterize, particularly, the Oligocene mid- to high-latitude planktonic foraminiferal assemblages.

Almost all forms with microperforate walls possess small tests. They often lack spinebases, but possess variously shaped surficial pustules. The microperforate, pustular walls can be easily differentiated from specimens of similar diameter, but with cancellate, spinose, or finely ($1.5\text{--}2\ \mu\text{m}$) or coarsely ($>2.0\ \mu\text{m}$) macroperforate walls. Some microperforate forms are stratigraphically restricted (e.g., *Candeina nitida* d’Orbigny, late Miocene-Holocene, and *Globerinatella insueta* Cushman and Stainforth, early Miocene). The separate taxonomic status of the microperforate *Globigerinita* from the macroperforate and cancellate *Catapsydrax* (both genera are bullate and grossly similar otherwise) now seems indisputable. Although variation in perforation size and density may correlate with changes of seawater temperature in *Orbulina universa* d’Orbigny and other species (Bé, 1968; Bé and others, 1976; Dow, 1977), it is not likely that the significant difference between microperforate and macroperforate walls is due to environmental effects. In many cases, biostratigraphy proves that microperforate walls are genetically controlled. However, it is not known whether the seemingly iterative occurrence of the microperforate wall structure in *Globuligerina* Bignot and Guyader (Late Jurassic-Early Cretaceous), *Favusella* Michael (Middle Cretaceous), *Parvularugoglobigerina* Hofker (basal Paleocene), *Globastica* Blow (early Paleocene) and *Tenuitella* Fleisher (late Eocene-Holocene) is due to evolutionary heredity in a single phylogeny or evolutionary convergence in several lineages (or to both).

Wall surface texture varies widely among planktonic foraminifera. This has led some authors to question its validity as a generic base (e.g., Stainforth and others, 1975), especially because differential post-mortem solution, the gametogenetic cycle (Bé, 1980) and eco-phenotypy (Kennett and Srinivasan, 1980) may alter the external texture of the tests. In any case, morphocharacters such as wall structure and texture must have evolved. Therefore, classifications (especially higher taxonomic categories) based solely on the wall structure, as suggested by Lipps (1966), by Steineck and Fleisher (1978) and by Saito and others (1981), are not universally accepted. Surface texture and ultrastructure of the walls have been employed, however (usually with other criteria), to characterize phyletically associated species groups, such as those referred here to *Tenuitella*.

¹ Present address: Department of Geology, Zhongshan University, Guangzhou, People’s Republic of China.

Although many forms of Fleisher's *Tenuitella* are still placed in *Globorotalia* or *Turborotalia* by some authors (e.g., Stainforth and others, 1975; Blow, 1979; Saito and others, 1981), it is becoming widely accepted that this taxon is a valid and important one (Banner, 1982; Loeblich and Tappan, 1984). More than 20 species have been proposed, which may belong to, or be related to, this group. These include *Globorotalia gemma* Jenkins, *Globigerina postcretacea* Myatliuk, *Globorotalia munda* Jenkins, *Turborotalia clemenciae* Bermúdez, *Globorotalia minutissima* Bolli and *Globorotalia anfracta* Parker. These species are morphologically similar and possess microperforate walls. Because some of these species have not been clearly defined by differential diagnoses, some workers may find themselves unable to differentiate satisfactorily between them. Authors tend either to include similar forms under a commonly used name (e.g., *G. gemma* or *G. postcretacea*), or to split them into species that were originally recorded as being stratigraphically separate (ignoring their morphologic similarity). The published stratigraphic range of any given species of *Tenuitella* represents no more than a synthesis of the records of that species, and cannot, therefore, be more reliable than the species concepts employed. For example, *Globorotalia gemma*, originally designated as the type species of *Tenuitella* by Fleisher (1974), was first recorded from the lower Oligocene of New Zealand (Jenkins, 1966). It superficially resembles forms placed by other authors in *Globigerina postcretacea* Myatliuk (e.g., Subbotina, 1953; Saito and Bé, 1964; Stainforth and others, 1975; Stainforth and Lamb, 1981); however, the original of *G. postcretacea* shows little similarity to forms subsequently reported under that name. If we assume that these forms are taxonomically identical, a problem still arises from the various stratigraphic ranges given. For example, *Globorotalia gemma* has been recorded from the late Eocene to the early Oligocene (Jenkins, 1966, 1971, 1985), whereas *Globigerina postcretacea* ranges from the late Eocene to the early Miocene (Stainforth and Lamb, 1981). It is difficult to trace phylogenetic relationships based on such records.

I have examined the phylogenetic relationships between species of *Tenuitella* and among the higher taxonomic groups to which *Tenuitella* may be related. When Banner (1982) proposed the subfamily Tenuitellinae, he indicated a discontinuous range in the early Paleocene, late Eocene and Oligocene, and suggested that *Tenuitella* may have originated (but with no known intermediates) from the small, equally microperforate, earliest Paleocene globigerinids, such as *Parvularugoglobigerina eugubina* (Luterbacher and Silva). Recent studies of well-preserved *P. eugubina* (Smit, 1982) have revealed the totally smooth microperforate wall, and extraordinarily elongate, wholly extraumbilical aperture of that species, indicating that it probably has no close relationship to *Tenuitella* and should be excluded from the Tenuitellinae. Though this subfamily has been adopted by Loeblich and Tappan (1984), they modified the range of the Tenuitellinae (without substantiating

data) to one from middle Eocene to middle Miocene. Kennett and Srinivasan (1983) had suggested, however, that the lineage *G. munda*-*G. clemenciae*-*G. anfracta* was wholly referable to Neogene *Tenuitella*, thus confirming the stratigraphic range of the genus (and therefore of the subfamily) throughout the Neogene and Quaternary, as suggested originally by Fleisher (1974). An earlier assertion that *Tenuitella* may be taxonomically closely linked with, and arose phylogenetically prior to, the genus *Globigerinita* (Fleisher, 1974) was also followed by Loeblich and Tappan (1984), who placed the Tenuitellinae and the Globigerinitinae in the family Globigerinitidae. Kennett and Srinivasan (1983) accepted the tenuitelline ancestry of *Globigerinita* and suggested that *Tenuitella* (*T. clemenciae*) was also the ancestor of *Turborotalia*. The origin of *Tenuitella* has not been adequately demonstrated, however, nor has appropriate systematic work on the Paleogene-Miocene Tenuitellinae been carried out so far.

MATERIALS AND METHODS

I examined samples from late Eocene to Quaternary sediments, placing special emphasis on late Eocene, Oligocene and Miocene sections. Only well-preserved materials were used for detailed studies of wall structure and other morphological characteristics.

Samples from the Eocene to Miocene succession of Trinidad (Bolli, 1957a, b; Bolli and Saunders, 1985) were initially used for this study. However, the Eocene sediments from Trinidad yielded only larger planktonic forms in poorly preserved condition. Thus samples of broadly equivalent strata were taken from several localities of the Jackson Group in the United States Gulf Coast (Table 1). The Oligocene and Miocene material was obtained from the type localities and type samples of Bolli (1957a) (except for that of the *Globorotalia kugleri* Zone; see Table 2).

For Pliocene sediments, samples from the Caloosahatchee Marl of Florida, the Santa Barbara Formation of California, the Pissouri Marls of southern Cyprus, and several samples from the Miocene-Pliocene rocks of Sardinia were studied, but they contained few forms referable to *Tenuitella*. Three samples of modern seabed sediments (two from the Tasman Sea and one off southwest Ireland) and ten core samples from the Quaternary of the Zante Channel (IS/82) and northwestern Aegean (NA/78) were also examined.

Approximately 1,000 individuals were coated for observation under a JEOL-T20 scanning electron microscope. Some selected forms also were dissected in order to reveal detailed characters of the test wall and internal structure. All holotypes and paratypes of new taxa and the remaining figured specimens are deposited in the British Museum (Natural History), London.

SUBFAMILY AND GENERIC CHARACTERISTICS

The Tenuitellinae, like the Globigerinitinae, have small tests characterized by microperforate walls (maximum perforation diameter $< 1 \mu\text{m}$); the microperfora-

TABLE 1. Late Eocene samples from the United States Gulf Coast.^a

Sample	Zone	Strata	Locality
GS/424 ^b	P16-P17	Cocoa Sand, Jackson Group	Near Old Cocoa Post Office, near Melvin, Choctaw County, Alabama
GS/478	P16-P17	Jackson Group	Just below the Red Bluff Clay, eastern Shubuta, Clarke County, Mississippi
GS/479 ^b	P15-P16		
GS/480	P15		
GS/483	P16-P17	Jackson Group	Type locality of the Red Bluff Clay, Wayne County, Mississippi
GS/484	P15		
GS/429	P15	Moody's Branch Marl, Jackson Group	Type Moody's Branch Marl, at Jackson, Mississippi
GS/411	P15		

^a See Mancini and Waters (1986) for lithologic and biostratigraphic details.

^b Samples containing some tenuitelline forms.

tions are irregularly scattered (Pl. 1, Figs. 5, 10; Pl. 2, Figs. 12, 16, 19; Pl. 5, Figs. 4, 11). Surficial pustules are sparsely and irregularly distributed, but no spine bases or muricae are present. The two subfamilies have been united (Loeblich and Tappan, 1984) into the family Globigerinitidae Bermúdez, whose members differ from the dominantly Paleocene Eoglobigerinidae Blow in their finer perforations (3 to 4 μm perforations in *Eoglobigerina eobulloides*; Blow, 1979, pls. 60, 61, 65, 66 and 70) and in their possession of pustules. The Globigerinitidae differ from the Globuligerinidae Loeblich and Tappan in the sparsity of their pustules, which do not fuse laterally or align into ridges (e.g., *Globuligerina* Bignot and Guyader, 1971), and also by never possessing a "virguline" aperture with a lateral re-entrant depression (Wernli and Kindler, 1986; *Globuligerina oxfordiana*). The Globorotaliidae Cushman are characteristically macroporiferate (perforations arranged in regular patterns); the Globigerinidae Carpenter, Parker and Jones are similarly macroporiferate and possess true spines and often are deeply pitted (Pl. 5, Figs. 3, 6, 10, 13). These test wall characteristics, because of their constancy through geological time, characterize groups of species and genera that are related phylogenetically, and are therefore considered to be criteria of high taxonomic ranking.

Second in taxonomic importance are the coiling mode and the position and geometry of the primary aperture,

which are directly related to the position of successive chambers during growth (for example, a form with an intraumbilical aperture cannot have a planispiral growth mode). However, there is evidence that modification of apertural position, direction and geometry has occurred frequently during the evolution of the major phyletic groups of the Globigerinacea (e.g., the progressive intraumbilical restriction of the aperture in the phylogenies "*Globorotalia*" (vel. *Turborotalia*) *centralis* to "*Globigerina*" *pseudoamplioapertura*, and in "*Globorotalia*" (vel. "*Turborotalia*") *increbescens* to "*Globigerina*" *amplioapertura*; see Blow and Banner, 1962). This paper demonstrates that analogous trends have occurred in the Globigerinitidae. The appearance of bullae in the Catapsydracidae, and, independently, in the Turborotalitidae, Globigerapsidae and other families, indicates that the bulla has evolved iteratively in trochospiral and streptospiral forms, and must be of tertiary taxonomic significance. Its development in the Globigerinitidae parallels that of the Catapsydracidae, but is phylogenetically independent.

The distinction between the intraumbilical and intra-extraumbilical apertural positions (Bolli and others, 1957), has proved its importance over the years. Blow (1969, 1979) noted the additionally valuable distinction between apertures directed wholly into the umbilical cavity (e.g., *Globigerina*) and those in which the aperture, although still essentially intraumbilical,

TABLE 2. Oligocene to middle Miocene samples from Trinidad. See Bolli (1957a, p. 100–105) for detailed descriptions of locality and lithology of these samples (except JS 1399). The latter was taken from Mosquito Creek, middle part of the new co-type locality of the *Gr. kugleri* Zone, southern Trinidad.

Sample	Zone name	Zone number	Formation
KR 23425	<i>Globorotalia menardii</i>	N15	Lengua
KR 23422	<i>Globorotalia mayeri</i>	N13-14	
BO 355A	<i>Globorotalia fohsi robusta</i>	N12	Cipero
JS 32	<i>Globorotalia fohsi lobata</i>	N11-N12	
*BO 185B	<i>Globorotalia fohsi fohsi</i>	N10-N11	
*BO 202	<i>Globorotalia fohsi barisanensis</i> (now <i>Gr. peripheroronda</i>)	N9	
*RZ 108	<i>Globigerinatella insueta</i>	N7-N8	
*K 9397	<i>Catapsydrax stainforthi</i>	N6	
*BO 267	<i>Catapsydrax dissimilis</i>	N5	
*JS 1399	<i>Globorotalia kugleri</i> (B)	N4 (B)	
*BO 291A	<i>Globigerina ciperoensis</i>	P22	
*JS 20	<i>Globorotalia opima opima</i>	P21	
*SE 4668	<i>Globigerina amplioapertura</i>	P20	

* Samples containing some tenuitelline (and globigerinitine) forms.

is directed obliquely and anteriorly away from the axis of the umbilicus (as in *Subbotina*). This is as important as the distinction of forms where the aperture is intra-extraumbilical and from those where the aperture, still interiomarginal, is wholly extraumbilical (by closure of the primary true umbilicus as in streptospiral forms; e.g., *Pulleniatina*, in Banner and Blow, 1967; early growth stages of *Orbulina*, in Desai and Banner, 1985). The wholly extraumbilical aperture can arise both by wide opening and by total closing of the umbilicus even in trochospiral or planispiral forms. For simplification of description, I introduce the term “axiointraumbilical” for intraumbilical apertures directed toward the umbilical center (umbilical and coiling axis) and “anterointraumbilical” for apertures that are still intra-

umbilical, but directed to face anteriorly from this axis (Fig. 1).

These distinctions enable the genera of the Tenuitellinae and Globigerinitinae to be classified as follows:

FAMILY GLOBIGERINITIDAE BERMÚDEZ

Test trochospiral, small; wall microperforate in the adult, with scattered pustules; primary aperture single, interiomarginal, with narrow lip of uniform breadth; lacking consistent sutural apertures on spiral (“dorsal”) side.

SUBFAMILY TENUITELLINAE BANNER

Aperture intra-extraumbilical.

- (1) Trochospire low; evolute side flat or concave; umbilicus wide, open; aperture extends from anterior side of umbilicus to pe-

PLATE 1

Late Eocene tenuitelline species

(Fig. 4, $\times 1,000$; Figs. 5, 10, 22, $\times 2,500$; all others, $\times 250$).

1-5 *Praetenuitella impariapertura*, n. sp. 1, 2 Holotype, no. P51995; ventral and peripheral view; 3 final chamber removed to show high peripheral penultimate aperture; 4 enlargement of aperture; 5 surface of final chamber. Late Eocene, Zone P16 (sample GS/479). 6-10 *Praetenuitella patefacta*, n. sp. 6, 7 Holotype, no. P51999; 8 paratype A, no. P52000; 9 paratype B; 10 surface of final chamber no. P52001. Note globular chambers and relatively coarse perforations of earlier chambers. Late Eocene, Zone P16-P17 (all from GS/424). 11-22 *Praetenuitella praegemma*, n. sp. 11-13 Paratype A, no. P52003; 14, 15 paratype B, no. P52004; 16-18 holotype, no. P52002; 19-22 paratype C, no. P52005. Note ovoid, slowly enlarged chambers and consistently developed microperforations (about 0.9–1 μm in diameter). Late Eocene, Zone P16-P17 (paratype A from sample GS/479, all others from GS/424).

PLATE 2

Oligocene tenuitelline species

(Figs. 12, 16, 19, $\times 2,500$; Figs. 14, 15, 17, 18, $\times 200$; others, $\times 350$)

1-4 *Tenuitella neoclemenciae* n. sp. 1 Paratype A, no. P52007, Oligocene *G. ampliapertura* Zone; 2, 3 holotype, no. P52006, *G. opima opima* Zone; 4 paratype B, no. P52008, *G. ciperoensis* Zone. Note small umbilicus and apertural lip tending to reach periphery. 5 Form transitional between *T. gemma* and *T. clemenciae* with 4 chambers in final whorl, no. P52009, *Globorotalia opima opima* Zone. 6-8 *Tenuitella gemma* (Jenkins). 6 No. P52010; 7 no. P52011; 8 no. P52012. Note almost closed umbilicus and intra-extraumbilical aperture. 6, 7 From *Gr. opima opima* Zone, 8 from *G. ampliapertura* Zone. 9 *Tenuitella clemenciae* (Bermúdez). Atypical specimen, no. P52013, note final chamber is smaller than normal for growth-series. *Gr. opima opima* Zone. 10 Form transitional between *T. munda* (Jenkins) and *Tenuitellinata juvenilis* (Bolli), no. P52014, note quickly enlarging chambers and anteroextraumbilical aperture. *Gr. opima opima* Zone. 11, 12 Form transitional between *Tenuitella gemma* and *T. munda*. 11 Umbilical view to show inflated chambers and intra-extraumbilical aperture; 12 final chamber surface, no. P52015. *Globigerina ampliapertura* Zone. 13 *Tenuitella munda* (Jenkins). Atypical specimen with elongate chambers, no. P52016. *G. ampliapertura* Zone. 14, 16 Form of *Tenuitellinata* transitional between *Tenuitella gemma* and *Tenuitellinata angustiumbilicata* (Bolli). 14 Umbilical view to show inflated chambers and anteroextraumbilical aperture; 16 final chamber surface, no. P52017. *G. ciperoensis* Zone. This form may be referable to *Tenuitellinata* cf. *T. pseudoedita* (Subbotina). 15, 17-19 *Tenuitellinata angustiumbilicata* (Bolli). 15 Topotype no. P52018; 17-19 Topotype no. P52019. Note relatively high spired test and axiointraumbilical aperture. *G. ciperoensis* Zone.

PLATE 3

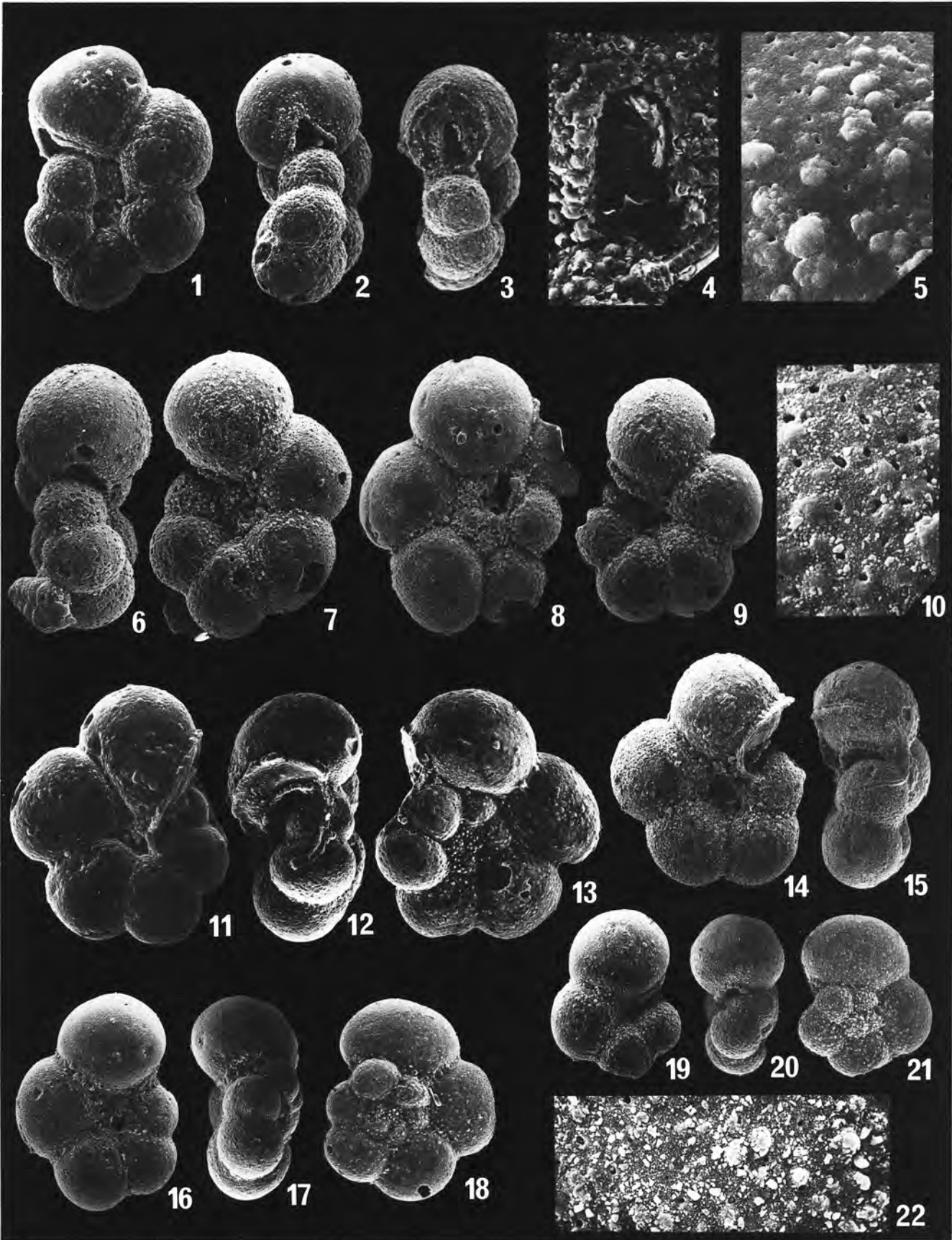
Early to middle Miocene species

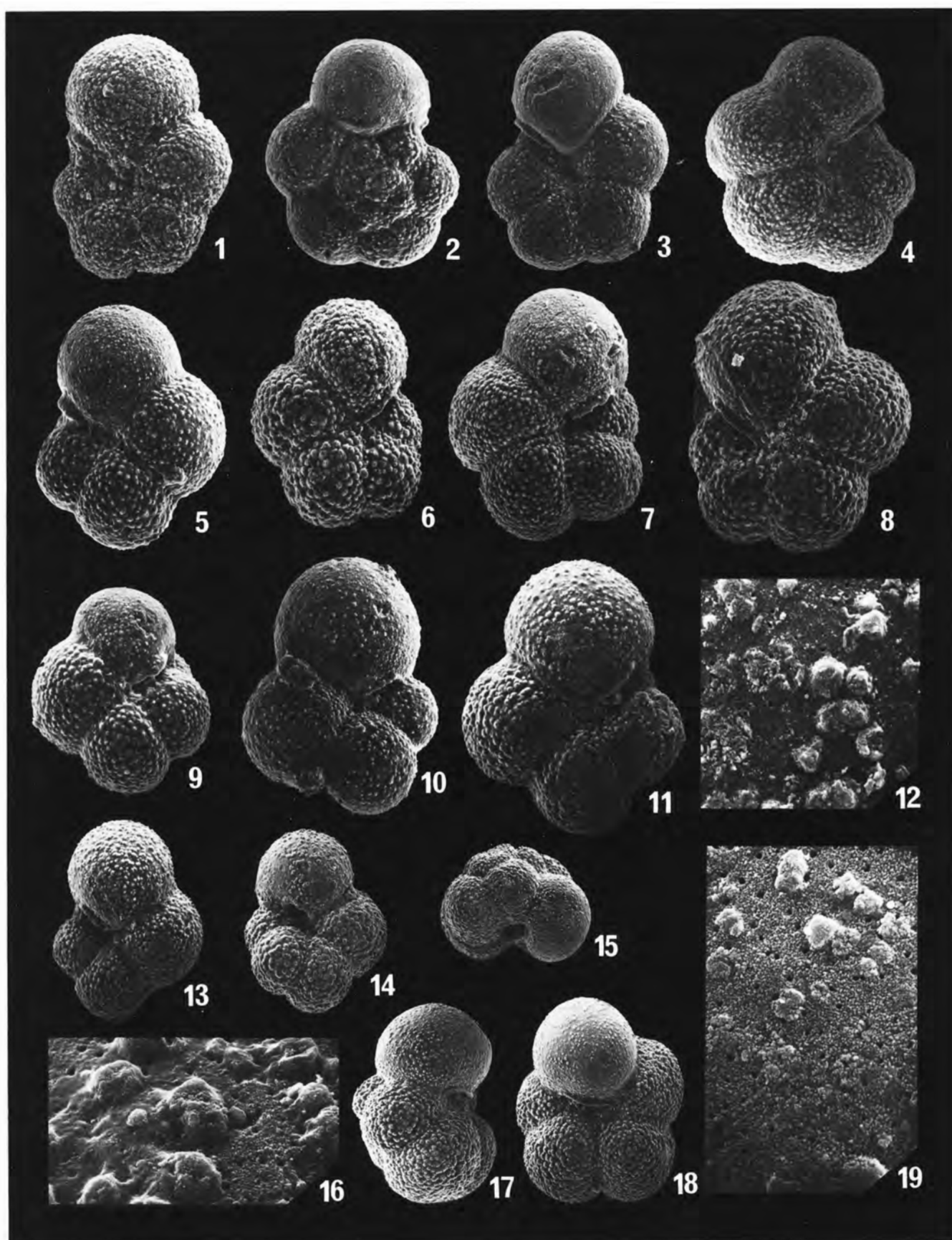
Figs. 5, 18, $\times 2,500$; Figs. 16, 17, $\times 250$; all others, $\times 350$

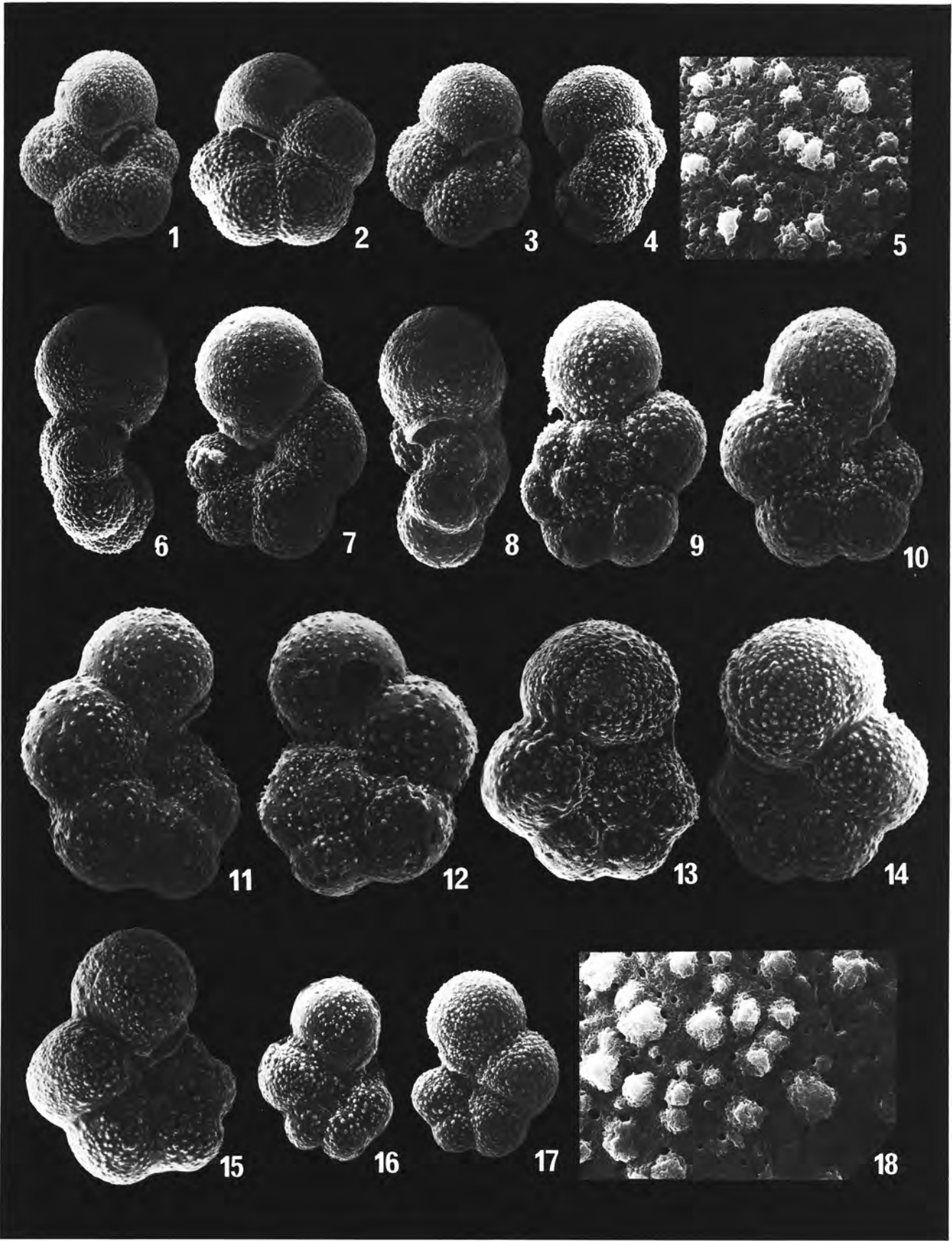
1-5 *Tenuitellinata* cf. *T. pseudoedita* (Subbotina). 1 No. P52020; 2 no. P52021; 3-5 no. P52022. Early Miocene, *Catapsydrax dissimilis* Zone. Note convex evolute side. 6-9 *Tenuitella minutissima* (Bolli). 6, 7 No. P52023, early Miocene, *C. dissimilis* Zone; 8, 9 no. P52024, middle Miocene, *Globorotalia fohsi fohsi* Zone. Note quickly enlarging, radially elongate chambers in final whorl. 10, 15 Specimens intermediate between *T. minutissima* and *T. neobrevispira*, n. sp. with quickly enlarging, radially elongate chambers and deep, open umbilicus. 10 no. P52026; 15 no. P52027. *G. fohsi fohsi* Zone. 11, 12 *Tenuitella minutissima* (Bolli). No. P52025. *G. fohsi fohsi* Zone. Note less densely pustulate test, closed umbilicus and tangentially elongate chambers. 13, 14 *Tenuitella neobrevispira*, n. sp. Holotype, no. P52028. Note quickly enlarging, ovate chambers and large, open umbilicus. *G. fohsi fohsi* Zone. 16-18 Pseudoplanispiral form with intraumbilical-peripheral aperture derived from *T. minutissima*. 16 “Dorsal,” less involute side; 17 “ventral or umbilical,” more involute side; 18 final chamber surface, no. P52029. *G. fohsi fohsi* Zone. Rare forms with consistently microperforate tests and low aperture, which extends equatorially onto “dorsal” side.

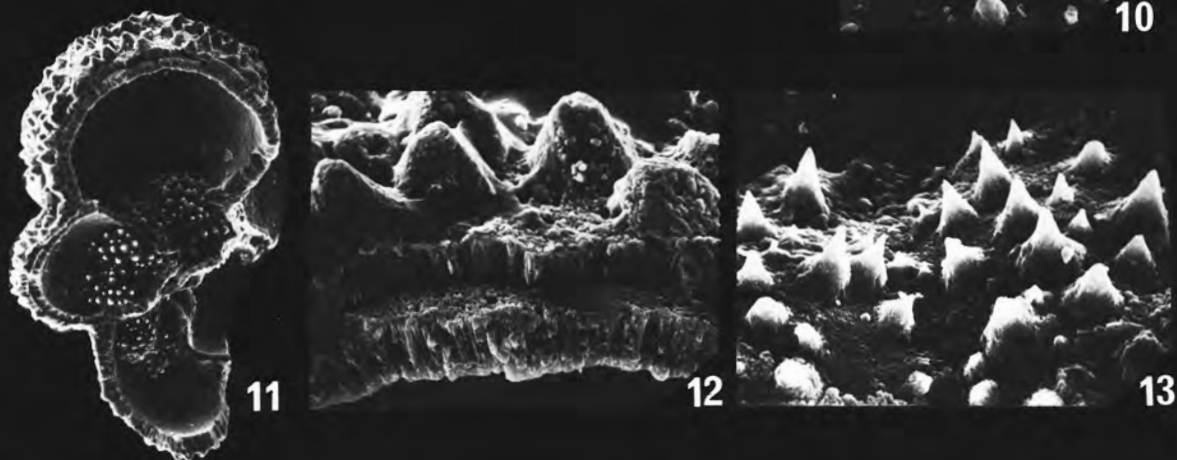
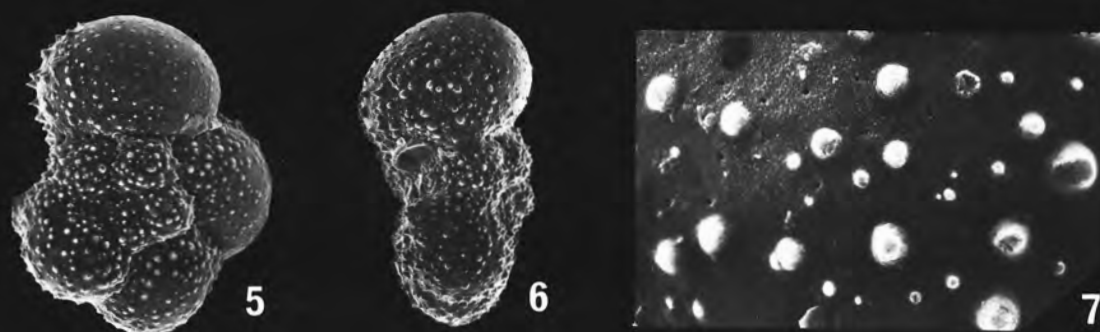
PLATE 4

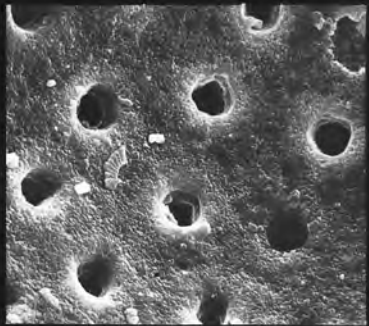
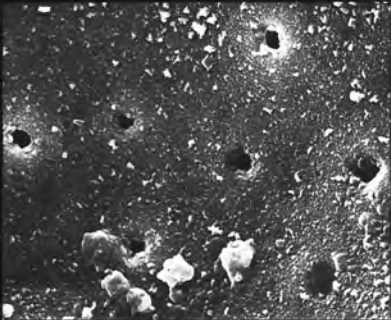
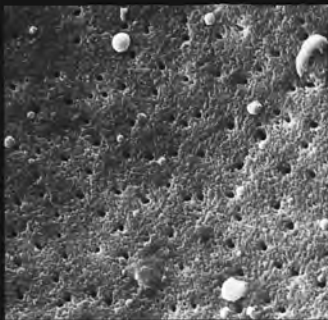
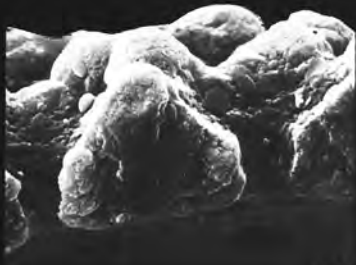
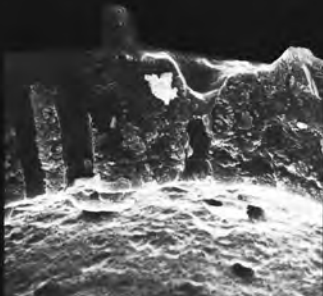
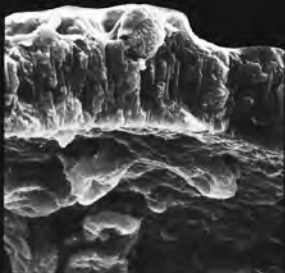
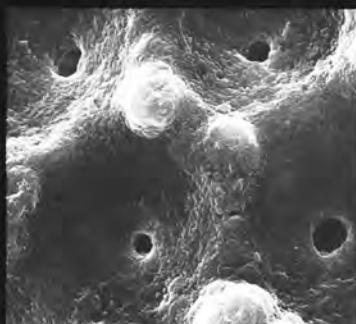
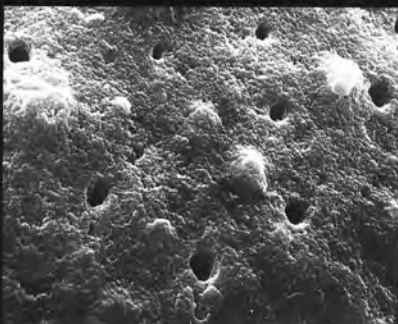
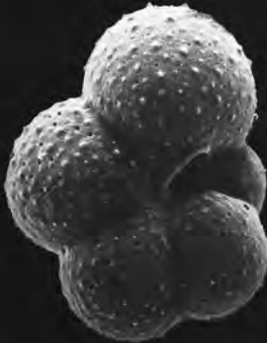
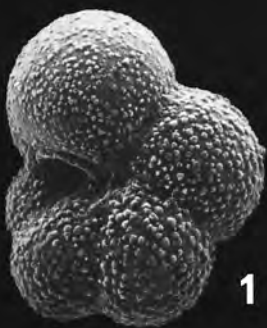
1-7 *Tenuitella fleisheri*, n. sp. 1-3 Holotype, no. P52030, $\times 350$; 4-7 paratype, no. P52031; 4-6, $\times 350$; 7 final chamber surface, $\times 2,500$. Note compressed tests and sparsely pustulate wall surface, holotype from sample IS/82/8, Zante Channel; paratype from sample NA/78/30, Aegean (both are late Quaternary). 8-10 *Tenuitellinata angustiumbilicata*. Topotype dissected to show ontogenetically early *Tenuitellinata* cf. *T. pseudoedita* stage with anteroextraumbilical-extraumbilical aperture (8 $\times 250$); cone-shaped, murica-like pustules on primary layer and secondarily deposited, thickened layer (encrustation) of penultimate chamber wall (9, 10 $\times 2,500$). *Globigerina ciperoensis* Zone. 11-13 Specimen of *Tenuitellinata* cf. *T. pseudoedita* dissected to show early whorl (11 $\times 350$), encrustation (2-layered wall structure, 12 $\times 2,500$), and sharp, cone-shaped pustules on surface of earlier chambers (13 $\times 2,500$), no. P52032. *G. ciperoensis* Zone.











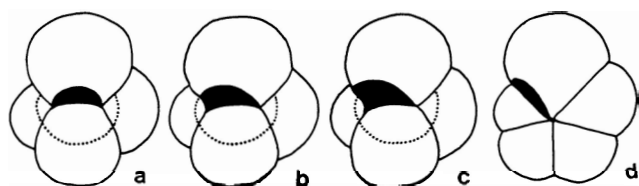


FIGURE 1. Schematic diagram showing position and shape of intraumbilical and extraumbilical apertures: **a** axiointraumbilical; **b** anterointraumbilical; **c** intraextraumbilical; and **d** extraumbilical (see text for explanation).

riphery of penultimate whorl (intraextraumbilical-peripheral); early chambers macroperforate, adult chambers microperforate: *Praetenuitella*, n. gen. (type species, *P. praegemma*, n. sp.). Late Eocene.

- (2) Trochospire low to medium, evolute side flat to convex; umbilicus small but open; aperture anterointraumbilical-extraumbilical; wall microperforate throughout.

(a) Lacking bulla; *Tenuitella* Fleisher (type species, *Globorotalia gemma* Jenkins). Early Oligocene-Holocene.

(b) With bulla: *Tenuitella*, n. gen. (type species, *Globigerinita iota* Parker). Quaternary.

SUBFAMILY GLOBIGERINITINAE BERMÚDEZ

Aperture intraumbilical (axiointraumbilical or anterointraumbilical).

- (a) Lacking bulla: *Tenuitellina*, n. gen. (type species, *Globigerina angustiumbilicata* Bolli). Late Oligocene-Holocene.
 (b) With bulla: *Globigerinita* Brönnimann (type species, *G. naparimaensis* Brönnimann). Late Oligocene-Holocene.
 (i) No accessory bullate tunnels: subgenus *Globigerinita* Brönnimann s.s. Late Oligocene-Holocene.
 (ii) Infralaminar multiple apertures at end of bullate extension tunnels: subgenus *Tinophodella* Loeblich and Tappan (type species, *T. ambitacrena* Loeblich and Tappan). Early Miocene-Holocene.

SPECIES CHARACTERISTICS

As tested by careful discrimination within the assemblages studied for this paper, spirality, chamber number in the final whorl, rate of chamber enlarge-

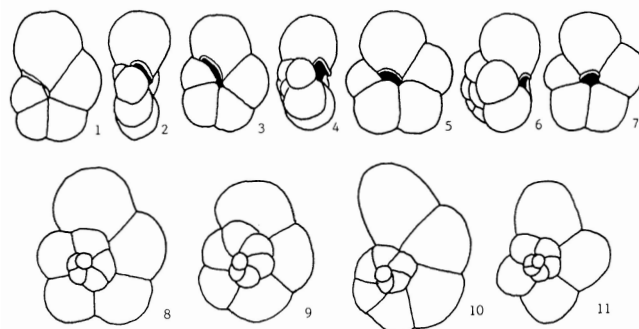


FIGURE 2. Morphocharacters used to differentiate species of Tenuitellinae and related forms. 1, 2 Very low trochospire with an extraumbilical aperture; 3, 4 low trochospire with an intraextraumbilical aperture; 5, 6 high trochospire with an anterointraumbilical aperture; 6, 7 high trochospire with an axiointraumbilical aperture; 8 slowly enlarging, globular-subglobular chambers; 9 slowly enlarging, ovoid (or subrescenscent) chambers; 10 quickly enlarging, (spiral) slightly elongate chambers; 11 quickly enlarging, radially elongate chambers.

ment, chamber shape, sutural indentation and obliquity, and umbilical and apertural characters (Fig. 2; Table 3) can all be employed to discriminate species in the Globigerinitidae, just as they are in other globigerine families. Lumping, solely because of their small size, is not justified, and has led to loss of biostratigraphic and phylogenetic information. The morphospecies described formally below have been discriminated on their persistence and (or) on their biostratigraphic significance. Iterative evolution rarely produces true homeomorphs; polyphyletic origins and the stratigraphic separation of superficially similar species (compare Pl. 1, Figs. 1–3, with Pl. 3, Figs. 16, 17) have created subtle morphologic distinctions between such forms.

At least 20 published species, attributed to *Globigerina* or *Globorotalia*, are probably referable to the Tenuitellinae or Globigerinitinae as herein described.

TABLE 3. Comparison of some changeable and unchangeable morphocharacters in *Tenuitella* spp. and related forms.

Characters changeable	Characters subject to little or no change
1. Test dimension: 90 → 200 μm (>200 μm?)	1. Microperforations (<1.0 μm)
2. Trochospirality: low → (medium) high	2. Pustular wall surface
3. Apertural position: intra-extraumbilical (-peripheral) → intraumbilical	3. Low-arched aperture
4. Umbilicus: open → small → closed	4. Thin apertural lip
5. Chambers: 8 → 13 (a single test); 4 → 6 (or 7, in the final whorl)	5. Rounded periphery, without keel
6. Chamber shape: globular-subglobular → ovoid-subrescenscent → slightly elongate	
7. Surface pustules: sparse → heavy	

PLATE 5

Comparison of the different wall structures and surfaces.

Fig. 1, ×350; Fig. 2, ×250; Fig. 3, ×185; all others, ×2,500.

1, 4, 7, 11 *Tenuitellina* cf. *T. pseudoedita*. No. P52033, *Globigerina ciperoensis* Zone; 1 umbilical view; 4 pustulate surface of microperforate final chamber; 7 microperforations in cross-section of wall; 11 internal surface of final chamber. 2, 5, 8, 9, 12 Juvenile specimen of *Globigerina*. No. P52034, early Miocene form from *Catapsydrax dissimilis* Zone; 2 umbilical view; 5 final chamber surface; 8, 9 funnel-shaped pores visible in cross-section; 12 internal surface of final chamber. 3, 6, 10, 13 *Globigerina angulisuturalis* Bolli. No. P52035, from *C. dissimilis* Zone; 3 umbilical view; 6 macroperforate, cancellate, final chamber surface, showing perforation-pits, inter-perforation ridges and spine bases; 10 cross-section of wall; 13 internal surface of penultimate chamber.

TABLE 4. Test morphocharacters that occur iteratively in the Globigerinitidae.

Morphocharacters	Examples*			
	Late Eocene	Oligocene	Miocene	Pliocene-Quaternary
1. Very low trochospirality (pseudoplanispirality)	<i>Praetenuitella</i> spp.	<i>Tenuitella neoclemenciae</i>	<i>Tenuitella minutissima</i>	
2. Axiointraumbilical apertures		<i>Tenuitellinata juvenilis</i> <i>T. angustiumbilocata</i>		<i>T. juvenilis</i>
3. Slightly elongately developed chambers			<i>T. minutissima</i>	" <i>T.</i> " <i>parkeri</i>
4. Ovoid (subcrescentic) chambers	<i>P. praegemma</i>	<i>T. neoclemenciae</i> <i>Tenuitellinata</i> cf. <i>T. pseudoedita</i>		<i>T. fleisheri</i>
5. Umbilical bullae		<i>Globigerinita praestainforthi</i>	<i>Globigerinita glutinata</i> s.l.	<i>Tenuitellita iota</i>

* See Figures 8A, B for the stratigraphic ranges of these taxa.

Their particular affinities have, on occasion, been recognized (e.g., the "*gemma-permicra* plexus" of Blow, 1979), but their small size has often led to barely adequate published descriptions and illustrations. Unless an SEM is employed, wall textures and apertural details frequently remain obscure. Therefore, pending restudy of primary or topotype specimens, there remains some uncertainty in the identification of species originally illustrated by drawings made with an optical microscope. Nevertheless, only about 10 previously described tenuitelline species (referable to the genera used here) are valid, the remainder being either synonyms or phylogenetically unrelated to globigerinitid stock. The species I have discriminated are comparatively diagnosed below.

KEY TO SPECIES

1. Aperture extraumbilical (or anterointra-extraumbilical); early test finely macroporulate, fully microporulate only in adult chambers; test very low trochospiral, flat to slightly concave or slightly convex on dorsal (evolute) side; chambers enlarging slowly as added, 5 to 6 (rarely 7) in final whorl.
 - 1.1. Chambers globular-subglobular; umbilicus wide, open.
 - 1.1.1. Dorsal side concave; aperture highly arched to subtriangular at periphery, becoming narrow, slit-like toward umbilicus: *Praetenuitella impariapertura*, n. sp.
 - 1.1.2. Dorsal side flat; aperture a low arch: *Praetenuitella patefacta*, n. sp.
 - 1.2. Chambers subglobular to subcrescentic; umbilicus narrow, open; dorsal side flat to slightly convex; aperture a low arch: *Praetenuitella praegemma*, n. sp.
2. Aperture intra-extraumbilical; microporulate throughout; test low trochospiral, flat to slightly convex on dorsal side; umbilicus small.
 - 2.1. Chambers enlarging slowly as added, 5 or more in final whorl.
 - 2.1.1. Apertural lip thin, narrow, extending to and along periphery: *Tenuitella neoclemenciae*, n. sp.
 - 2.1.2. Apertural lip a triangular plate, extending into umbilicus: *Tenuitella* sp.
 - 2.1.3. Apertural lip narrow, along much of the apertural length, on umbilical side only.
 - 2.1.3.1. Umbilicus small; with sporadic development of dorsal supplementary apertures: "*Tenuitella*" *nkbrowni* (Brönnimann and Resig).

- 2.1.3.2. Umbilicus very small to closed; surface heavily pustulate: *Tenuitella gemma* (Jenkins).
- 2.1.3.3. Umbilicus small, open; surface sparsely pustulate: *Tenuitella fleisheri*, n. sp.
- 2.2. Chambers enlarging less slowly, 4 in final whorl: *Tenuitella clemenciae* (Bermúdez).
- 2.3. Chambers enlarging rapidly as added.
 - 2.3.1. Umbilicus open; chambers subcrescentic, 5 in final whorl: *Tenuitella neobrevispira*, n. sp.
 - 2.3.2. Umbilicus small to closed.
 - 2.3.2.1. Chambers slightly (spirally) elongate, 5–6 in final whorl: *Tenuitella minutissima* (Bolli).
 - 2.3.2.2. Chambers slightly (radially) elongate, 4–4½ in final whorl; surface smooth: "*Tenuitella*" *parkeri* (Brönnimann and Resig).
 - 2.3.2.3. Chambers inflated spirally and ventrally, 4 in final whorl: *Tenuitella munda* (Jenkins).
3. Aperture intraumbilical (axiointraumbilical to anterointraumbilical); test low to medium trochospiral; chambers globular to subglobular.
 - 3.1. 5 chambers in final whorl.
 - 3.1.1. Aperture anterointraumbilical, tending to be intraextraumbilical: *Tenuitellinata* cf. *T. pseudoedita* (Subbotina).
 - 3.1.2. Aperture axiointraumbilical, tending to be anterointraumbilical: *Tenuitellinata angustiumbilocata* (Bolli).
 - 3.2. 4 chambers in final whorl; aperture axiointraumbilical.
 - 3.2.1. Without bulla: *Tenuitellinata juvenilis* (Bolli).
 - 3.2.2. With bulla: *Globigerinita glutinata* (Egger) s.l.
4. Intraumbilical-extraumbilical primary aperture covered by umbilical bulla; 5 chambers in final whorl.
 - 4.1. Primary aperture anterointraumbilical to axiointraumbilical: *Globigerinita praestainforthi* Blow.
 - 4.2. Primary aperture extraumbilical: *Tenuitellita iota* (Parker).

SYSTEMATIC CLASSIFICATION

Order FORAMINIFERIDA Eichwald, 1830

Suborder GLOBIGERINININA Delage and Hérouard, 1896

Superfamily GLOBOROTALIACEA Cushman, 1927

Family GLOBIGERINITIDAE Bermúdez, 1961

Subfamily TENUITELLINAE Banner, 1982, emend.

Description. Test small, commonly less than 200 µm in diameter; low trochospiral; chambers globular, subglobular to ovate, 8–13 (commonly 9–11) arranged in 1½–2 whorls, 4–6 chambers (rarely 7) in final whorl; sutures depressed, radial or slightly curved to oblique; periphery rounded, no carinae; umbilicus wide and open to small and closed; wall microporulate in adult, small "crystallite" pustules on outer surface; aperture interiomarginal, a low slit-like arch for most or all of its length, intraumbilical-extraumbilical to anterointraumbilical, bordered with a lip. Late Eocene-Holocene.

Genus *Praetenuitella*, n. gen.

Pl. 1, Figs. 1–22

Type species. Praetenuitella praegemma, n. sp.

Description. Test very low trochospiral; chambers globular to ovate, enlarging slowly as added, 4–6 in final whorl; sutures radial on both sides; umbilicus large and open; wall finely macroperforate in early test, later microperforate; surface sparsely pustulate; aperture antero-intra-extraumbilical to wholly extraumbilical, with thin lip.

Etymology. “prae-,” before; “before the genus *Tenuitella*.”

Stratigraphic range. Late Eocene.

Praetenuitella impariapertura, n. sp.

Pl. 1, Figs. 1–5

Description. Test concave on spiral side; chambers globular, 5–6 in final whorl; early chambers finely macroperforate, later chambers microperforate; aperture high, peripheral in early stage, becoming extraumbilical-peripheral in adult.

Type horizon. Late Eocene (P15–P16, ?P17).

Type locality. Just below the Red Bluff clays, eastern Shubuta, Clarke County, Mississippi; sample GS/479.

Etymology. “imparis,” unequal; unequally distributed aperture.

Remarks. The aperture of this new taxon is commonly developed in two distinct parts. A highly arched or subtriangular opening is situated at the periphery; this is connected to a narrow slit, which extends into the umbilicus. The early ontogenetic stage is planispirally coiled with a high aperture, suggesting that this species may be derived from a small, planispiral, finely macroperforate variant of, possibly, *Pseudohastigerina micra* s.l.

Praetenuitella patefacta, n. sp.

Pl. 1, Figs. 6–10

Description. Test flat on spiral side; chambers globular, 5–6 in final whorl; early chambers finely macroperforate, later chambers microperforate; umbilicus wide, shallow; aperture narrow, extraumbilical-peripheral.

Type horizon. Late Eocene (P16–P17).

Type locality. Near Old Cocoa Post Office, near Melvin, Choctaw County, Alabama; sample GS/424.

Etymology. “patefacio,” to open up, to make accessible.

Praetenuitella praegemma, n. sp.

Pl. 1, Figs. 11–22

Description. Spiral side of test flattened to slightly convex; chambers ovoid, 4–5 in final whorl, subscentric on spiral side; early chambers finely macroperforate, later chambers microperforate; aperture a low slit-like arch, extraumbilical-antero-intraumbilical.

Type horizon. Late Eocene (P16–P17).

Type locality. Near Old Cocoa Post Office, near Melvin, Choctaw County, Alabama; sample GS/424.

Etymology. “prae-,” “before; before the species *gemma*.”

Remarks. This species differs from its immediate descendant, *Tenuitella gemma*, in having a less pustulate test with rather sparsely distributed, fine, macroperforations in early chambers and true microperforations in adult chambers. *Globorotalia insolita* Jenkins from the upper Eocene of New Zealand is superficially similar, and may be related, but is characterized by an extraumbilical, highly arched aperture and a closed umbilicus.

Genus *Tenuitella* Fleisher, 1974, emend.

Type species. Globorotalia gemma Jenkins.

Description. Test small, low trochospiral; chambers globular to ovate, 4–6 (commonly 5 in final whorl); sutures radial on umbilical side, radial to obliquely curved on spiral side; wall consistently densely microperforate and pustulate; umbilicus small, open to closed; aperture a low arch, bordered with a thin lip, extraumbilical to antero-intraumbilical-extraumbilical.

Stratigraphic range. Early Oligocene to Holocene.

Tenuitella clemenciae (Bermúdez)

Pl. 2, Fig. 9

Turborotalia clemenciae BERMÚDEZ, 1961, p. 1321, pl. 17, fig. 10.

Remarks. The holotype specimen of this species, as originally described, is larger (300 μ m, see Fig. 3: 25, 26) than those recorded subsequently under that name. Although a re-examination of type material is highly recommended, the published concept of many authors is followed here (forms with less inflated chambers, four in the final whorl). Its status as either a senior synonym of *Globorotalia munda* (see Blow, 1979, and below), or of forms like *Tenuitella minutissima* with 5-chambered tests (e.g., Kennett and Srinivasan, 1983) is not adequately proved because neither the test size nor the 5-chambered test can be used for its discrimination. Specimens referable to this taxon, although very rare and atypical, were encountered from the lower Oligocene *Globigerina ampliapertura* Zone to the lower Miocene *Catapsydrax dissimilis* Zone; they show gradation into *T. munda* in the lower Oligocene samples.

Tenuitella fleisheri, n. sp.

Pl. 4, Figs. 1–7

Tenuitella anfracta (Parker).—FLEISHER, 1974, p. 1133, figs. 9, 10.—KENNETT and SRINIVASAN, 1983, p. 164, pl. 40, figs. 7–9.

Description. Test small, compressed on both sides; chambers ovoid to subglobular 4½–5 in final whorl, increasing moderately in size as added; umbilicus small to closed; wall microperforate and pustulate; aperture antero-intraumbilical-extraumbilical, a low arch.

Type horizon. Late Quaternary.

Type locality. Zante Channel, sample IS/82/8.

Etymology. Named for R. L. Fleisher, in honor of his work on *Tenuitella*.

Remarks. Forms referable to this taxon have previously been recorded as *Globorotalia anfracta* Parker (Fig. 3: 22–24). The latter species, however, possesses more inflated chambers with a smooth, macroperforate wall (e.g., Brönnimann and Resig, 1971, pl. 43, figs. 2, 3, 6; pl. 48, fig. 4; Rögl and Bolli, 1973, pl. 8, figs. 1–7; Quilty, 1976, pl. 11, figs. 9, 10; Poore, 1979, pl. 2, figs. 7–9). Robert L. Fleisher (written communication, 1986) has checked the holotype of *G. anfracta* and confirms this distinction. The distinct morphocharacters possessed by *T. fleisheri*, such as small size of the test, microperforate wall and pustulate surface, indicate that it is not Parker's taxon, but is a modern representative of *Tenuitella*. This species differs from all of the Oligocene-Miocene tenuitellines in having a compressed test, which is more densely pustulate on the early whorl and on the umbilical-apertural face. It seems to have evolved into the bullate *Tenuitellita iota* (Parker).

Tenuitella gemma (Jenkins)

Pl. 2, Figs. 6–8

Globorotalia gemma JENKINS, 1966, p. 1115–1118, fig. 11, nos. 97–103. (See Fig. 3: 4–6.)

Remarks. I reject the assertion that *Tenuitella gemma* may be a junior synonym of *Globigerina postcretacea* Myatliuk (e.g., Stainforth and others, 1975; Stainforth and Lamb, 1981; see notes on *G. postcretacea* below). *Tenuitella gemma* can be distinguished by its 5-chambered, low trochospiral and heavily pustulate test, and its intraextraumbilical aperture, on which a thin lip may develop.

Jenkins (1966, 1971, 1985) recorded that this species is restricted to the *G. brevis* Zone (uppermost Eocene to basal Oligocene) in southern mid-latitudes. However, it apparently ranges into the “*Globorotalia*” *opima opima* Zone (P21) in Trinidad. There is evidence that this taxon gave rise to forms such as *T. clemenciae* and *Tenuitellinata* cf. *T. pseudoedita* during the Oligocene.

Tenuitella minutissima (Bolli)

Pl. 3, Figs. 6–9, 11, 12

Globorotalia minutissima BOLLI, 1957a, p. 119, pl. 29, fig. 1. (See Fig. 3: 16–18.)

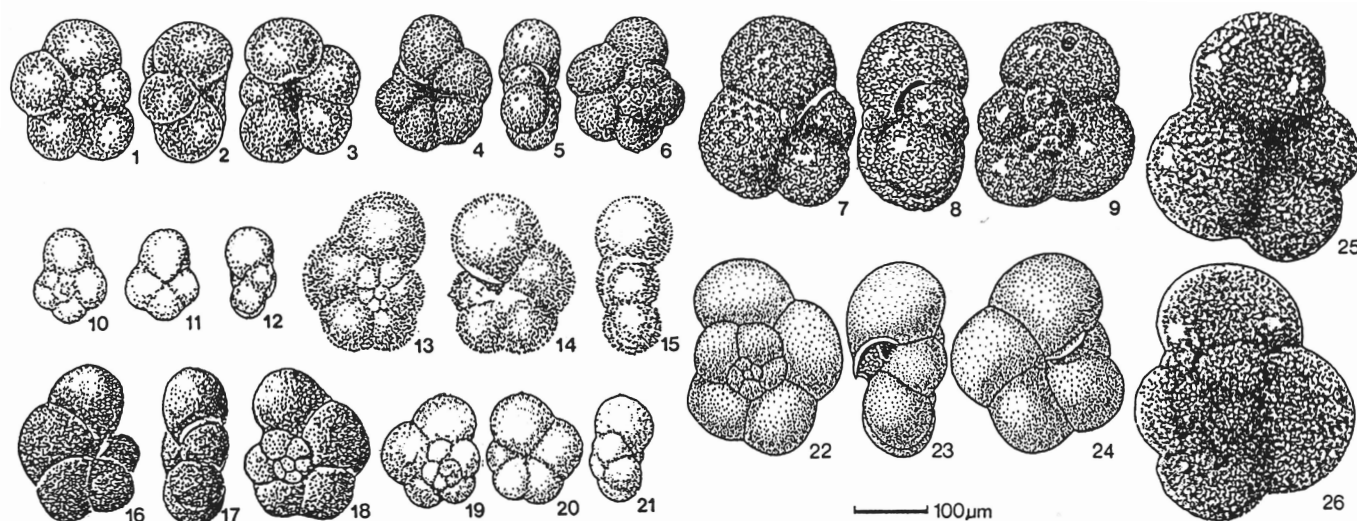


FIGURE 3. Type illustrations of some selected species that have been considered as belonging to, or related to, the Tenuitellinae (*Tenuitella*): 1-3 *Globigerina postcretacea* Myatliuk (1950, pl. 4, fig. 3, holotype); 4-6 *Globorotalia gemma* Jenkins (1966, fig. 11, nos. 97-99, holotype); 7-9 *Globorotalia munda* Jenkins (1966, fig. 14, nos. 126-128, holotype); 10-15 *Globigerina brevispira* Subbotina (1960, pl. 11, fig. 4, holotype [10-12], fig. 5, paratype [13-15]); 16-18 *Globorotalia minutissima* Bolli (1957a, pl. 29, fig. 1, holotype); 19-21 *Globigerina pseudoedita* Subbotina (1960, pl. 11, fig. 1, holotype); 22-24 *Globorotalia anfracta* Parker (1967, pl. 28, fig. 3, holotype); 25, 26 *Turborotalia clemenciae* Bermúdez (1961, pl. 17, fig. 10, holotype).

Globigerina brevispira SUBBOTINA, in Subbotina and others, 1960, p. 56, pl. 11, figs. 4, 5 (not fig. 6).

Remarks. This species is characterized by a test having rapidly enlarging, slightly spirally elongate chambers and a small-to-closed umbilicus. Individuals with slightly radial chambers, referable to *Globigerina brevispira* Subbotina (see Fig. 3: 10-15, and Pl. 3, Figs. 6-9), are considered to be within the range of variation of this taxon; both forms were commonly encountered together from the lower Miocene *Catapsydrax dissimilis* Zone to the middle Miocene *Globorotalia fohsi fohsi* Zone (N10-N11).

***Tenuitella munda* (Jenkins)**

Pl. 2, Fig. 13

Globorotalia munda JENKINS, 1966, p. 1121-1122, fig. 14, nos. 126-133. (See Fig. 3: 7-9.)

Remarks. This mid-latitude form (Kennett and Srinivasan, 1983), showing many similarities to 4-chambered *T. clemenciae*, has led some authors (e.g., Blow, 1979) to consider that it is possibly a junior synonym of the latter. However, the spirally and ventrally strongly inflated chambers of *T. munda* distinguish it from *T. clemenciae*.

An early Oligocene lineage, *munda-juvenilis*, first recognized by Jenkins (1966), has been confirmed by subsequent studies (e.g., Jenkins and Srinivasan, 1985).

***Tenuitella neobrevispira*, n. sp.**

Pl. 3, Figs. 13, 14

Globigerina brevispira SUBBOTINA, in Subbotina and others, 1960, p. 56, pl. 11, fig. 6 (not figs. 4, 5).

Description. Test very low trochospiral, with a flat to concave spiral side; chambers ovoid, 5 in final whorl, increasing rapidly as added; umbilicus open, medium in size; wall microperforate and pustulate; aperture extraumbilical.

Type horizon. Middle Miocene, *Gr. fohsi fohsi* Zone.

Type locality. On east bank of cricket ground southwest of Golconda Estate house which is about one-sixth mile south of Golconda Village, south Trinidad (Bolli, 1957a, p. 101); sample Bo 185A.

Remarks. This species can easily be distinguished from related forms by its subpentagonal test, quickly enlarging ovate chambers

and well-defined umbilicus. It seems to have derived from *T. minutissima* in the middle Miocene.

***Tenuitella neoclemenciae*, n. sp.**

Pl. 2, Figs. 1-4

Description. Test small, low trochospiral, spiral side flat or concave; chambers subglobular, 5 or 6 in final whorl, enlarging slowly as added; umbilicus small; wall microperforate and pustulate; aperture extraumbilical.

Type horizon. Lower Oligocene, *Gr. opima opima* Zone (P21).

Type locality. Cipero type section, between 20 and 240 ft southwest from fixed point (Bolli, 1957a, p. 100, 103); sample JS 20.

Remarks. This species differs from both *T. gemma* and *T. clemenciae* in possessing a fully extended extraumbilical-peripheral aperture and five or more chambers in the final whorl and a flattened to concave spiral side. The apertural lip in *T. neoclemenciae*, unlike in other forms, develops towards the periphery. In Trinidad sections, *T. clemenciae* ranges through the lower and upper Oligocene interval.

"*Tenuitella*" *nkbrowni* (Brönnimann and Resig)

Globorotalia (*Turborotalia*) *nkbrowni* BRÖNNIMANN and RESIG, 1971, p. 1279-1280, pl. 40, figs. 1-8.

Remarks. This taxon is similar to *T. gemma*, but differs in having a sutural supplementary aperture on the evolute (spiral) side (at least in the holotype specimen), a more highly arched primary aperture and typically 6 (rather than 5) chambers in the adult whorl. It has been reported only from the upper Oligocene (N3/P22).

"*Tenuitella*" *parkeri* (Brönnimann and Resig)

Globorotalia (*Turborotalia*) *parkeri* BRÖNNIMANN and RESIG, 1971, p. 1280-1281, pl. 43, fig. 7 (not fig. 10); pl. 47, figs. 2, 3.

Remarks. This Quaternary form, which Fleisher (1974) suggested placing in *Tenuitella*, differs from all other species of the genus in 4-4½ slightly radial, rapidly enlarging chambers in the final whorl and a smooth, although microperforate, wall structure (see also Saito and others, 1981, p. 120, pl. 39, fig. 2). These morphologic differences make its tenuitelline status dubious with respect to the generic concept defined here, and further work on its evolutionary phylogeny is recommended.

Tenuitella sp.

Globorotalia sp. 4. JENKINS and ORR, 1972, pl. 18, figs. 7–12.

Remarks. This form is characterized by a large apertural lip or plate, which extends onto the umbilicus. It may be derived from *Tenuitellinata* cf. *T. pseudoedita* or some related forms in the early Miocene (see Fleisher, 1974, p. 1134).

Tenuitellita, n. gen.

Type species. *Globigerinita iota* Parker, 1962.

Description. Test small, low trochospiral; 5 chambers in final whorl, enlarging slowly to moderately in size as added; sutures radial on both sides; wall microperforate and pustulate; primary aperture antero-intraumbilical-extraumbilical, covered with umbilical bulla.

Stratigraphic range. Quaternary.

Remarks. This new genus is distinguished from *Tenuitella* and *Globigerinita* by its bullate, intraextraumbilical, primary aperture. It may have been derived directly from *Tenuitella* (possibly *T. fleisheri*), whereas bullate *Globigerinita* with intraumbilical primary apertures developed also from *Tenuitella*, but via a transitional stage, which is recognized as *Tenuitellinata* spp. The Oligocene-Miocene bullate species, *Globigerinita praestainforthi* Blow, is superficially similar to the forms included here, but possesses an antero-intraumbilical primary aperture (see Fig. 4), and is correctly assigned to *Globigerinita*.

Subfamily GLOBIGERINITINAE Bermúdez, 1961**Tenuitellinata, n. gen.**

Type species. *Globigerina angustiumbilitata* Bolli, 1957.

Description. Test small, low to medium trochospiral, with convex spiral side; chambers globular to subglobular, about 11–13 slowly enlarging chambers arranged in 2 whorls, 4–5 chambers in final whorl; sutures radial on umbilical (involute) side, radial to slightly curved on spiral (evolute) side; umbilicus small to closed; wall microperforate and pustulate; aperture a low arch, intraumbilical, bordered with a thin lip, but lacking a bulla.

Stratigraphic range. Eocene?–Oligocene to Holocene.

Remarks. *Tenuitellinata* is superficially similar to *Tenuitella*, but differs in apertural details. In *Tenuitella*, the aperture is always umbilical-extraumbilical (-peripheral), but species of *Tenuitellinata* possess an intraumbilical aperture. *Tenuitellinata* may have evolved from *Tenuitella* by migration of the aperture to the umbilicus; hence they are phylogenetically closely related. Separation of this new genus from *Tenuitella* is to mark an evolutionary stage, which may then have evolved into bullate *Globigerinita*.

Tenuitellinata angustiumbilitata (Bolli)

Pl. 2, Figs. 15, 17–19

?*Globigerina postcretacea* MYATLIUK, 1950, p. 280, pl. 4, fig. 3.

Globigerina ciperoensis angustiumbilitata BOLLI, 1957a, p. 109, pl. 22, figs. 12 (paratype), 13 (holotype); p. 164,

cf. *Globigerina ciperoensis angustiumbilitata* Bolli.—BOLLI 1957b, p. 164, pl. 36, fig. 6.

Description emended. Test a medium trochospire, with 5 ventrally inflated, globular chambers in final whorl; umbilicus closed; wall densely microperforate and pustulate; aperture a low arch, antero-intraumbilical to axiointraumbilical, lacking a bulla.

Type horizon. Late Oligocene (P22).

Type locality. Cipero type section, between 60 northeast and 20 southwest of fixed point (Bolli, 1957a, p. 100, 103); sample Bo 291A (also the source of the specimens used here).

Remarks. Fleisher (1974) noted that *G. angustiumbilitata* Bolli was an exceptional globigerine species in that it did not seem to belong to the spinose group of species typified by *Globigerina bulloides* and with roots in the late Eocene *G. officinalis* stock. Fleisher was able to re-examine the holotype in December, 1986, and has informed me (written communication, 1986) that the assignment of this species to *Tenuitellinata* is correct and that the test “has microperforate wall texture rather than a spinose one.” Therefore, the identifications of this species by Jenkins and Orr (1972, pl. 4, fig. 6

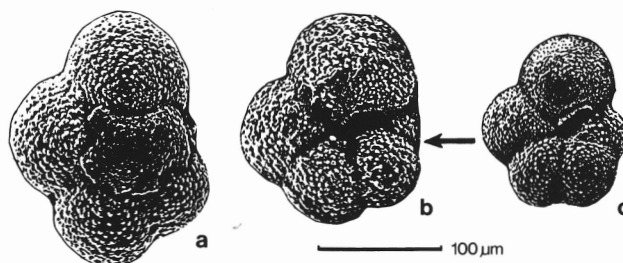


FIGURE 4. Phylogenetic development from *Tenuitellinata* (*T. cf. T. pseudoedita*) to *Globigerinita* (*G. praestainforthi*). **a** Whole specimen of *G. praestainforthi*; **b** final chamber (same specimen) removed to show the antero-intraumbilical primary aperture as in **c** *T. cf. T. pseudoedita* (see Pl. 3, Fig. 1). All from the early Miocene *Catapsydrax dissimilis* Zone (N5).

[not fig. 5], pl. 5, figs. 6–8), Quilty (1976, pl. 1, figs. 12, 13) and Kennett and Srinivasan (1983, pl. 4, figs. 3–5) are to be accepted, while those of other authors, who have given this species name to macroperforate, spinose representatives of *Globigerina*, are incorrect. Such misidentification has been frequent, because, as Fleisher has written, “it has never been very difficult to find a small, macroperforate form that was generally similar to Bolli’s illustration. . . . This problem arose, I think, because the holotype illustration of *G. angustiumbilitata* is a drawing made 30 years ago, when details of wall texture were not considered important. The drawing shows a fine macroperforate texture that is not present on the (holotype) specimens; the roughened, pustulose surface was apparently taken for a lightly pitted one. The surface pattern illustrated (in Bolli, 1957a) is essentially identical with that shown for *Globigerina juvenilis*, which . . . is microperforate.” Consequently, in this paper, *G. angustiumbilitata* Bolli is designated the type species of *Tenuitellinata*, a designation with which Fleisher (written communication, 1986) agrees.

The specimen of *T. angustiumbilitata* illustrated here was obtained from sample Bo 291A and is strictly a topotype (Pl. 2, Figs. 15, 17–19); it is believed by Fleisher (written communication, 1986) to be very similar to the holotype of this species, “except that the final chamber (of the holotype) is slightly larger, relative to the size of the test, and that the spire (of the figured specimen) is slightly higher. I (Fleisher) believe that they are synonymous.” In view of the unreliability of the depictions of surface texture in the original illustrations of this species, Bolli’s (1957b) record from the late Eocene San Fernando Formation (Zone P16) needs confirmation by review of the hypotype (Bolli, 1957b, pl. 36, fig. 6). The grossly homeomorphic, but spinose and macroperforate species called “*G. angustiumbilitata*” by many authors, needs a new and distinct species name. Kennett and Srinivasan (1983) correctly identified *T. angustiumbilitata* and recorded it to range as high as zones N19/20 (middle Pliocene).

Tenuitellinata juvenilis (Bolli)

Globigerina juvenilis BOLLI, 1957a, p. 110, pl. 24, figs. 5, 6.

Remarks. This taxon is still in dispute because it has been considered either as a synonym of *Globigerinita glutinata* (e.g., Kennett and Srinivasan, 1983) or, as originally described, as a separate species of “*Globigerina*” (e.g., Jenkins, 1985). However, its phylogenetic relationship to *Tenuitella munda*, as recognized by Jenkins (1966), and further demonstrated by Jenkins and Srinivasan (1985), indicates that this microperforate form is not a true *Globigerina*, but a *Tenuitellinata*, as defined here. A stratigraphic gap between the first occurrence of the non-bullate *T. juvenilis* species in the early Oligocene and that of the bullate *Globigerinita glutinata* s.s. in the early Miocene also confirms that their taxonomic status is distinct; if the two forms were merely different forms of the same biological species, their stratigraphic ranges would be the same. On the contrary, their successive appearance in time suggests that *Globigerinita glutinata* is a direct descendant of *Tenuitellinata juvenilis*.

Tenuitellinata cf. *T. pseudoedita* (Subbotina)

Pl. 3, Figs. 1–5; Pl. 4, Figs. 11–13;

Pl. 5, Figs. 1, 4, 7, 11

cf. *Globigerina pseudoedita* SUBBOTINA, in Subbotina and others, 1960, p. 55–56, pl. 11, figs. 1–3.? *Globorotalia (Tenuitella) clemenciae* (Bermúdez).—KENNETT and SRINIVASAN, 1983, pl. 40, figs. 3–6 (not figs. 1, 2).

Remarks. This species is characterized by a slightly convex spiral side and a low arched (often variable) aperture, which is strongly anterointraumbilical. The specimens observed are similar to forms described as *G. pseudoedita* by Subbotina (in Subbotina and others, 1960), but the extent of the aperture in the latter, although originally described as extending along the basal suture (i.e., interiomarginal and, possibly, extraumbilical), has not yet been properly illustrated (see Fig. 3: 19–21, for Subbotina's holotype specimen). For this reason, its taxonomic status as a synonym of *G. angustiumbilitata* Bolli, as suggested by Blow (1979), is still questionable. *Tenuitellinata* cf. *T. pseudoedita* was found in the upper Oligocene and lower Miocene samples, and many Oligocene-Miocene specimens show progressive gradation into both *T. angustiumbilitata* and bullate *Globigerinita praestainforthi*. Kennett and Srinivasan (1983) recorded a long ranging species, *Tenuitella clemenciae*, some forms of which are possibly within the variation of *Tenuitellinata* cf. *T. pseudoedita* rather than *Tenuitella clemenciae*.

NOTES ON OTHER SYNONYMS AND SIMILAR BUT UNRELATED FORMS

Globigerina inconspicua Howe subsp. *aculeata* Jenkins (1966, upper Eocene, New Zealand)

Fleisher (1974) first regarded this taxon as a species of *Tenuitella*. However, its macroperforate wall and spinose surface texture (see Jenkins and Srinivasan, 1985, pl. 2, fig. 4) refute this removal from *Globigerina*.

Globorotalia anfracta Parker (1967, Holocene, Caribbean)

Fleisher (1974), Srinivasan and Kennett (1981), and Kennett and Srinivasan (1983) considered this taxon as a *Tenuitella*. However, its finely macroperforate and smooth wall, demonstrated earlier by Rögl and Bolli (1973, pl. 8, figs. 1–7), prevents its assignment to *Tenuitella*. The forms described previously as *T. anfracta* (by the authors cited above), which Rögl (written communication, 1986) regarded as *T. iota* (Parker), are now included in *T. fleisheri*, n. sp.

Globigerina brevispira Subbotina (1960, early Miocene, USSR)

Rapidly enlarging, slightly elongate chambers shown in the original figures 4, 5 (see Fig. 3: 10–15) may represent a variant of *T. minutissima* (Bolli); they are provisionally considered as synonyms. Some different morphocharacters shown in Subbotina's paratype (fig. 6), such as the open umbilicus and dorsal subcrescentic chambers, may be of specific value, and characterize the new species, *T. neobrevispira*.

Globorotalia (Turborotalia) cifellii Brönnimann and Resig (1971, late Oligocene, Equatorial Pacific)

This species (in part) was regarded by Fleisher (1974) as belonging to *Tenuitella*. However, its strongly, although sparsely, spinose test and typically macroperforate wall (perforations 2–3 μ m, as originally described), indicate that it does not.

Globorotalia denseconnexa Subbotina (1960, Oligocene, USSR)

Although Blow (1979) did suggest that this taxon may belong to his "gemma-permicra plexus," forms with strongly oblique dorsal sutures (such as possessed by this species) have not yet been reported to be microperforate, and referable to *Tenuitella*. Re-examination of the type material of *G. denseconnexa* is necessary.

Globorotalia insolita Jenkins (1966, late Eocene, New Zealand)

This species, referred to *Tenuitella* by Fleisher (1974), shows many differences from *Tenuitella*. It possesses 2–3 (rather than 1½–2) whorls,

an extraumbilically high aperture with a bifid apertural lip and, more importantly, a smooth and macroperforate wall (see Jenkins and Srinivasan, 1985). Nevertheless, this taxon may be related to forms recognized here as *Praetenuitella*.

Globigerina khadumica Bykova and *Globigerinella liverovskae* Bykova (1960, early Oligocene, USSR)

No holotypes were originally designated for these two species. According to Bykova, however, *G. liverovskae* possesses some characters intermediate between planispiral *Globigerinella* and low trochospiral *Globigerina*, and the species was said to include the forms described as *Globigerina postcretacea* by Subbotina (1953). Samuel and Salaj (1968) considered *G. khadumica* as a synonym of *G. liverovskae* and proposed a lectotype (Bykova's 1960, fig. 3 of *G. liverovskae*) for the latter. Since then, neither the name *liverovskae*, nor *khadumica* was used until Blow (1979) included this species in his concept of the "gemma-permicra plexus." If *liverovskae* does contain forms with a very low trochospire or pseudoplanispire, it might be a senior synonym of *Globorotalia gemma* Jenkins, as that taxon also was described to include Subbotina's *G. postcretacea*. However, although Bykova's taxa were described much earlier than *G. gemma*, their lectotype was not proposed until two years after the founding of *G. gemma* by Jenkins. Because of the confusion over the nature and status of *G. liverovskae* and *G. khadumica* no convincing proposals about them can be made before Bykova's types are restudied.

Globorotalia (Turborotalia) permicra Blow and Banner (1962, early to middle Oligocene, Tanzania)

Blow (1979) suggested that this species is a component of the "gemma-permicra plexus," a group of small species with microperforate walls referable to *Tenuitella* as defined herein. The species *G. permicra*, however, was described as possessing a highly arched aperture, and its metatype illustration shows a pitted, macroperforate wall (Blow, 1969, pl. 35, fig. 9); if this is correct, the species cannot be regarded as a true *Tenuitella*. Blow (1979, pl. 245, fig. 4) also illustrated a microperforate "ideotype," which closely resembles *T. clemenciae* (Bermúdez). Apparently, neither Blow (1969, 1979) nor Blow and Banner (1962) clearly discriminated between wall structures and textures when dealing with these very small species (F. T. Banner, oral communication, 1986).

Globigerina postcretacea Myatliuk (1950, Oligocene, USSR)

This taxon is poorly defined, as it has been used for various form-species, which are quite different in the detailed nature of their aperture and wall structure. Subbotina (1953) recognized forms with umbilical-extraumbilical-peripheral apertures as *postcretacea*, and noted great variation in the test size and in the apertural position. However, none of the specimens figured by Subbotina (Subbotina, 1953, pl. 2, figs. 16–20) possesses an intraumbilical aperture as in the type of *G. postcretacea* (see Fig. 3: 1–3). Bykova (1960) first drew attention to this and proposed two new species, *Globigerina khadumica* and *Globigerinella liverovskae* (see above). Subsequently, Jenkins (1966) pointed out that *G. postcretacea* should not be confused with *Globorotalia gemma* Jenkins. Thus there are now two different views on *postcretacea* and *gemma*: 1) those who follow Subbotina (1953) apparently lump together these form-taxa, as well as their allies (e.g., Stainforth and others, 1975; Stainforth and Lamb, 1981); 2) those who agree with Jenkins (1966), consider each as an independent species (e.g., Jenkins, 1971, 1985; Banner, 1982; Krashennikov and Basov, 1983), even though the actual taxonomic position of *G. postcretacea* has never been completely understood (Blow, 1979, p. 804). I found forms with intraumbilical apertures in at least two species groups having different wall structures. The axiointraumbilical aperture suggests that *G. postcretacea* may fall within the range of *Tenuitellinata angustiumbilitata* (Bolli). Its true wall structure remains to be determined by restudy of the type material.

DISCUSSION

Praetenuitella and *Tenuitella*, stratigraphically the most important genera of this group, are distinguished

by their small, low trochospiral tests with an extraumbilical aperture. They differ conspicuously from *Globanomalina* Haque (Paleocene-early Eocene; type species *G. ovalis* Haque), which has a much larger test and a smooth, macroperforate wall. *Parvularugoglobigerina* Hofker (type species *Globigerina eugubina* Luterbacher and Silva) of Danian age, possesses a small, microperforate test, similar to that of *Tenuitella*, but has an extraumbilically arched aperture. Hofker (1978, pl. 2, fig. 6) and Banner (1982, p. 202) indicated that it possesses a finely muricate wall texture with sparsely distributed "fine mural pores," as in "*Globorotalia* (*Turborotalia*)" *archeocompressa* Blow (see Blow, 1979, p. 1049–1052, pl. 58, figs. 2, 6–9; pl. 64, figs. 2, 3, 5, 6). However, Smit (1982) has redescribed *P. eugubina* from its zone in southeast Spain (correlated also on magnetostratigraphy), and has clearly illustrated the smooth, microperforate wall (as well as the highly arched, wholly extraumbilical aperture) of that species (which is recognized to be a senior synonym of "*Globorotalia* (*Turborotalia*)" *longiapertura* Blow, 1979). It seems to be phyletically (and stratigraphically) separated from *Tenuitella*. Bullate, microperforate forms with an anterointraumbilical primary aperture, such as *Globigerinita praestainforthi* Blow, which Fleisher (1974) suggested belong to *Tenuitella*, I now retain in *Globigerinita* (see Fig. 4), even though *G. naparimaensis* has an axiointraumbilical aperture. I do this because the apertural extent varies considerably within the umbilicus between different species of *Globigerinita*. The "globorotaline" forms with an intra-extraumbilical aperture (like *T. gemma*) are grouped in the genus *Tenuitella*, which, if the primary aperture is covered by a bulla, produces forms now referred to *Tenuitellita* (not *Globigerinita*). *Turborotalita* Blow and Banner (type species *Truncatulina humilis* Brady) is distinguished by the ampullate final chamber and the macroperforate wall, and therefore differs greatly from both *Tenuitellita* and *Globigerinita*.

Fleisher (1974) differentiated *Globigerinita* from *Tenuitella* by its intraumbilical primary aperture, which may be covered by bulla. Forms placed in *Globigerinita glutinata* (Egger) by Kennett and Srinivasan (1983) include both bullate *Tinophodella ambitacrena* (and *Globigerinita naparimaensis*) and non-bullate *Globigerina juvenilis* Bolli. The "lumping" in the case of *Globigerinita glutinata* obscures phylogenetic relationships. The non-bullate "*G.*" *juvenilis* occurred first, in the middle to late Oligocene (Jenkins, 1966; Jenkins and Srinivasan, 1985), whereas the bullate *Globigerinita glutinata* s.l. first occurred in the early to middle Miocene (Saito and others, 1981; Bolli and Saunders, 1985). As currently understood, it seems that *Globigerinita* is of polyphyletic origin, even if species of *Catapsydrax* are excluded from it. A definite generic boundary must be drawn to exclude *Globigerinita* from phylogenetically ancestral forms; otherwise, the separation of *Tenuitella* from *Globigerinita* may also be obscured. I distinguish *Globigerinita* from equally microperforate *Tenuitella* by its bullate structure and its apertural extent (see key to the genera). Those transi-

tional forms between *Tenuitella* and *Globigerinita* having an intraumbilical aperture but lacking bullae, I assign to the new genus, *Tenuitellinata*. Unlike *Tenuitellinata*, some other genera characterized also by intraumbilical (although highly arched and often non-rimmed) apertures, such as *Globigerina* d'Orbigny (type species *G. bulloides* d'Orbigny) and *Globastica* Blow (type species *Globigerina daubjergensis* Brönnimann), possess either rather large, spinose tests with a macroperforate wall (as in the former), or small, muricate tests with a microperforate wall (as in the latter). Finally, the new genus *Praetenuitella* is distinguished by: 1) its very low trochospiral test; 2) finely macroperforate walls in the earlier test, developing into a microperforate wall in the adult chambers; and 3) a wide and open umbilicus.

ORIGIN AND PHYLOGENY OF THE TENUITELLINAE

ORIGIN OF THE TENUITELLINAE

Gould's (1977) models of evolutionary punctuated equilibrium and phyletic gradualism were discussed by Banner and Lowry (1985) with regard to planktonic foraminiferal phylogeny. Progressive and continuous modification of test morphocharacters in geological time (e.g., the *Pulleniatina* lineage, discussed by Banner and Blow [1967] and the *Globorotalia peripheroronda*-*G. fohsi fohsi* lineage of Bolli [1957a] and Blow and Banner [1966]) exemplify phyletic gradualism. On the other hand, the abrupt, cryptogenic appearance of other distinctive species (e.g., *Hantkenina* spp.) were believed to illustrate punctuations in phylogeny. The ancestor of *Tenuitella* was previously unknown and the appearance of the tenuitellines in the late Eocene has seemed to be a cryptogenic example of evolutionary punctuation. The stratigraphic range of one suggested ancestor, *Parvularugoglobigerina* (see Banner, 1982), is separated from that of *Tenuitella* by at least 13 my (early and middle Eocene).

The problems of finding the ancestor of *Tenuitella* have been aggravated by preconceived ideas regarding its likely nature (F. T. Banner, oral communication, 1985). Within the *Globigerinitina*, most lineages evolved unidirectionally; microperforate tests (as in *Globuligerina*) occurred before macroperforate ones, so the ancestor to *Tenuitella* has been assumed to be microperforate. Trochospiral taxa have repeatedly given rise to planispiral ones (Banner, 1982) and the reverse has not been noted; therefore, the ancestor to *Tenuitella* has been assumed to be trochospiral. There is a tendency, common to many known lineages, for tests to increase in size with evolutionary development; therefore, the tenuitellid ancestor has been supposed to be as small as, or smaller than, *Tenuitella* itself. In summary, if phyletic unidirectional gradualism has produced known species of *Tenuitella*, then the ancestral form should have been small, microperforate and trochospiral, much like *Tenuitella gemma*. The absence of such forms in the early and middle Eocene produced a phyletic problem with no obvious solution;

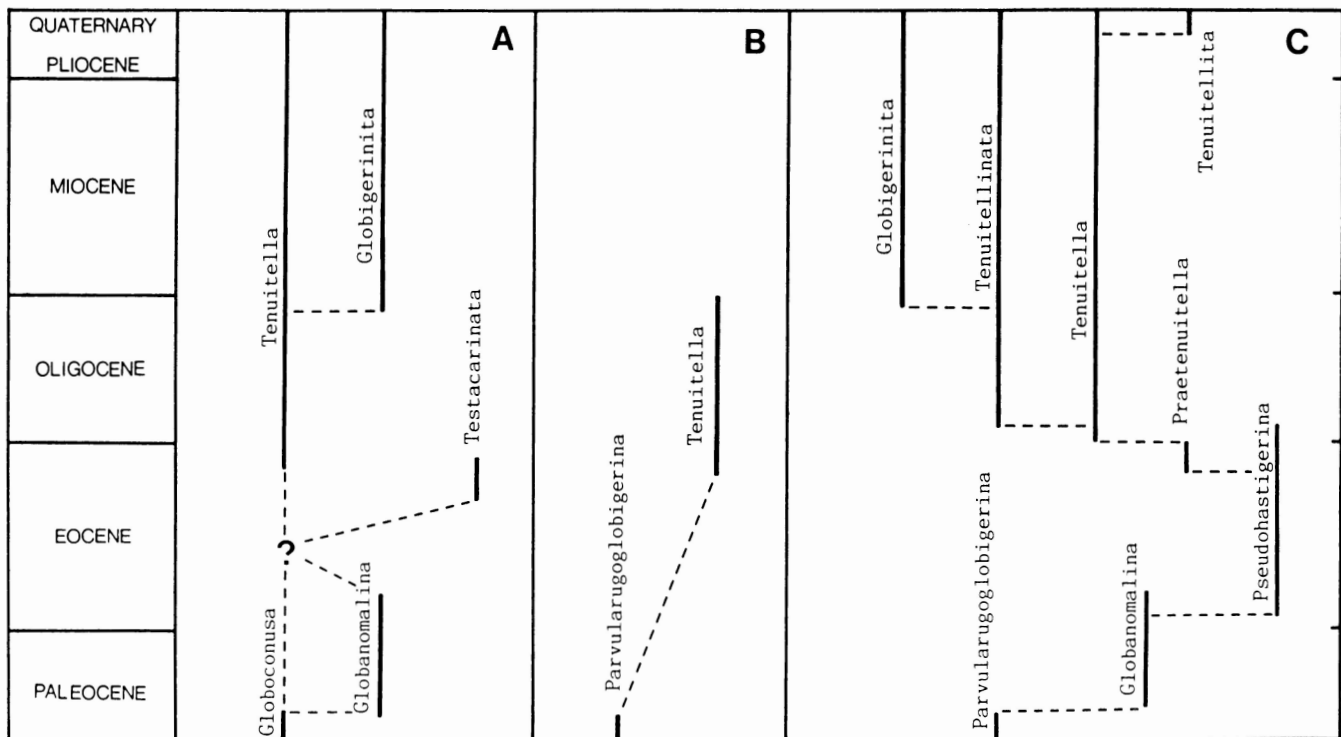


FIGURE 5. Probable phylogenetic affinities of, and lineages involving, *Tenuitella*. **A** based on Fleisher (1974); **B** Banner (1982); **C** this paper.

to call the origin of *Tenuitella* cryptogenic, or an example of punctuation, merely tended to conceal ignorance of the early phylogeny of the genus. Even to suggest *Globanomalina*, a relatively large and macroperforate form, as a possible ancestor (Fleisher, 1974; Fig. 5A, this paper), did not overcome the stratigraphic gap between the supposed ancestor and its alleged descendant.

When Banner and Lowry (1985) outlined the evolutionary history of the Globigerinacea, they listed only two examples of demonstrated reversal of previously established evolutionary patterns (Fig. 7B). One example was the Tertiary lineage from unkeeled *Globorotalia zealandica* to keeled *G. conoidea* and then, in turn, to unkeeled *G. inflata*. The other was the Cretaceous evolution of unkeeled *Ticinella* through variously keeled taxa related to *Rotalipora*, followed by loss of the keel in the ultimate descendant of the stock, *Anaticinella*. I suggest a third example (Fig. 5C). It involves a reversal of coiling mode (trochospiral to planispiral to trochospiral) and the diminution of perforation diameters to produce microperforate descendants from macroperforate ancestors. *Praetenuitella* provides evidence for this.

Blow (1979) suggested that low trochospiral, microperforate tests in the Danian ("*Globorotalia* (*Turborotalia*)" *archeocompressa* Blow) gave rise to larger, macroperforate species "*G. (T.)*" *compressa* (Plummer) in the later Paleocene. "*Globorotalia*" *archaeocompressa* is undoubtedly closely related to "*G. (T.)*" *longiapertura* Blow (believed by Smit [1982] to be the same as *Globigerina eugubina*). "*Globorotalia*" *compressa* is an early species of *Globanomalina*. The evi-

dence indicates that small, microperforate *Parvularugoglobigerina* (of Hofker, 1978), or perhaps "*Globigerina*" (of Smit, 1982, among others), of the earliest Paleocene, evolved into larger, macroperforate *Globanomalina* by mid-Paleocene time, with essentially low trochospirality retained. From *Globanomalina* evolved *Pseudohastigerina*, by migration of the extraumbilical aperture over the interiomarginal periphery and the achievement of planispirality (Berggren and others, 1967; Banner, 1982; Banner and Lowry, 1985) by the earliest Eocene. In the late Eocene samples studied here (Jackson Formation; GS/424 and GS/479), the finer size fraction (63–250 μm) yielded not only *Pseudohastigerina danvillensis* (Howe and Wallace), characterized by its planispiral, wholly macroperforate test, but also species of *Praetenuitella* with very low adult trochospirality (approaching pseudoplanispirality), microperforate later chambers and a planispiral, macroperforate early ontogenetic stage. The two species, together, comprised some 60% of the fossil assemblage (in the <250 μm fraction), and the morphological affinity between them is evident. *Praetenuitella impariapertura*, in particular (from GS/479 only), has an aperture that is not only fully peripheral initially, but which also is characterized by the height of the peripheral portion of the aperture even after adult (low) trochospirality is achieved (see Fig. 6). This emphasizes the (palaeogenetic) affinity of *P. impariapertura* with a *Pseudohastigerina* (possibly *P. danvillensis*) immediate ancestor. The descendant, typically post-Eocene *Tenuitella*, with its full trochospirality and wholly microperforate test, is grossly homeomorphic to the distant *Parvularugoglobigerina* ancestor, thus

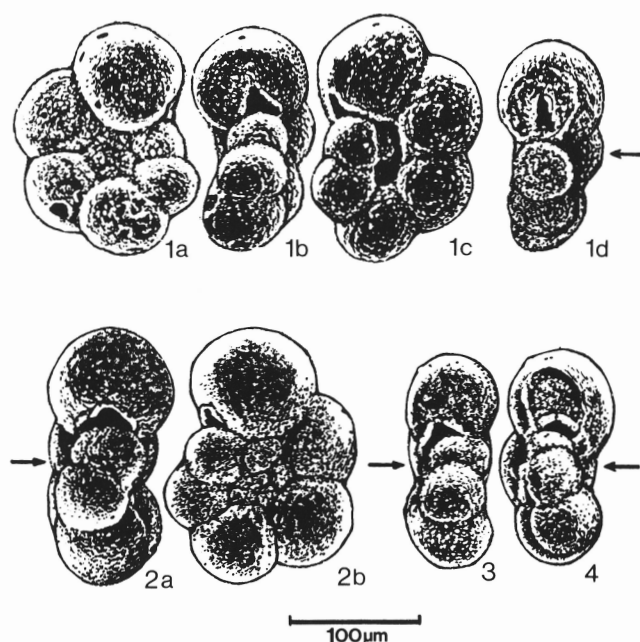


FIGURE 6. Apertural variation in *Praetenuitella impariapertura*, n. sp. 1 Holotype (see also Pl. I, Figs. 1–5); 2 paratype A, no. P51996; 3 paratype B, no. P51997; 4 a transitional form between *P. impariapertura* and *P. patefacta*, n. sp., no. P51998. Note the subtriangular aperture in the peripheral portion and the concave dorsal side (arrow points to umbilicus). All from the late Eocene Zone P15–P16, sample GS/479.

providing the completion of an example of “reversed” morphological evolution as depicted diagrammatically in Fig. 7B.

PHYLOGENETIC EVOLUTION OF TENUITELLINE AND GLOBIGERINITINE SPECIES

Three recognizable species, *Praetenuitella impariapertura*, *P. patefacta* and *P. praegemma*, evolved successively in the late Eocene. The evolving pattern of these primitive types, which is phylogenetically continuous, shows that such a process was achieved by the modifications of: 1) spirality (pseudoplanispiral to low trochospiral); 2) apertural characters (peripheral-extraumbilical to intra-extraumbilical); 3) chamber geometry (globular-subglobular to ovoid or subcrescentic); and 4) perforation pattern (finely macroperforate, $> 1.5 \mu\text{m}$, to microperforate, $< 1.0 \mu\text{m}$).

The advent of a global climatic crisis in the late Eocene-early Oligocene (e.g., Loubere, 1985) is believed to have influenced, actively or passively, the development of the Tenuitellinae. The test morphology changed through a further reduction of test dimensions and an increase of the density of the surface pustules, as seen in *Tenuitella gemma* and *T. neoclemenciae*. It seems that the cooling climate did not hamper any potential speciation of this group, as a continuous evolution can still be recognized. Within the early Oligocene, a genuine microperforate wall structure was established in *Tenuitella* and became a fixed character among those subsequently evolving tenuitelline species. The umbilicus, which is large and open in *Praetenui-*

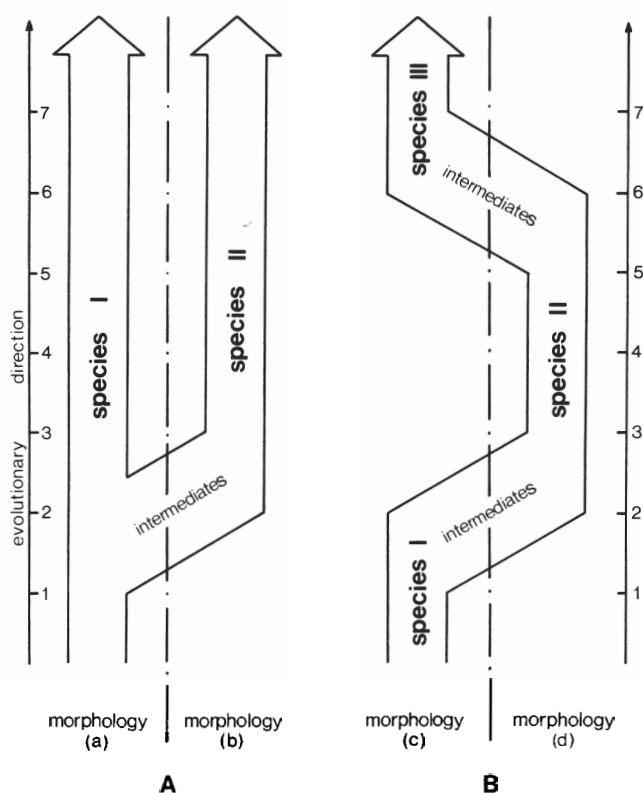


FIGURE 7. Two evolutionary trends in the planktonic foraminifera. **A** “Unidirectional” evolution: after the stasis of species I alone, an evolutionary offshoot (species II) arises by gradualistic change in the 1–2 interval; if that interval is geologically short, it will appear to be a “punctuation,” and if very short, and accompanied by major morphological change, species II will appear to be cryptogenic. After interval 2–3, both species are separate and each has achieved a period of “phyletic equilibrium.” **B** Evolutionary morphological “reversal”: as in **A** periods of “equilibrium” may be followed by observable evolutionary change, for which the fossil record may provide evidence, by forms intermediate between species I and species II (and then again with species II–III intermediates), for “phyletic gradualism.” Here, however, species III returns to the essential morphology (e.g., coiling mode or peripheral characters) of the ancestral species I. True homeomorphy between species I and species III is, however, rarely, if ever, achieved.

tella, became smaller and, finally, tended to close. Low trochospiral tests developed a slightly convex dorsal side. Individuals referable to *Tenuitella clemenciae*, with 4 chambers in the final whorl and an intra-extraumbilical aperture (which seldom reaches the periphery) made their first appearance in the early Oligocene. I believe that this taxon subsequently evolved into equally 4-chambered but ventrally and spirally strongly inflated *T. munda* in mid to high latitudes. *Tenuitella munda*, in turn, gave rise to *Tenuitellina juvenilis* (Jenkins, 1966; Jenkins and Srinivasan, 1985), and, finally, in the early Miocene (Fig. 8A), to some bullate forms (e.g., *Globigerinita ambitacrena* and *G. glutinata*). Further umbilical centralization of the aperture, which is associated with a progressively higher coiling mode, was first seen in the *Globorotalia opima opima* Zone (P21) (e.g., the appearance of *T. juvenilis*), but did not become common until the *Globigerina ciperoensis* Zone (P22), where forms developed antero-

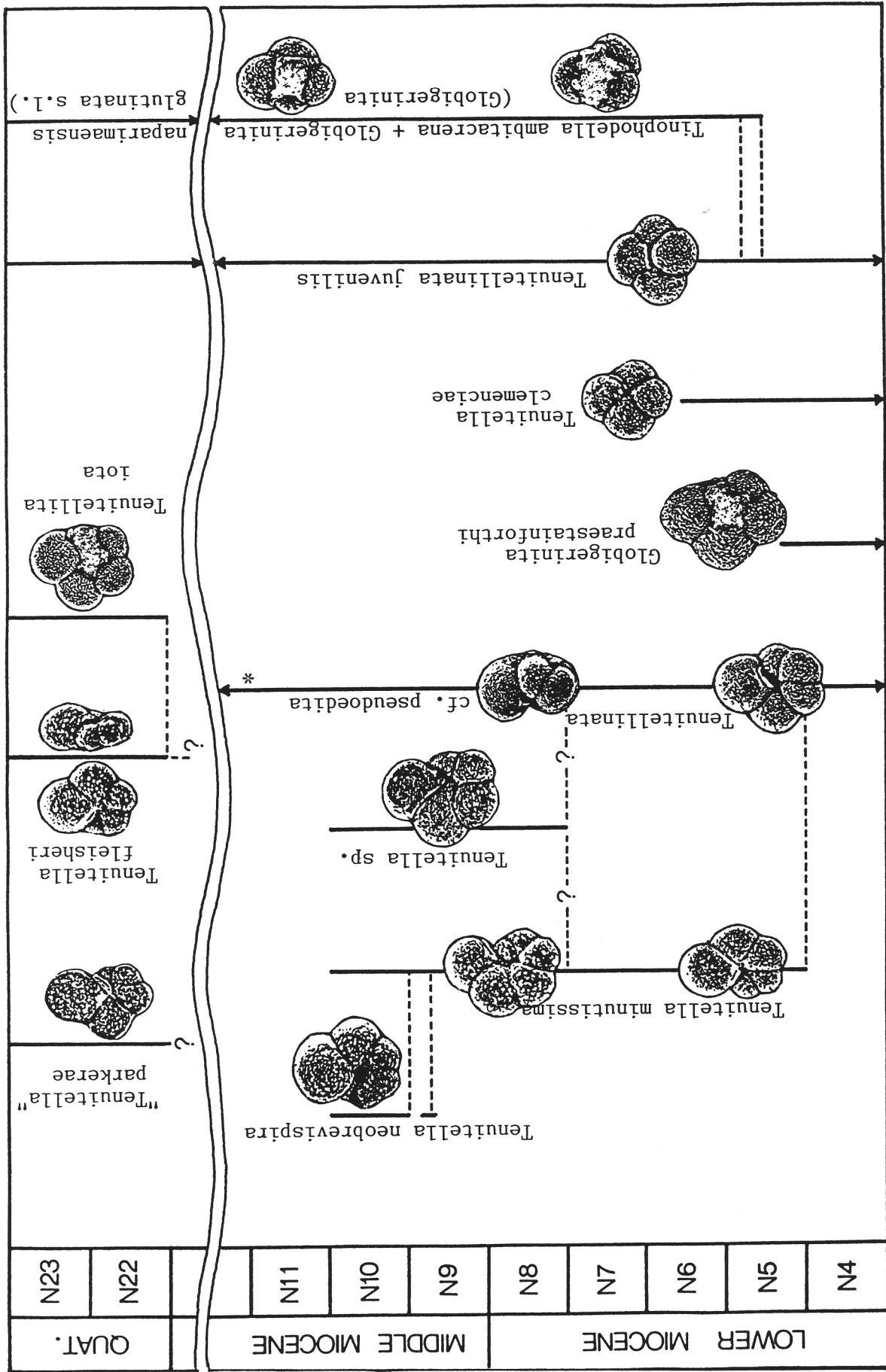


FIGURE 8A. Phylogenetic lineage of the Miocene to Quaternary Globigerinitidae. Note that Kennett and Srinivasan (1983) recorded *T. clemenciae* (now *T. cf. T. pseudoedita*) through the late Miocene interval in deep sea sediments.

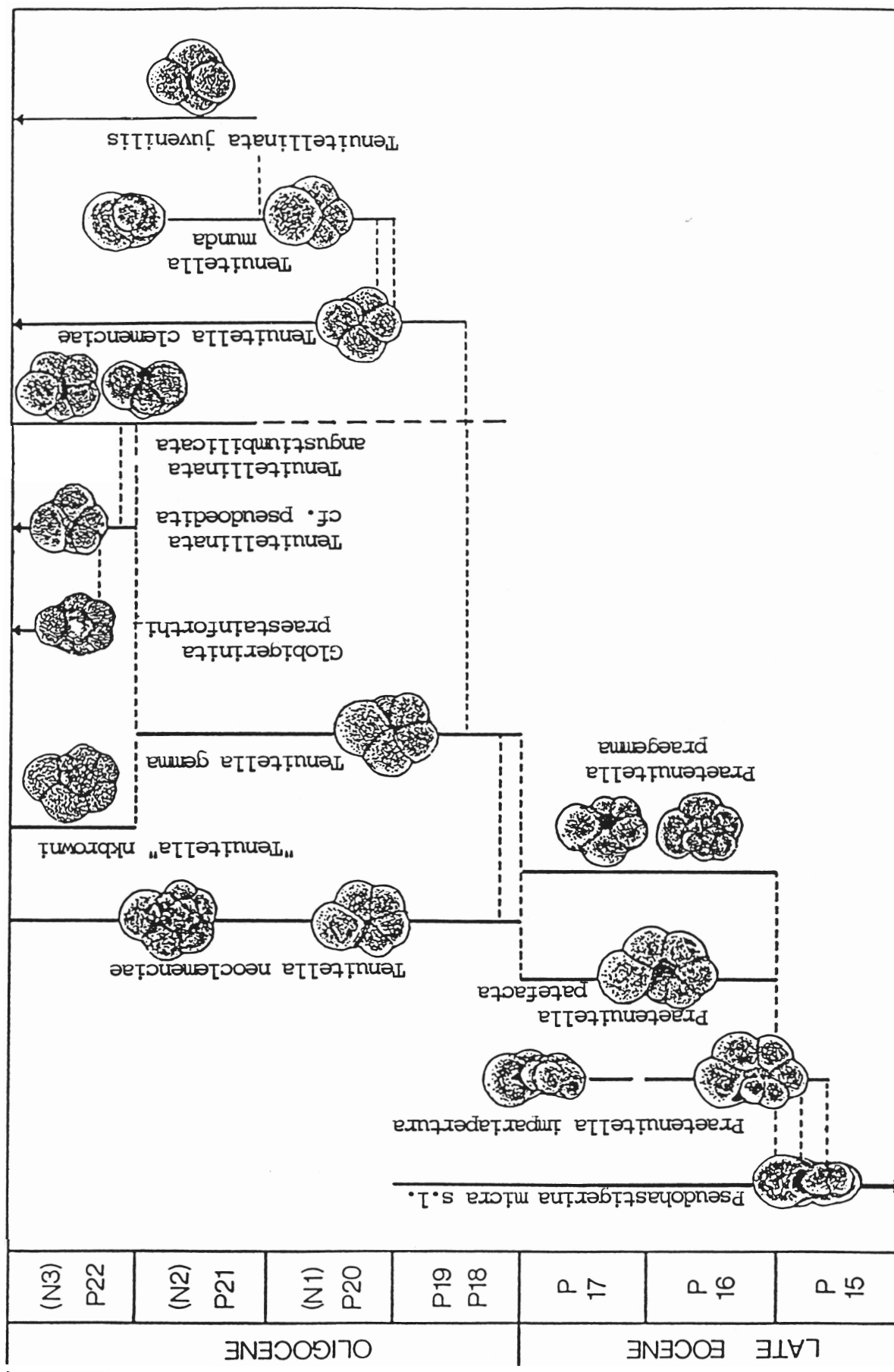


FIGURE 8B. Phylogenetic lineage of the Eocene-Oligocene Globigerinitidae.

intraumbilical apertures (*Tenuitellinata* cf. *T. pseudoedita*) and axiointraumbilical apertures (*T. umbilicata*). Some other variants or descendants from either *Tenuitella gemma* or *Tenuitellinata* cf. *T. pseudoedita*, such as "*Tenuitella*" *nkbrowni* and bullate *Globigerinita praestainforthi*, also first occurred in Zone P22. *Tenuitella gemma*, a stratigraphically useful species, became extinct at the top of the *opima opima* Zone (Fig. 8B).

The early Miocene saw, first, the continuous evolution of some Oligocene species with slowly enlarging chambers (e.g., *Tenuitella clemenciae* and *Tenuitellinata* cf. *T. pseudoedita* and, then, forms with rapidly enlarging chambers (Fig. 8A; *Tenuitella minutissima*, *T. neobrevispira*). The stratigraphically most important tenuitelline species first occurred in the early-middle Miocene. The evolution of the Tenuitellinae was suddenly interrupted, for no known reason, at the top of the *Globorotalia fohsi fohsi* Zone (N10–11), and disappeared from the Trinidad sections. Some globigerinitine species, referable to *Tenuitellinata juvenilis* and *T. cf. T. pseudoedita*, survived elsewhere, however, through the late Miocene (Kennett and Srinivasan, 1983, as *Tenuitella clemenciae*). The microperforate, pustulate *Globigerinatella insueta*, which appeared cryptogenically in the early Miocene (N6), probably arose directly from either *Globigerinita* or *Tenuitellinata* by the adoption of umbilically-directed streptospirality; *Globigerinatella* is a globigerinitid homeomorph of the Orbulinidae, and should be transferred from that latter family accordingly.

Forms referable to, or related to, the Tenuitellinae are not well known from Pliocene sequences. The evolutionary history of the subfamily at this stage, at least in the Mediterranean region, is unclear. No evidence of *Tenuitella* has been found in my samples of Pliocene marine sediments collected from Sardinia or Cyprus, or from Pliocene faunas published before. Nevertheless, *Tenuitellinata juvenilis* and its allies have been frequently recorded. I believe that the evolution of this globigerinitine group continued during the Pliocene, although the tenuitelline stocks have not yet been recognized.

Tenuitella fleisheri resembles, in many respects, the Oligocene-Miocene tenuitelline species, but it occurs only in the Quaternary. The bullate *Tenuitellita iota* may be directly descended from *T. fleisheri*; the origin of *T. fleisheri* still remains unknown. Together with these forms, "*Tenuitella*" *parkeri* and *Tenuitellinata juvenilis* (and its closely related *Globigerinita glutinata* s.l.) may also be encountered in Quaternary and modern marine deposits (Fig. 8A.)

Apparently, the evolutionary history of the *Tenuitella* plexus, as demonstrated herein, is continuous from the late Eocene to the Quaternary. Its greatest speciation occurred in the Oligocene and Miocene and its species tend to dominate the globigerinitid planktonic foraminiferal faunas of that interval in mid to high latitudes (Subbotina, 1953—USSR; Jenkins, 1966, 1985—New Zealand; Poore, 1979—North Atlantic). The stratigraphic importance of tenuitellines decreases

rapidly towards the tropical-subtropical regions where larger globigerinacean taxa are more useful (Bolli, 1957a, and Bolli and Saunders, 1985—Caribbean [Trinidad]; Banner and Blow, 1965, and Blow, 1969—low latitudes; Jenkins and Orr, 1972—Equatorial Pacific; Fleisher, 1974, 1977—northern Indian Ocean). During the whole evolutionary history of the Tenuitellinae, some morphological characters occurred iteratively, even though complete homeomorphs have not been found. For example, tests with very low trochospirality are seen in *Praetenuitella*, *Tenuitella neoclemenciae* and *T. minutissima*. The development of an umbilical bulla on some *Tenuitella* species gave rise to both *Globigerinita* and *Tenuitellita* (see Table 4). The lack of muricae in any member of the Globigerinitidae meant that none could develop muricocarinae, and no tenuitellines evolved true carinae either.

CONCLUSIONS

The microperforate wall structure is a definitive and fixed morphocharacter in both the Tenuitellinae and Globigerinitinae. The family Globigerinitidae is an important stock from which many Neogene-Quaternary planktonic foraminiferal groups developed. A phylogenetic change from pustular, microperforate to spinose or cancellate, macroperforate wall structure, or vice versa, seems, untenable, although the evolutionary pattern of the family may have become convergent to a certain extent. The wall structure is a meaningful phylogenetic reference and taxonomic parameter for phylogenetic reconstruction within this family group.

Detailed systematic work on the Tenuitellinae reveals that this group dominates the Oligocene to early middle Miocene small planktonic foraminifera, and that *Tenuitella* is directly descended from *Praetenuitella* (late Eocene), which evolved from a small variant of *Pseudohastigerina micra* s.l. This evolution is seen through a process of: 1) apertural migration from peripheral to extraumbilical-umbilical; and 2) progressive reduction of the perforations from finely macroperforate ($>1.5 \mu\text{m}$) to microperforate ($<1.0 \mu\text{m}$). Three closely linked new species, *Praetenuitella impariapertura*, *P. patefacta*, and *P. praegemma*, are restricted to the late Eocene. *Praetenuitella praegemma* is believed to be ancestral to *Tenuitella*.

Oligocene tenuitelline species are characterized by a diverse speciation of *Tenuitella* with slowly enlarging test chambers. Low trochospired forms possessing intra-extraumbilical apertures, such as *T. gemma* and *T. neoclemenciae*, are stratigraphically important in the early to middle Oligocene, together with some 4-chambered (in the final whorl) species, particularly, *T. clemenciae* and *T. munda*. Several new forms, derived from *Tenuitella*, first appeared in the late Oligocene and became extinct soon afterwards. Intraumbilical restriction of the aperture produced *Tenuitellinata* in the Oligocene (*T. juvenilis*) and possibly (but not proven) in late Eocene (doubtful records of *T. angustiumbilicata*). Its bullate descendants rapidly evolved (*Globigerinita*, and its subgenus *Tinophodella*); both

Tenuitellinata and *Globigerinita* persist to the present. *Globigerinatella* probably arose abruptly from this group in the late early Miocene.

Tenuitelline species with slowly enlarging chambers, as seen first in the Oligocene, continued to evolve in the early to middle Miocene, while species having rapidly enlarging chambers and tests (such as *T. minutissima* and *T. neobrevispira*) also became important in this period.

During the mid-middle Miocene to Pliocene the evolution of the Tenuitellinae slowed; forms referable to this group are few and have little stratigraphic value (as seen in *Tenuitellinata juvenilis* and its allies). This trend seems to have continued into the Quaternary where only *Tenuitella fleisheri* and a few related forms may be occasionally encountered.

ACKNOWLEDGMENTS

The author sincerely thanks F. T. Banner of University College London for prompting this research, for his supervision, discussion and, especially, a very careful, critical reading and valuable correction of the manuscript, which greatly improve this presentation. A. R. Lord is thanked for donating the study material from the Jackson Group (collected by T. F. Grimsdale) and from some Pliocene and Quaternary sequences mentioned in the text, and for use of facilities in the Postgraduate Unit of Micropalaeontology, U.C.L. Robert L. Fleisher, Chevron Overseas Petroleum Inc., San Ramon, CA, is sincerely thanked for his valuable comments and for communicating the results of his re-examination of the holotypes of *Globorotalia anfracta* Parker and "*Globigerina*" *angustiumbilitata* Bolli. Special thanks are also due to T. Barnard and D. Curry for the Trinidad material, and to M. M. Gay for technical assistance. I wish to thank Liam Gallagher, Ian Boomer and Gavin Gillmore, my research fellows at U.C.L., for discussion and encouragement.

This project was carried out at U.C.L. after the author finished his M.Sc. degree course. The financial support was received from the Chinese Government, which is gratefully acknowledged.

REFERENCES

- BANNER, F. T., 1982, A classification and introduction to the Globigerinacea, in Banner, F. T., and Lord, A. R. (eds.), *Aspects of Micropalaeontology*: George Allen and Unwin, London, p. 142–239.
- , and BLOW, W. H., 1965, Progress in the planktonic foraminiferal biostratigraphy of the Neogene: *Nature*, v. 208, p. 1164–1166.
- , and —, 1967, The origin, evolution and taxonomy of the foraminiferal genus *Pulleniatina* Cushman, 1927: *Micropalaeontology*, v. 13, p. 133–162.
- , and LOWRY, F. M. D., 1985, The stratigraphical record of planktonic foraminifera and its evolutionary implications, in Cope, J. C. W., and Skelton, P. W. (eds.), *Evolutionary Case Histories from the Fossil Record*: Palaeontological Association, London, Special Papers in Palaeontology, No. 33, p. 117–130.
- BÉ, A. W. H., 1968, Shell porosity of recent planktonic foraminifera as a climatic index: *Science*, v. 161, p. 881–884.
- , 1980, Gametogenic calcification in a spinose planktonic foraminifer, *Globigerinoides sacculifer* (Brady): *Marine Micropalaeontology*, v. 5, p. 283–310.
- , HARRISON, S. M., FRERICHS, W. E., and HEIMAN, M. E., 1976, Variability in test porosity of *Orbulina universa* d'Orbigny at two Indian Ocean localities, in Takayanagi, Y., and Saito, T. (eds.), *Progress in Micropalaeontology*: American Museum of Natural History, Micropalaeontology Press, p. 1–9.
- BERGGREN, W. A., OLSSON, R. K., and REYMENT, R. A., 1967, Origin and development of the foraminiferal genus *Pseudohastigerina* Banner and Blow, 1959: *Micropalaeontology*, v. 13, p. 265–288.
- BERMÚDEZ, P. J., 1961 (1960), Contribucion al estudio de las Globigerinidea de la region Caribe-Antillana (Paleoceno-Reciente): *Boletín Geología (Venezuela)*, Special Publication 3, p. 1119–1393.
- BIGNOT, G., and GUYADER, J., 1971, Observations nouvelles sur *Globigerina oxfordiana* Grigelis, in Farinacci, A. (ed.), *Proceedings of the Second Planktonic Conference (Rome, 1970)*: Edizione Tecnoscienza, Rome, p. 79–83.
- BLOW, W. H., 1969, Late middle Eocene to Recent planktonic foraminiferal biostratigraphy, in Brönnimann, P., and Renz, H. H. (eds.), *Proceedings of the First International Conference on Planktonic Microfossils (Geneva, 1967)*: Brill, Leiden, p. 199–422.
- , 1979, The Cainozoic Globigerinida: Brill, Leiden, parts II and III, p. 735–1413.
- , and BANNER, F. T., 1962, The mid-Tertiary (Upper Eocene to Aquitanian) Globigerinaceae, in Eames, F. E., Banner, F. T., Blow, W. H., and Clarke, W. J. (eds.), *Fundamentals of mid-Tertiary Stratigraphical Correlation*: Cambridge University Press, Cambridge, England, p. 61–151.
- , and —, 1966, The morphology, taxonomy and biostratigraphy of *Globorotalia barisanensis* LeRoy, *G. fohsi* Cushman and Ellisor, and related taxa: *Micropalaeontology*, v. 12, p. 286–302.
- BOLLI, H. M., 1957a, Planktonic foraminifera from the Oligocene-Miocene Cipero and Lengua formations of Trinidad, B.W.I.: *U.S. National Museum Bulletin* 215, p. 97–123.
- , 1957b, Planktonic foraminifera of the Eocene San Fernando and Navet Formations of Trinidad, B.W.I.: *U.S. National Museum Bulletin* 215, p. 155–172.
- , LOEBLICH, A. R., JR., and TAPPAN, H., 1957, Planktonic foraminiferal families Hantkeninidae, Orbulinidae, Globorotaliidae and Globotruncanidae: *U.S. National Museum Bulletin* 215, p. 3–50.
- , and SAUNDERS, J. B., 1985, Oligocene to Holocene low latitude planktic foraminifera, in Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), *Plankton Stratigraphy*: Cambridge University Press, Cambridge, England, p. 155–262.
- BRÖNNIMANN, P., and RESIG, J., 1971, A Neogene globigerinacean biochronologic time-scale of the south-western Pacific, in Winterer, E. L., and others, *Initial Reports of the Deep Sea Drilling Project*, volume 7: U.S. Government Printing Office, Washington, DC, p. 1235–1469.
- BRUMMER, G.-J. A., HEMLEBEN, C., and SPINDLER, M., 1986, Planktonic foraminiferal ontogeny and new perspectives for micropalaeontology: *Nature*, v. 319, p. 50–52.
- BYKOVA, N. K., 1960, K voprosu o tsiklichnosti filogeneticheskogo rosvitiya v foraminifer (On the question of cyclicity of phylogenetic development in the foraminifera): *Trudi, Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI)*, Leningrad, Geology, Sbornik 5, p. 309–328.
- DESAI, D., and BANNER, F. T., 1985, The ontogeny of, and relationships between, middle Miocene and Quaternary *Orbulina* (foraminifera): *Journal of Micropalaeontology*, v. 4, p. 81–91.
- DOW, R. L., 1977, Test porosity in *Neoglobobulimina pachyderma* in late Miocene to Recent, DSDP site 284, South Pacific: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 21, p. 157–162.
- FLEISHER, R. L., 1974, Cenozoic planktonic foraminifera and biostratigraphy, Arabian Sea, Deep Sea Drilling Project, Leg 23A, in Whitmarsh, R. B., Weser, O. E. Ross, D. A., and others,

- Initial Reports of the Deep Sea Drilling Project, volume 23: U.S. Government Printing Office, Washington, DC, p. 1001-1072.
- , 1975, Oligocene planktonic foraminiferal biostratigraphy, Central North Pacific Ocean, DSDP Leg 32, in Larson, R. L., Moberly, R., and others, Initial Reports of the Deep Sea Drilling Project, volume 32: U.S. Government Printing Office, Washington, DC, p. 753-763.
- , 1977, Oligocene planktonic foraminiferal assemblages from Deep Sea Drilling Project sites in the Indian Ocean, in Heintzler, J. R., Bolli, H. M., Davies, T. A., Saunders, J. B., and Sclater, J. G. (eds.), Indian Ocean Geology and Biostratigraphy: American Geophysical Union, Washington, DC, p. 459-467.
- GOULD, S. J., 1977, Ontogeny and Phylogeny: Harvard University Press, Cambridge, MA, 501 p.
- HOFKER, J., 1978, Analysis of a large succession of samples through the upper Maastrichtian and the lower Tertiary of Drill Hole 47.2, Shatsky Rise, Pacific, Deep Sea Drilling Project: Journal of Foraminiferal Research, v. 8, p. 46-75.
- HUANG, CHENG-YI, 1981, Observations on the interior of some late Neogene planktonic foraminifera: Journal of Foraminiferal Research, v. 11, p. 173-190.
- JENKINS, D. G., 1966, Planktonic foraminiferal zones and new taxa from the Danian to lower Miocene of New Zealand: New Zealand Journal of Geology and Geophysics, v. 8, p. 1088-1126.
- , 1971, New Zealand Cenozoic planktonic foraminifera: New Zealand Geological Survey Paleontological Bulletin, v. 42, 278 p.
- , 1985, Southern mid-latitude Paleocene to Holocene planktonic foraminifera, in Bolli, H. M., Saunders, J. B., and Perch-Nielsen, K. (eds.), Plankton Stratigraphy: Cambridge University Press, Cambridge, England, p. 263-282.
- , and ORR, W. N., 1972, Planktonic foraminiferal biostratigraphy of the east equatorial Pacific—DSDP Leg 9, in Hays, J. D., and others, Initial Reports of the Deep Sea Drilling Project, volume 9: U.S. Government Printing Office, Washington, DC, p. 1059-1193.
- , and SRINIVASAN, M. S., 1985, Cenozoic planktonic foraminifera from the Equator to the sub-Antarctic of the southwest Pacific, in Kennett, J. P., von der Borch, C. C., and others, Initial Reports of the Deep Sea Drilling Project, volume 90: U.S. Government Printing Office, Washington, DC, p. 795-834.
- KENNETT, J. P., and SRINIVASAN, M. S., 1980, Surface ultrastructure variation in *Neoglobobulimina pachyderma* (Ehrenberg): phenotypic variation and phylogeny in the Late Cenozoic, in Sliter, W. V. (ed.), Studies in Marine Micropaleontology: Cushman Foundation for Foraminiferal Research, Special Publication 19, p. 134-162.
- , and ———, 1983, Neogene planktonic Foraminifera, a phylogenetic atlas: Hutchinson Ross Publishing Company, Stroudsburg, PA, 265 p.
- KRASHENINNIKOV, V. A., and BASOV, I. A., 1983, Cenozoic planktonic foraminifera of the Falkland Plateau and Argentine Basin, Deep Sea Drilling Project Leg 71, in Ludwig, W. J., Krasheninnikov, V. A., and others, Initial Reports of the Deep Sea Drilling Project, volume 71: U.S. Government Printing Office, Washington, DC, p. 821-858.
- LIPPS, J. H., 1966, Wall structure, systematics and phylogeny studies of Cenozoic planktonic foraminifera: Journal of Paleontology, v. 40, p. 1257-1274.
- LOEBLICH, A. R., JR., and TAPPAN, H., 1984, Suprageneric classification of the Foraminiferida (Protozoa): Micropaleontology, v. 30, p. 1-70.
- LOUBERE, P., 1985, Population diversity of planktonic foraminifera and stable-isotope record across the Eocene-Oligocene boundary: Hole 549A, in Graciansky, P. C. de, Poag, C. W., and others, Initial Reports of the Deep Sea Drilling Project, volume 80: U.S. Government Printing Office, Washington, DC, p. 557-566.
- MANCINI, E. A., and WATERS, L. A., 1986, Planktonic foraminiferal biostratigraphy of upper Eocene and lower Oligocene strata in southern Mississippi and southwestern and south-central Alabama: Journal of Foraminiferal Research, v. 16, p. 24-33.
- MYATLIUK, E. V., 1950, Stratigrafiya fishevykh osadkov severnykh Karpat v sveta dannyykh fauny foraminifer (The stratigraphy of the flysch deposits of the northern Carpathian Mountains according to the foraminiferal faunas): Trudi, Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI), Leningrad, n. ser., v. 51 (Mikrofauna SSSR, sbornik 4.), p. 225-287.
- PARKER, F. L., 1967, Late Tertiary biostratigraphy (planktonic foraminifera) of tropical Indo-Pacific deep-sea cores: Bulletins of American Paleontology, v. 52, p. 115-208.
- POORE, R. Z., 1979, Oligocene through Quaternary planktonic foraminiferal biostratigraphy of the North Atlantic: DSDP, Leg 49, in Luyendyk, B. P., Cann, J. R., and others, Initial Reports of the Deep Sea Drilling Project, Volume 49: U.S. Government Printing Office, Washington, DC, p. 447-517.
- QUILTY, P. G., 1976, Planktonic foraminifera DSDP Leg 34—Nazca Plate, in Yeats, R. S., Hart, S. R., and others, Initial Reports of the Deep Sea Drilling Project, volume 34: U.S. Government Printing Office, Washington, DC, p. 629-703.
- ROGL, F., and BOLLI, H. M., 1973, Holocene to Pleistocene planktonic foraminifera of Leg 15, site 147 (Cariaco Basin (trench), Caribbean Sea) and their climatic interpretation, in Edgar, M. T., Saunders, J. B., and others, Initial Reports of the Deep Sea Drilling Project, volume 15: U.S. Government Printing Office, Washington, DC, p. 553-615.
- SAITO, T., and BÉ, A. W. H., 1964, Planktonic foraminifera from the American Oligocene: Science, v. 145, p. 702-705.
- , THOMPSON, P. R., and BREGER, D., 1981, Systematic Index of Recent and Pleistocene Planktonic Foraminifera: University of Tokyo Press, Tokyo, 190 p.
- SAMUEL, O., and SALAJ, J., 1968, Microbiostratigraphy and Foraminifera of the Slovak Carpathian Paleogene: Geologický Ústav Dionýza Štura, Bratislava, 232 p.
- SMIT, J., 1982, Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous Tertiary boundary: Geological Society of America, Special Paper 190, p. 329-352.
- SRINIVASAN, M. S., and KENNETT, J. P., 1981, A review of Neogene planktonic foraminiferal biostratigraphy: applications in the equatorial and South Pacific, in Warme, J. E., Douglas, R. G., and Winterer, E. L. (eds.), The Deep Sea Drilling Project: A Decade of Progress: Society of Economic Paleontologists and Mineralogists, Special Publication 32, p. 395-432.
- STAINFORTH, R. M., and LAMB, J. L., 1981, An evaluation of planktonic foraminiferal zonation of the Oligocene: University of Kansas Paleontological Contributions, Paper 104, 34 p.
- , LUTERBACHER, H., BEARD, J., and JEFFORDS, R. M., 1975, Cenozoic Planktonic Foraminiferal Zonation and Characteristics of Index Forms: University of Kansas Paleontological Contributions, Article 62, 425 p.
- STEINECK, P. L., and FLEISHER, R. L., 1978, Towards the classical evolutionary reclassification of Cenozoic Globigerinacea (Foraminiferida): Journal of Paleontology, v. 52, p. 618-635.
- SUBBOTINA, N. N., 1953, Globigerinidi, Hantkeninidi i Globobuliminidi: Iskopaemie Foraminiferi SSSR, Trudi, VNIGRI v. 76, 296 p. (English translation: Fossil foraminifera of the USSR, by E. Lees, Collet's Ltd., London and Wellingborough.)
- , PISHVANOV, L. S., and IVANOVA, L. V., 1960, Stratigrafiya oligotsenovikh i miotsenovikh otlozheniy Predkarpatsya po foraminiferam (Stratigraphy of the Oligocene and Miocene deposits of the Cisrarpethians according to the foraminifera): Mikrofauna SSSR, 11, Trudi, Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI), Leningrad, v. 153, p. 5-127.
- WERNLI, P. R., and KINDLER, P., 1986, Les "Protoglobigerines" du Callovo-Oxfordien de Chatillon-sur-Cluses (Préalpes internes, Haute-Savoie, France): Ecologiae Geologicae Helveticae, v. 79, p. 137-147.

Received 2 September 1986
Accepted 3 March 1987