

WALL TEXTURE CLASSIFICATION OF PLANKTONIC FORAMINIFERA GENERA IN THE LOWER DANIAN

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ABSTRACT

The early Danian planktonic foraminifera from Zones P0, P α , and P1a can be classified into four groups based on surface wall texture: microperforate, normal perforate smooth-walled, normal perforate cancellate non-spinose, and normal perforate cancellate spinose. One new genus, *Praemurica*, is erected for the cancellate nonspinose group and another new genus, *Parasubbotina*, is erected for species in the *pseudobulloides* lineage within the cancellate spinose group. Only two Cretaceous genera, *Guembelitria* s.l. and *Hedbergella*, are believed to have given rise to the early Danian planktonic foraminifera, *Guembelitria* to the microperforate group and *Hedbergella* to the smooth-walled and cancellate groups. No other Cretaceous planktonic foraminifera are involved in the phylogeny of the Danian planktonic foraminifera. The microperforate taxa are the most diverse group in the Danian and include the genera *Parvularugoglobigerina*, *Guembelitria*, *Woodringina*, *Chiloguembelina*, and *Globoconusa* and are included in the Superfamily Heterohelicacea. This group rapidly declined and most species became extinct before the end of the Danian. The great radiations of planktonic foraminifera of the Paleogene and Neogene are linked to the three other groups. The genera (with at least fifteen species) recognized in these groups include *Globanomalina* (smooth-walled), *Praemurica* (cancellate nonspinose), and *Eoglobigerina*, *Parasubbotina*, and *Subbotina* (cancellate spinose) which are placed in the Superfamily Globigerinacea.

The absence or rarity of cancellate wall species in lowermost Danian sections such as at El Kef is most probably due to lack of preservation.

INTRODUCTION

Much attention in recent years has been directed at the response of planktonic foraminifera to the Cretaceous/Paleogene boundary event. Such studies (Smit, 1982; Smit and Romein, 1985; Brinkhuis and Zachariasse, 1988; Keller, 1988, 1989a, 1989b; Barrera and Keller, 1991; d'Hondt and Keller, 1991) have focused on the early Paleocene biostratigraphy, phylogeny, evolution, extinction, and survivorship of planktonic foraminiferal species in stratigraphic sections at Gredero, Spain; El Kef, Tunisia; Brazos River, Texas; and some deep sea (DSDP, ODP) sites. A comparison of species and generic usage in these

studies reveals many inconsistencies in species and generic identification. None of these studies has addressed the taphonomy of the earliest planktonic foraminifera. Notwithstanding the question of Cretaceous survivors, the appearance of new species in these stratigraphic sections may be a result of preservational bias as well as other paleoecologic factors. For instance, it is clear from examination of material from Gredero and El Kef that species of certain globigerine forms in the lowermost part of the Paleocene have scattered stratigraphic occurrences and are poorly preserved. As a consequence, there is confusion and misunderstanding and, perhaps, erroneous reconstructions of ancestor-descendant lineages. The purpose of this study, which is based on test architecture and wall texture, is to state as clearly as possible our understanding of the basic groups of early Paleocene planktonic foraminifera. We have examined over 1000 specimens of planktonic foraminifera by scanning electron microscopy in order to gain a clearer understanding of their basic morphology and ontogeny. There are many problems of species identification which are partly due to a lack of first hand examination of species erected by Russian workers but, nevertheless, have been used in the above K/P boundary studies. We have attempted to clarify this situation by our study of Russian material in our collections (WAB) and those of H. P. Luterbacher at Tübingen. In addition, W. A. Berggren has made several visits to the Soviet Union to examine type specimens and collections of Russian workers.

In order to conduct this study we have sought to use the best preserved material that is available from the lower Paleocene. In recognizing and selecting appropriate material for this study it was necessary to distinguish various steps in the calcification of the living planktonic foraminiferal test and the diagenetic effect on the test during burial. This is explained in a following section. Most of the material used in this study is from a K/P boundary section at Millers Ferry, Alabama (Olsson, 1970; Olsson and Liu, 1990) where the preservation is the best that we have observed. This is supplemented with various material from other locations as outlined in the text.

Our studies focus on wall texture and architecture since this is a direct result of the living activity of the planktonic foraminifera, and studies have shown that it is a functional adaptation of each species (Hemleben and others, 1989). Our studies recognize four basic types of wall texture which are similar to those observed in living planktonic foraminifera. These are microperforate, normal perforate smooth-walled, normal perforate cancellate spinose, and normal perforate cancellate nonspinose. Normal perforate walls (Bé, 1968) have a pore size range of 1 to 7 μm in diameter. All of the planktonic species known to us that occur in the basal Paleocene sections can be placed in one of these groups. In the case of living planktonic foraminifera wall surface texture has been shown to be a fundamental higher

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level taxonomic character. We believe that this establishes a firm taxonomic base within which phylogenetic and biostratigraphic studies can be conducted. Also it should provide a better understanding of the recovery of planktonic foraminifera from the K/P boundary event. Hemleben and others (1991) first showed that the spinose habit, well-known in living planktonic foraminifera, could be traced to the earliest Paleocene. Well preserved specimens of the species *Eoglobigerina eobulloides* were shown to contain a characteristic pattern of tiny cylindrical holes in a weakly cancellate surface texture, holes which in living spinose planktonic foraminifera are fitted with long thin spines which are utilized in capturing food (Hemleben and others, 1989). The nonspinose cancellate wall texture had been observed in one species, *Praemurica taurica*. In this study we have investigated more extensively the cancellate spinose and nonspinose wall texture in the earliest Paleocene species at Millers Ferry and elsewhere. In addition, we have extended our studies to include the two other basic types of wall texture that are present in the earliest Paleocene, the microporiferate type and the smooth-walled normal perforate type. The objective of this paper is to document the four types of wall texture and to present our interpretation of the taxonomy of the various species that are found in the earliest Paleocene. We believe that this taxonomic division will be useful to other workers who study the impact of the K/P boundary event on the evolution and recovery of planktonic foraminifera. We also present our interpretation on the phylogeny of the early Paleocene planktonic foraminifera which is based on this taxonomic division. However, we do not address the question of survivorship of Cretaceous planktonic species other than *Guembelitra cretacea*. The possible survivorship of other Cretaceous species (Keller, 1989a, b) is not important to this study since none of the proposed survivor species belong to the four basic groups. In this study we use the biostratigraphic zonation of Berggren and Miller (1988) and P0 Zone of Smit (1982).

In the following section we delineate the characters which distinguish the main taxa which form the radiation at the base of the Cenozoic. A complete synonymy of all Danian taxa awaits completion of additional comparative studies on type material housed in various museums.

Specimens used for SEM study are contained in the micropaleontology SEM collections at the Institut und Museum für Geologie und Paläontologie der Universität Tübingen. Hypotypes (USNM 461191-461200) of species from Millers Ferry, Alabama are deposited at the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.

WALL TEXTURE CLASSIFICATION AND PRESERVATION

The wall texture of planktonic foraminifera is formed by calcification as chambers are added and at first is smooth and pierced with pore holes (Hemleben and others, 1989). This first stage in the calcification process is then followed by additions of calcite in the adult stage which develops the characteristic wall texture of the species. In most instances the final stage of calcification is the only one observed in early Paleocene specimens. In addition to the calcification stages in the life cycle of the living planktonic foraminifera,

diagenesis during preburial and postburial can and often does alter the original architecture by deposition of diagenetic calcite on and over the original calcite wall, by recrystallization of the original wall including any diagenetic calcite, and by dissolution of part or all of the test. In general, diagenetic calcification obscures and alters the original architecture of the test wall. The recognition and separation of diagenetic calcite from primary calcite is essential to identifying the original wall texture. The best preservation is, of course, where little or no diagenetic calcite is present. This is rarely the case in most sections of the Paleocene but a few such as Millers Ferry contain this kind of preservation although not at all levels. Thus, it is important to examine carefully the preservational state in each section in order to develop reliable data on wall texture. Two features that are important to recognize in the classification of wall texture are spines and pustules (Hemleben, 1975; Hemleben and others, 1989, 1991) as they serve different functions in the living planktonic foraminifera and are constructed quite differently.

Study of modern spinose planktonic foraminifera (Hemleben, 1975; Saito and others, 1976; Hemleben and others, 1989) shows that spines are elongate single crystals that are implanted in the wall as secondary structures originating at the primary organic matrix or at one of the outer organic layers. As chambers are added lamellar calcification builds up around the spines and they are surrounded by a characteristic spine collar. During gametogenesis the spines are shed and resorbed; calcite is then deposited as gametogenic calcite over the ridges and spine holes surrounding the pores. Thus, spinose species of planktonic foraminifera can rarely be identified as fossils by observing spines protruding from the test wall. However, as demonstrated by Hemleben and others (1991) they can be readily identified if spine holes are observed. As this study pointed out, spine holes can be covered and obscured by gametogenic calcification and in fossil foraminifera heavy diagenetic calcification frequently makes it impossible to detect spine holes. Breakage of the test wall can be used to view the spine hole in cross-section but is more time consuming and destroys the test. The approach used in this study was to select the best preserved material and view numerous specimens under the SEM. This improves the chances of finding specimens with the least amount of gametogenic and diagenetic calcite.

Pustules have an entirely different origin than spines as they are an integral part of the test wall and are not lost during gametogenesis. Hence, pustules are preserved in fossils. Pustules (the pseudospines of Benjamini and Reiss, 1979) are layered like the test wall and are developed in different shapes and patterns according to taxonomic assignment (Hemleben, 1975; Hemleben and others, 1977; Benjamini and Reiss, 1979). Unlike spines, pustules grow larger as they develop. They may be rounded in shape or sharp and pointed. They may branch or form aggregates. Features such as hispid structures, rugosities, pseudospines, protuberances, and tubercles are all different forms of pustules (Hemleben and others, 1989).

Spines and pustules in living planktonic foraminifera serve similar functions in the sense that they serve as anchor bases for radiating rhizopods for food gathering. The spines, in contrast to pustules, are able to support long

strands of rhizopods which are efficient in snaring and digesting large quantities of zooplankton. The pustulose foraminifera appear to be largely herbivorous or passive grazers (Anderson and others, 1979; Spindler and others, 1984). Thus, it appears that many of the earliest species of planktonic foraminifera in the Paleocene were adapted in ways similar to living species. Below we list the four groups of wall texture observed in basal Paleocene planktonic foraminifera with examples of each.

CANCELLATE SPINOSE

This wall texture is observed in one of two trochospiral globigerinid groups in the earliest Paleocene. The buildup of the cancellate wall is weakly developed at first, but then becomes more strongly developed. The spines are situated, as in modern cancellate spinose species at the juncture of, and along, the cancellate ridges. Spine holes are clearly visible in specimens from Millers Ferry. The genera *Eoglobigerina*, *Parasubbotina* gen. nov., and *Subbotina* belong to this group. Within this group the following species and forms are recognized with comments on synonymies based on studies of type materials and collections.

Eoglobigerina

Eoglobigerina eobulloides (Morozova) 1959 occurs at Millers Ferry in Zones P0, P α , and P1a (Pl. 1, Figs. 1–7). It has a moderately elevated trochospire, globular chambers, an umbilical to slightly extraumbilical rounded aperture which is bordered by a narrow, slightly flaring lip. Four to four and one-half chambers in the final whorl increase moderately in size. The umbilicus is small but open to the previous chambers. The cancellate wall texture is very weakly developed and difficult to view with the light microscope, especially where preservation of the wall is poor. The pores which are on average about 1 μ m in diameter at the narrowest point occur at the base of a shallow pit which is surrounded by the cancellate ridges. The wall ranges from 4 μ m to 7 μ m in thickness and the overall size of the test is generally less than 250 μ m.

Four chambered forms of this species were named by Blow (1979) as the subspecies *E. eobulloides simplicissima* (Pl. 1, Fig. 1). This form seems to be the same as *Globigerina moskvini* Shutskeya 1953, a name that could be used for this taxon except that some of the Shutskeya collections were destroyed during the 1960's and, thus the usage of this name is not advisable. Blow's (1979) illustrations of *E. eobulloides* agree well with the holotype which was examined in the micropaleontological collections of the Geological Institute of the Academy of Sciences, Moscow, during a visit by one of us (WAB) in 1988. The small size of *E. eobulloides* and its very thin pore filled walls makes this species very susceptible to dissolution. In the well preserved assemblages at Millers Ferry it occurs consistently, except in intervals with much cementation where it is rare or absent. Our observations indicate that this species occurs sporadically at El Kef where it is very poorly preserved in the basal Paleocene.

Eoglobigerina edita Subbotina 1953 occurs in Zones P α and P1 at Millers Ferry (Pl. 2, Figs. 1–7). The species is characterized by a moderately high trochospiral test, globular chambers, and an umbilical rounded aperture which is

bordered by a narrow lip. The five to five and one-half chambers in the final whorl increase gradually in size. The umbilicus is small but open to the previous chambers. The cancellate wall is weakly developed. The pore size and location is similar to *E. eobulloides*. The wall thickness ranges from 4 μ m to 7 μ m and the overall size of the test is generally less than 250 μ m.

Synonyms of this species include *Globigerina* (*Eoglobigerina*) *hemisphaerica* Morozova 1961 and *Globigerina* (*Eoglobigerina*) *pentagona* Morozova 1961. The form named as *Globigerina edita* var. *polycamera* by Khalilov 1956 differs from typical *E. edita* in having more chambers in the final whorl (Pl. 2, Fig. 6). This is not the form figured as this species by Blow (1979). This species is not as common at Millers Ferry as *E. eobulloides* but, like this species, it is very susceptible to dissolution. Its occurrence in the Millers Ferry section is persistent in contrast to El Kef where it is almost absent in the basal Paleocene.

Parasubbotina gen. nov.

Parasubbotina Olsson, Hemleben, Berggren, and Liu, new genus
Plate 3, Figures 1–7

Type species: *Globigerina pseudobulloides* PLUMMER 1926

Test very low trochospiral with 10–12 chambers, and with 4 to 5 chambers in the ultimate whorl. The chambers which are inflated globular and slightly ovoid in shape increase rapidly in size. The aperture is interiomarginal, umbilical to extraumbilical, a high rounded arch which is bordered by a narrow lip. The umbilicus is narrow, deep and open to the previous chambers. The wall is weakly to strongly cancellate and spinose. Spine holes are numerous and located at the juncture of and along the cancellate ridges. They may be obscured by gametogenetic and/or diagenetic calcification.

Parasubbotina first appears in the upper part of Zone P0 and occurs rarely in Zone P α . It ranges probably into Zone P4 but its total range is not yet established. Two species are identified in the early Paleocene Zone P1, *P. pseudobulloides* and *P. varianta*. The earliest form referable to *Parasubbotina* is identified here as *P. aff. pseudobulloides* and occurs in Zones P0 and P α . *Parasubbotina* is distinguished from *Eoglobigerina* by its very low trochospiral test, chambers that increase rapidly in size in the ultimate whorl, and by the high-arched umbilical to extraumbilical aperture. The first two characteristics separate it from the nonspinose genus *Praemurica* gen. nov. The rate of size increase of chambers in the ultimate whorl in *Praemurica* is much lower than in *Parasubbotina*. The number of chambers in the ultimate whorl in *Parasubbotina* never exceeds 5 whereas in *Praemurica* there is often 6 or more.

Parasubbotina pseudobulloides (Plummer) 1926 has a very low trochospiral test, globular to slightly ovate chambers that increase rapidly in size in the ultimate whorl, and an umbilical to extraumbilical high arched, rounded aperture that is bordered by a narrow lip. The umbilicus is narrow and deep but open to the previous chambers. The cancellate wall is weakly developed in the early forms of this species but becomes stronger in later forms. The pore diameter averages about 1 μ m at the narrowest point and the pores are located at the base of pore pits. The wall thickness ranges from 4 μ m to 7 μ m and the overall size of the test is generally greater than 250 μ m.

The species has a persistent and frequent occurrence in Zone P1 at Millers Ferry (Pl. 3, Figs. 1–7) where it is well preserved except in intervals where cementation and dissolution are evident. Morphologically related forms referred to as *P. aff. pseudobulloides* occur very rarely in Zones P0 and P α (Pl. 4, Figs. 1–4). The aff. forms are smaller than

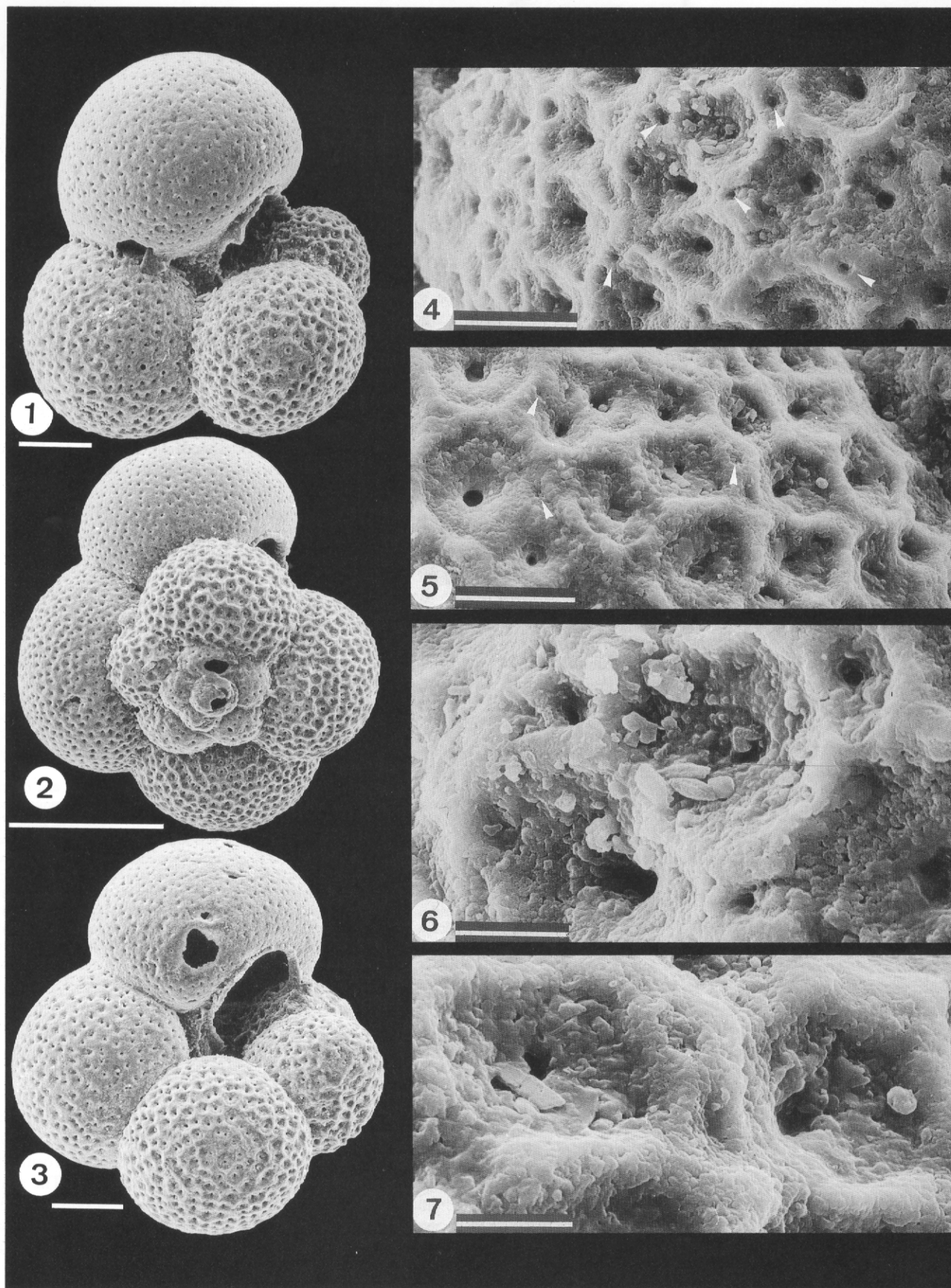


PLATE 1

Figs. 1–7 *Eoglobigerina eobulloides*, Early Danian, (Zone P α), Clayton Basal Sands, Millers Ferry, Alabama, umbilical (Figs. 1, 3; bar = 40 μ m) and spiral (Fig. 2; bar = 100 μ m) views showing weakly cancellate wall texture. Detail of wall texture exhibiting gametogenic calcification and spine holes is shown in Figs. 4–7. Some of the spine holes in Figs. 4 and 5 are pointed out by the small arrowheads (Fig. 4; bar = 10 μ m and Fig. 6; bar = 4 μ m from prepenultimate chamber of Fig. 1; Fig. 5; bar = 10 μ m and Fig. 7; bar = 4 μ m from prepenultimate chamber of Fig. 3).

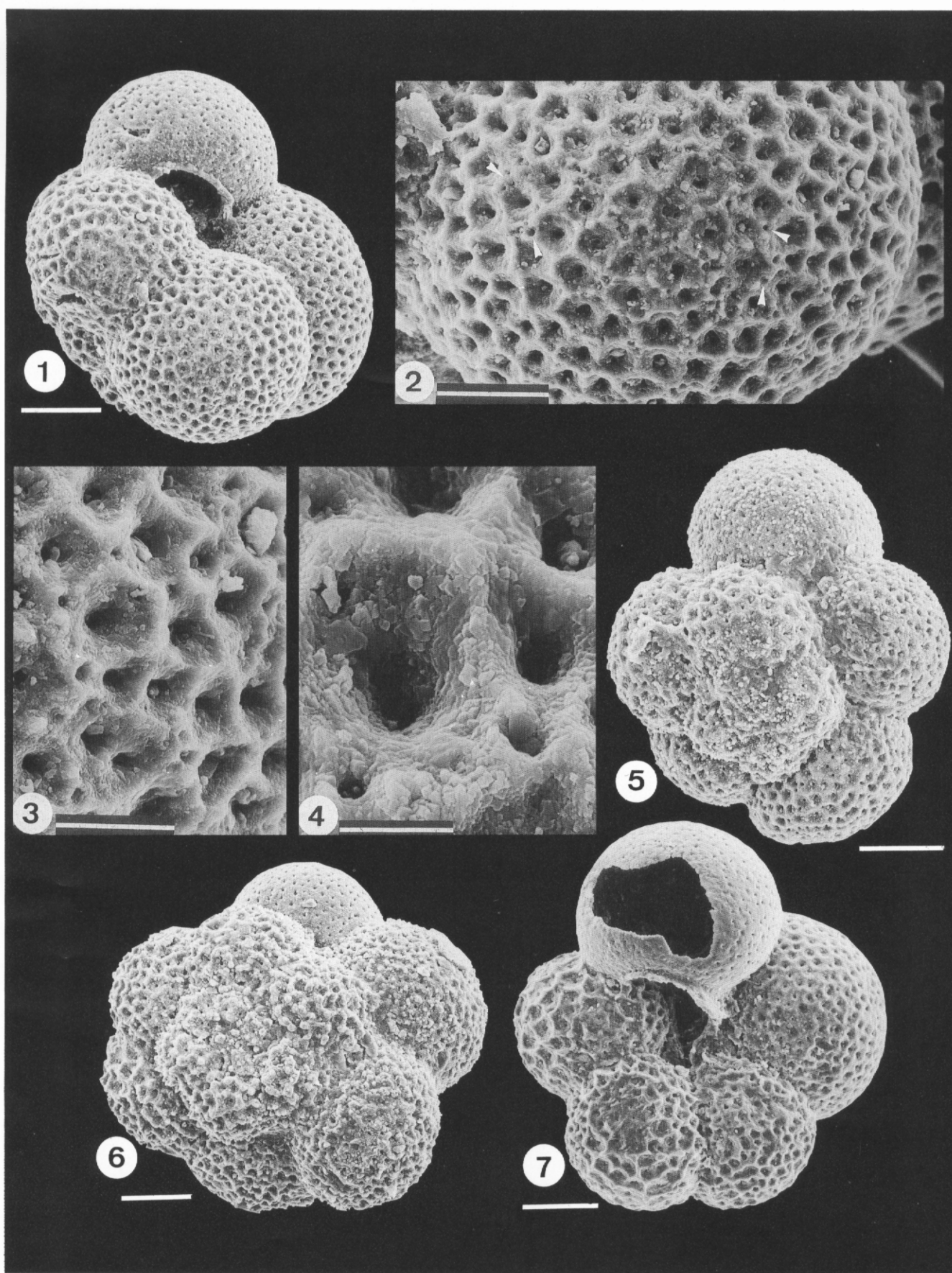


PLATE 2

Figs. 1-7 *Eoglobigerina edita*, Early Danian, Millers Ferry, Alabama, showing edge (Fig. 1; bar = 40 µm, Zone Pα, Clayton Basal Sands), spiral, and umbilical (Figs. 5 and 7; bar = 40 µm, Pine Barren Member, Clayton Formation) views showing weakly cancellate wall texture. Detail of wall texture exhibiting gametogenic calcification (slightly recrystallized) and numerous spine holes is shown in Figs. 2-4. Some of the spine holes in Fig. 2 are pointed out by the small arrowheads (Fig. 2; bar = 20 µm, Fig. 3; bar = 10 µm, and Fig. 4; bar = 4 µm from prepenultimate chamber of Fig. 1). Fig. 6 *Eoglobigerina edita polycamera*, Early Danian, (Zone P1a) Pine Barren Member, Clayton Formation, Millers Ferry, Alabama, showing spiral view (bar = 40 µm) multichambered specimen which exhibits a weakly cancellate wall texture.

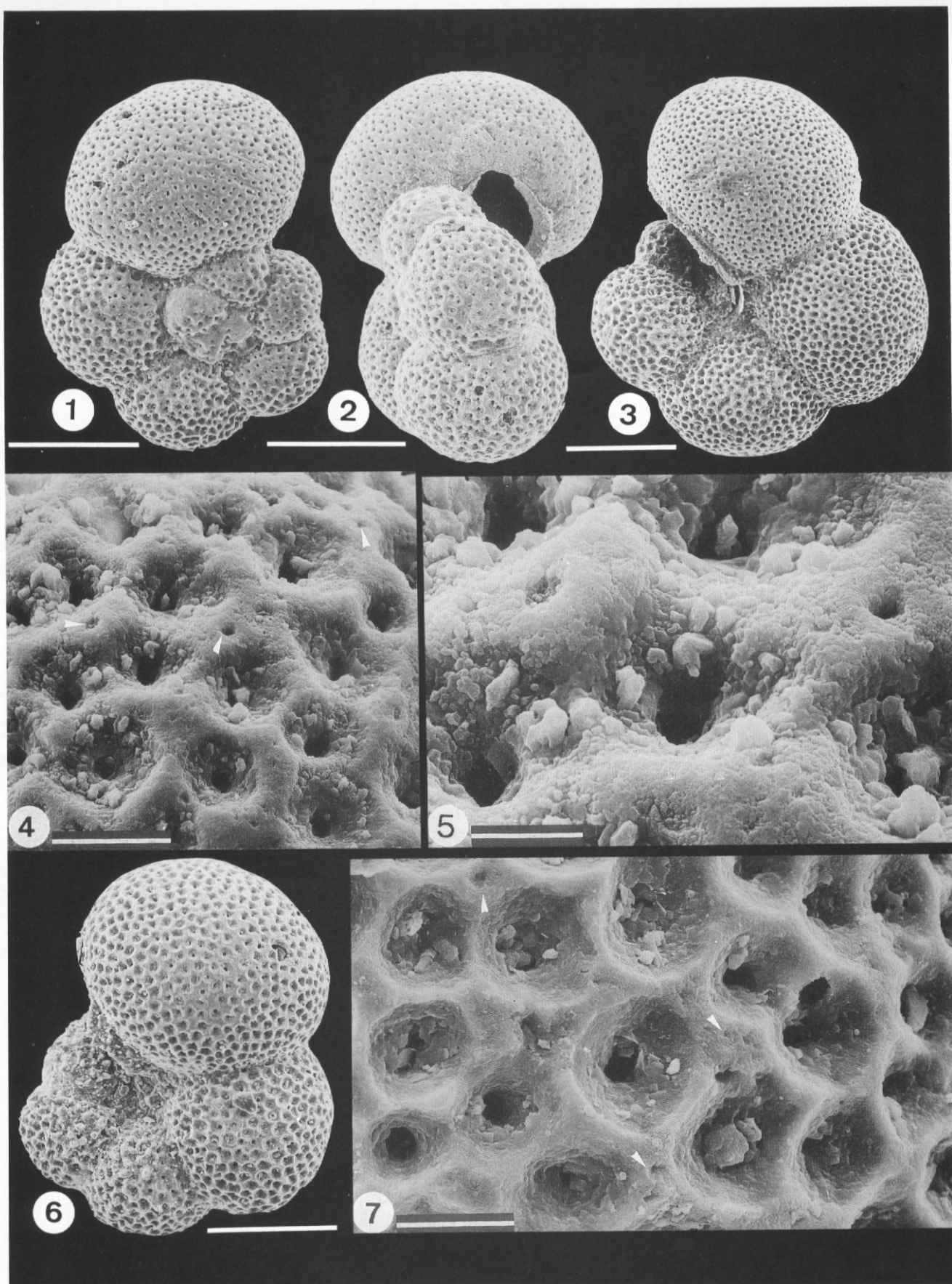


PLATE 3

Figs. 1–3 *Parassubbotina pseudobulloides*, Early Danian, showing the cancellate wall texture. Figs. 1–3 (bar = 100 μm) spiral, edge, and umbilical views of specimens from Zone P1a, Pine Barren Member, Clayton Formation, Alabama; detail of anteprepenultimate chamber of Fig. 2 showing gametogenic calcification (slightly recrystallized) and spine holes (pointed out by small arrowheads) is shown in Fig. 4 (bar = 10 μm) and Fig. 5 (bar = 4 μm); Fig. 6 (bar = 100 μm) and Fig. 7 (bar = 10 μm) showing a more strongly developed cancellate texture of specimens from Zone P2, upper Midway Formation, Texas, Fig. 7 from penultimate chamber of Fig. 6 showing gametogenic calcification and spine holes (pointed out by small arrowheads).

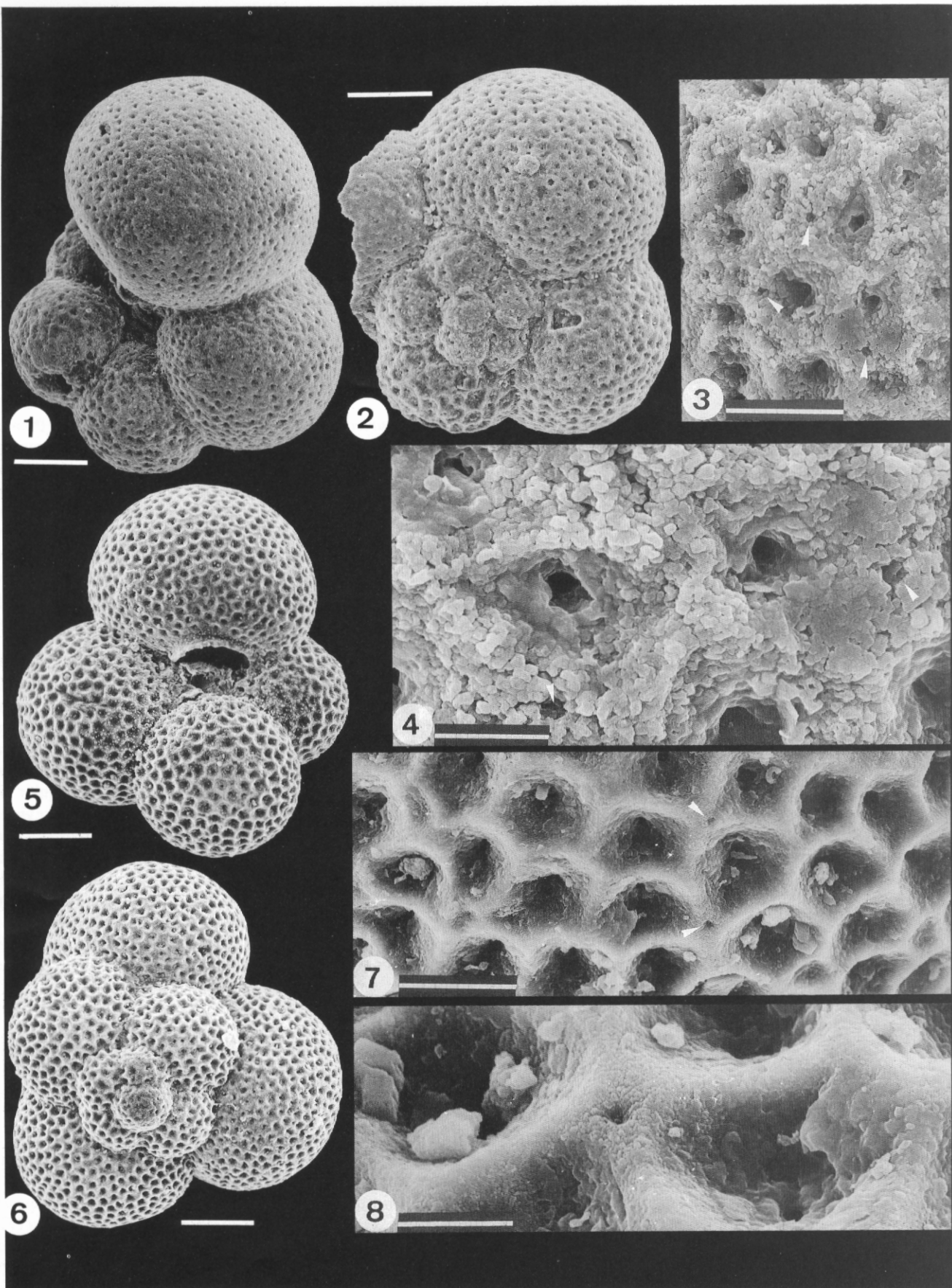


PLATE 4

Figs. 1–4 *Parasubbotina* aff. *pseudobulloides*, Early Danian, (Zone Pα) Clayton Basal Sands, Millers Ferry, Alabama showing a rather smooth surface with weakly developed cancellate texture and spine holes (pointed out by small arrowheads) visible in a recrystallized surface (Fig. 1 and 2: bar = 40 μm; Fig. 3: bar = 10 μm and Fig. 4: bar = 4 μm from prepenultimate chamber of Fig. 2). Figs 5–8 *Subbotina trivialis*, Early Danian, (Zone P1a) Pine Barren Member, Clayton Formation, Millers Ferry, Alabama showing cancellate wall texture, gametogenic calcification and spine holes. Some of the spine holes in Fig. 7 are pointed out by small arrowheads (Figs. 5 and 6: bar = 40 μm, Fig. 7: bar = 10 μm and Fig. 8: bar = 4 μm from prepenultimate chamber of Fig. 5).

P. pseudobulloides, being about 150 μm in largest test diameter and the cancellate wall is very weakly developed. The aff. forms are often referred to the species *Globigerina fringa* Subbotina 1950 which is a low spired 4 chambered form, although this species could be the same as *E. eobulloides*. Clarification of the synonymy of these two forms awaits examination of type material in collections in St. Petersburg, Russia by WAB.

We would include the cancellate spinose *Globigerina varianta* Subbotina in *Parasubbotina* and believe it evolved from *P. pseudobulloides* in the upper part of Zone P1.

Subbotina

Subbotina trivialis (Subbotina) 1953 occurs in the upper part of Zone P α and in Zone P1a at Millers Ferry (Pl. 4, Figs. 5–8). The species is characterized by its low trochospiral, tightly coiled test with 3½ chambers in the final whorl and an umbilical aperture with a thin lip. The wall is weakly cancellate and spinose. The spines are set at the junctures of the cancellate ridges. The umbilicus is small and nearly closed by the tight coiling. The pore size and location is similar to *Eoglobigerina eobulloides* from which the species is derived. The wall thickness ranges from 4 μm to 7 μm and the overall size of the test is generally less than 250 μm .

We regard *trivialis* as the first species of the genus *Subbotina* and believe it is derived from *Eoglobigerina*. The distinguishing features of the genus are the tightly coiled tripartite test with an umbilical aperture. *Eoglobigerina* has a more loosely coiled test and an umbilical to somewhat extraumbilical aperture. The umbilicus is open and distinct in contrast to *Subbotina* where the umbilicus becomes closed. The spines in *Subbotina* appear to be more regularly positioned at the juncture of the cancellate ridges whereas in *Eoglobigerina* the spines appear to occur along the cancellate ridges as well as at the juncture of the ridges. In later species of *Subbotina*, such as *S. triloculinoidea* (Plummer), the wall texture becomes more coarsely cancellate and the apertural lip becomes broader and extends over and covers the umbilical area.

CANCELLATE NONSPINOSE

In general appearance the cancellate wall texture is similar to the cancellate spinose planktonic foraminifera. In morphologic detail the wall texture is nearly identical to the living species *Neoglobobulimina dutertrei*. The wall texture develops by pustulose buildup of calcite plaques between the pores. The plaque buildups coalesce into ridges which form the honeycomb texture. Further calcification during gametogenesis enhances the cancellate texture. In detail not all of the pores are surrounded by ridges but several may lie at the base of elongate ridges (Pl. 5, Figs. 7, 8; Pl. 6, Figs. 4, 5, 7). An appropriate generic name does not exist into which these simple nonspinose globigerine forms of the early Paleocene can be placed. They are believed to be ancestral to the muricate morozovellids and acarininids of the mid-Paleocene but lack the typical morphologic features of these genera. Consequently, a new genus, *Praemurica*, is proposed for these early Paleocene forms.

Praemurica gen. nov.

Praemurica Olsson, Hemleben, Berggren, and Liu, new genus
Plate 5, Figures 1–8

Type species: *Globigerina (Eoglobigerina) taurica* MOROZOVA 1961

Test very low trochospiral with 10–15 chambers, and with 5–6, but occasionally more in the ultimate whorl. The chambers which are globular to slightly ovoid in shape increase very gradually in size. The arrangement of chambers in the coil is nearly planispiral although the last one or two chambers may be shifted slightly towards the umbilicus. The aperture is interiomarginal, umbilical to extraumbilical, a low to high arch which is bordered by a narrow lip that often is somewhat wider in the umbilical area. The umbilicus can vary from narrow and deep to fairly broad and wide but is open to the previous chambers. The wall is weakly to strongly cancellate and nonspinose.

Praemurica first appears in the upper part of Zone P0 and it occurs frequently to commonly in Zone P α . It ranges probably into Zone P3 but its total range is not yet established. Three species are identified in the earliest Paleocene, *P. inconstans*, *P. pseudoinconstans* and *P. taurica*. *Globigerina trinidadensis* Bolli and *Acarinina praecursoria* Morozova probably belong in this genus but have not yet been adequately investigated. The forms identified as *Globorotalia (Turborotalia) polycamera* (Khalilov) by Blow (1979) from Zones P α and P1 belong to this genus but, as noted above, not to Khalilov's species.

Praemurica taurica (Morozova) 1961 occurs in the Zones P0, P α , and P1 (Pl. 5, Figs. 1–8) at Millers Ferry. It is a very low trochospiral form with a somewhat flat spiral side. The six globular chambers that make up the ultimate whorl increase very gradually in size. The aperture forms a high arch and is bordered by a narrow lip which broadens in the umbilical area and becomes somewhat triangular in shape. In well preserved specimens the lips from previous chambers project as small flaps into the umbilicus. The umbilicus is fairly wide and broad with a deep depression which opens to the previous chambers. The cancellate wall texture is weakly developed. The pores which average about 1 μm in diameter at the narrowest point are set in the chamber wall at the base of the cancellate ridges. The walls are about 4 μm to 7 μm thickness and the overall size of the test is generally less than 200 μm .

The species is rare in Zones P0 and P α but it becomes more frequent in Zone P1 at Millers Ferry. Because of its thin test walls with numerous pores this species is susceptible to dissolution as are the eoglobigerinids. In the El Kef section it is poorly preserved and its occurrence is very rare and highly sporadic. This comparison between El Kef and Millers Ferry suggests that the lack of primitive cancellate forms in basal Paleocene sections may be due to preservational factors rather than evolutionary factors.

Praemurica pseudoinconstans (Blow) 1979 first appears in Zone P α and ranges through Zone P1 at Millers Ferry (Pl. 6, Figs. 1–7). It is a very low trochospiral form with a flattened spiral side. The five to five and one-half chambers that make up the ultimate whorl increase gradually in size at first but then more rapidly in the final few chambers. In some specimens the final chamber may be offset slightly towards the umbilical side. The aperture is a high rounded arch which is bordered by a narrow lip. The apertural lip broadens into the umbilical area but is not as pronounced as in *P. taurica*. The umbilicus is narrow and deep and is open

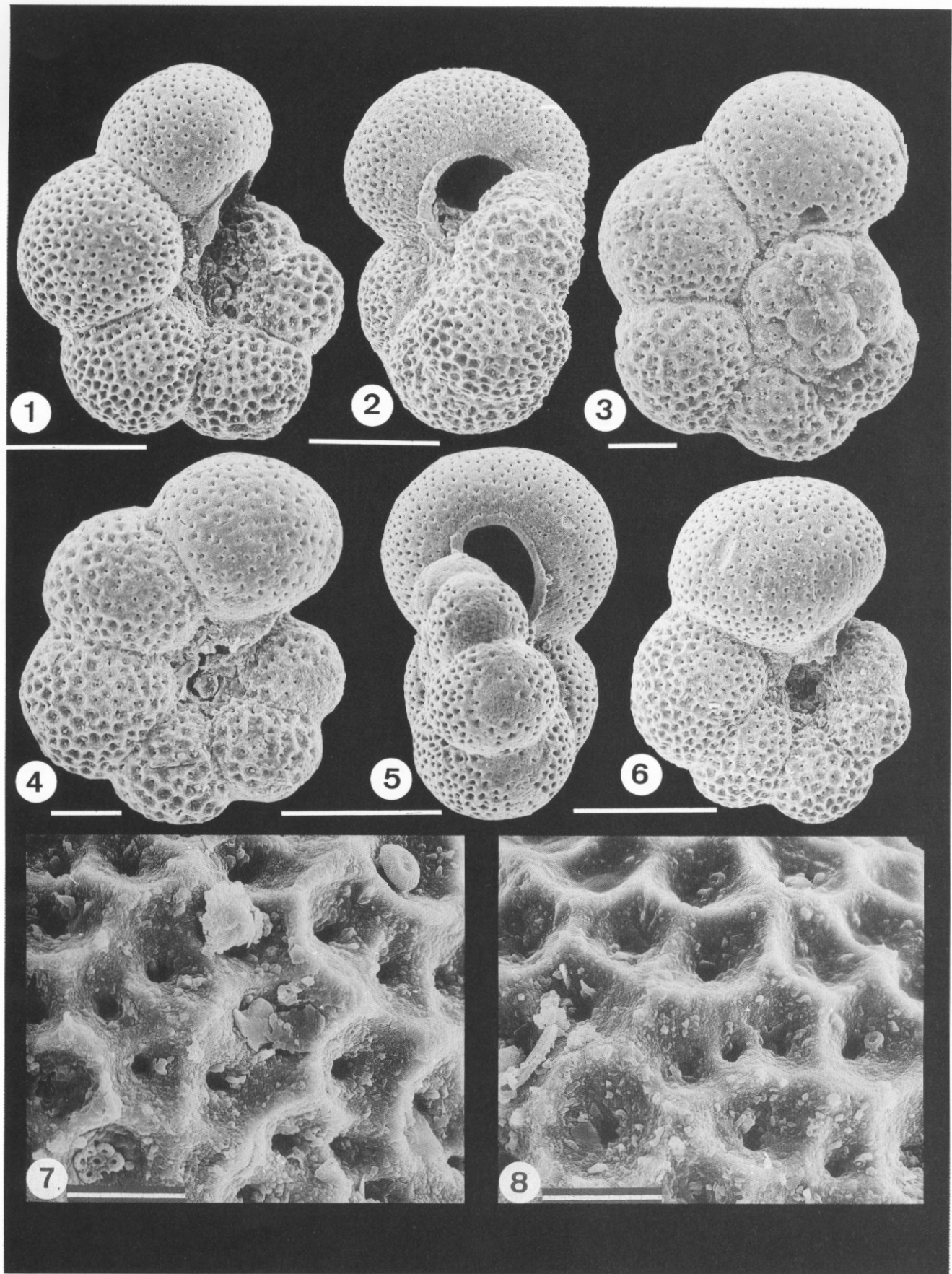


PLATE 5

Figs. 1-8 *Praemurica taurica*, Early Danian, (Zone P1a) Pine Barren Member, Clayton Formation, Millers Ferry, Alabama showing weakly developed cancellate wall texture. Figs. 1-6 spiral, edge, and umbilical views (Figs. 3 and 4: bar = 40 μm , Figs. 1, 2, 5, 6: bar = 100 μm); Figs. 7 and 8: bar = 10 μm showing nonspinoso wall texture with pores surrounded by rather parallel ridges and less developed ridges oblique to the main ridges (Fig. 7 prepenultimate chamber and Fig. 8 antepenultimate chamber of Fig. 6). Figs. 1, 2, and 6 show the broadening of the apertural lip into triangular-like flaps which project into the umbilicus.

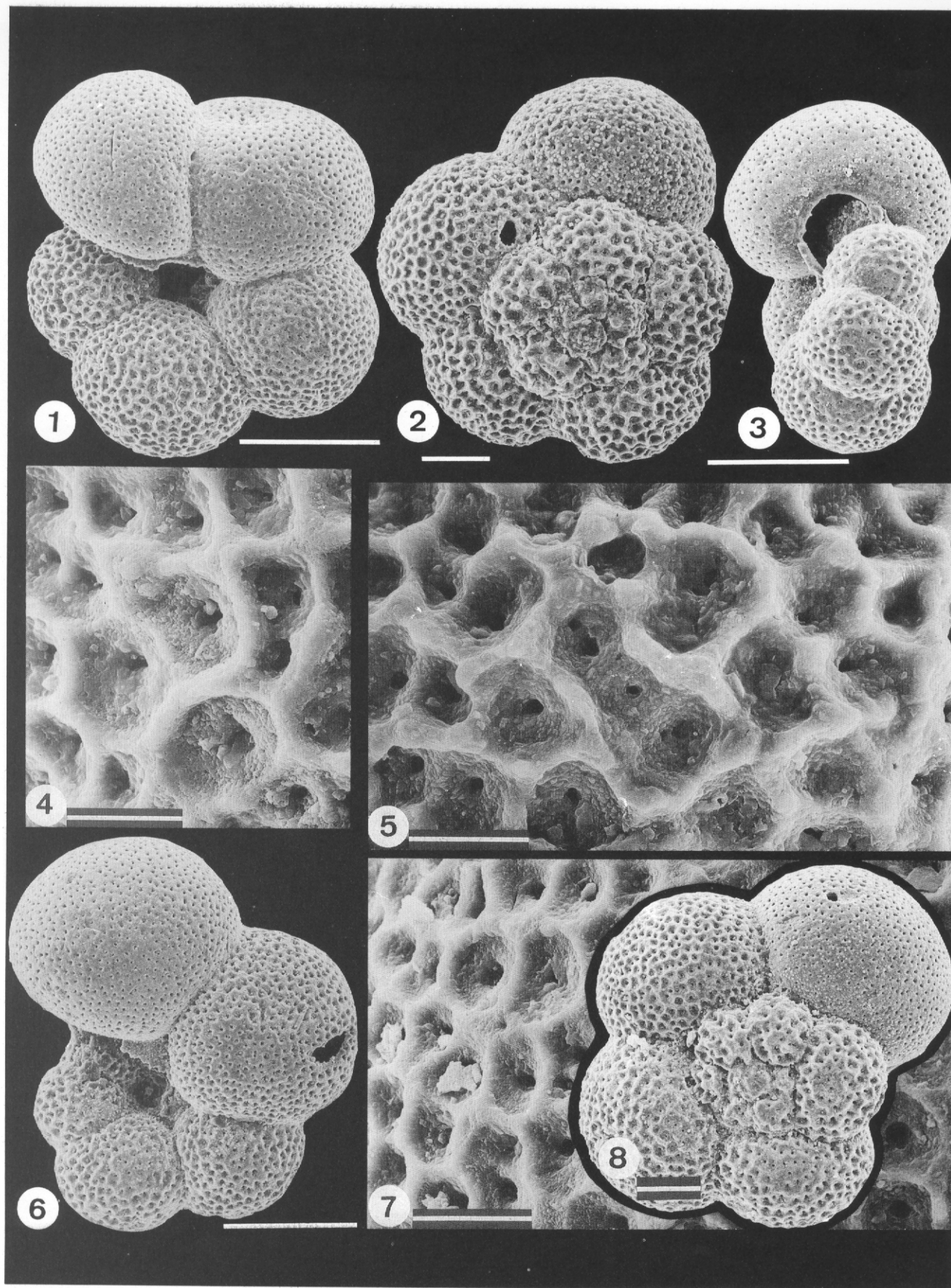


PLATE 6

Figs. 1–8 *Praemurica pseudoinconstans*, Early Danian, Millers Ferry, Alabama showing umbilical (Fig. 1 and Fig. 6; bar = 100 μ m), spiral (Fig. 2 and Fig. 8; bar = 40 μ m), and edge (Fig. 3; bar = 100 μ m) views and weakly developed cancellate wall texture. Fig. 1 and Fig. 4 from Zone P α , Clayton Basal Sands; other figs. from Pine Barren Member, Clayton Formation. Figs. 4, 5, 7; bar = 10 μ m showing nonspinoso wall texture with gametogenic calcification and pores surrounded by rather parallel ridges with less developed ridges parallel to the main ridges. Fig. 6 shows tendency of apertural lip to broaden in the umbilical area.

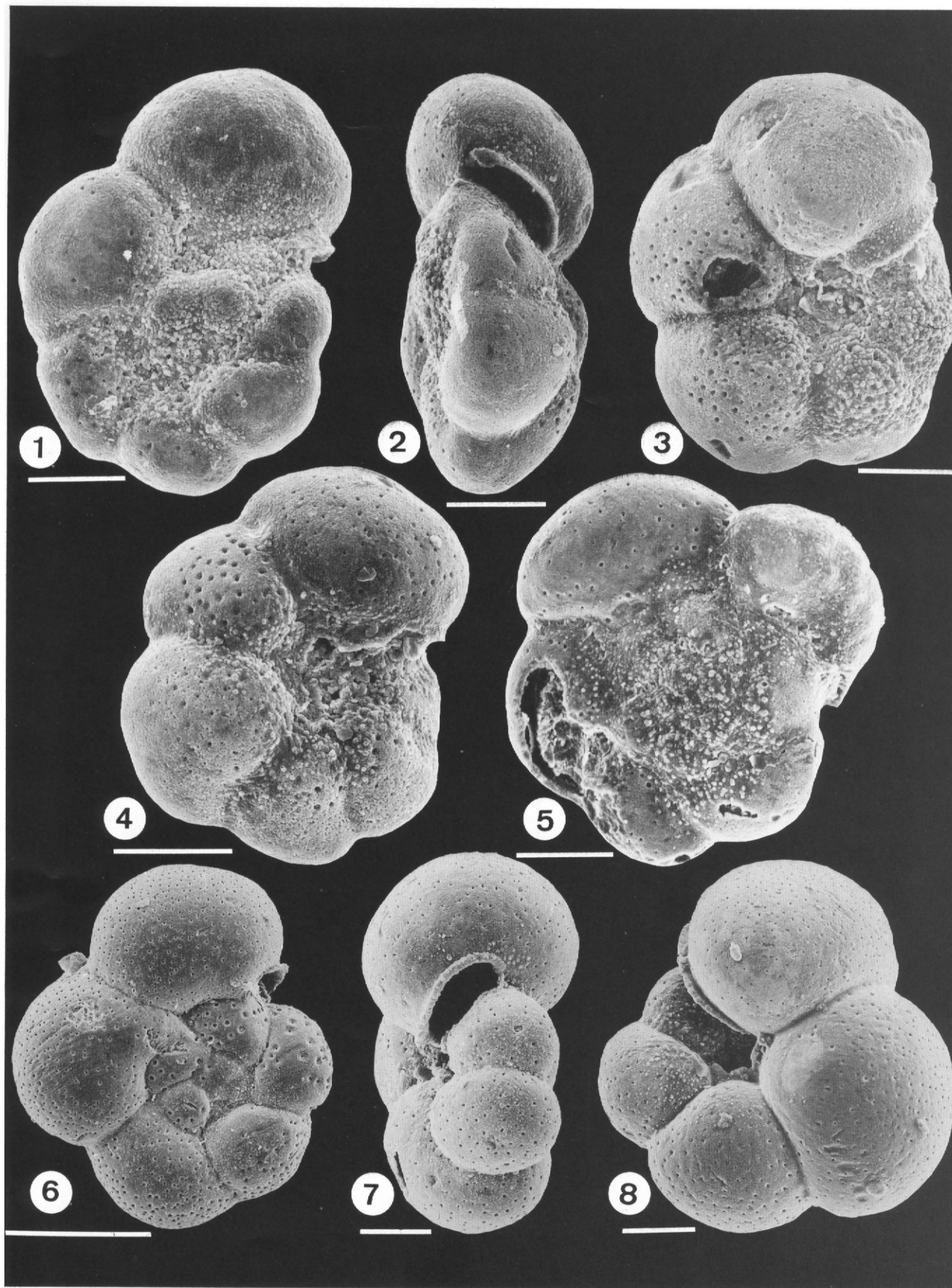


PLATE 7

Figs. 1-5 *Globanomalina archeocompressa*, Early Danian, (Zone P0) Clayton Basal Sands, Millers Ferry, Alabama, spiral, edge, and umbilical views showing the small compressed, smooth-walled test with weak pustule development in the umbilical area and in the spiral area. Pores are scattered on the umbilical and spiral sides with the periphery largely imperforate. Figs. 1-5: bar = 10 µm. Fig. 6-8 *Globanomalina planocompressa*, Early Danian, (Zone P1a) Pine Barren Member, Clayton Formation, Millers Ferry, Alabama, spiral, edge, and umbilical views showing wall, compressed test with pores distributed over entire wall. Fig. 6: bar = 100 µm, Figs. 7 and 8: bar = 40 µm.

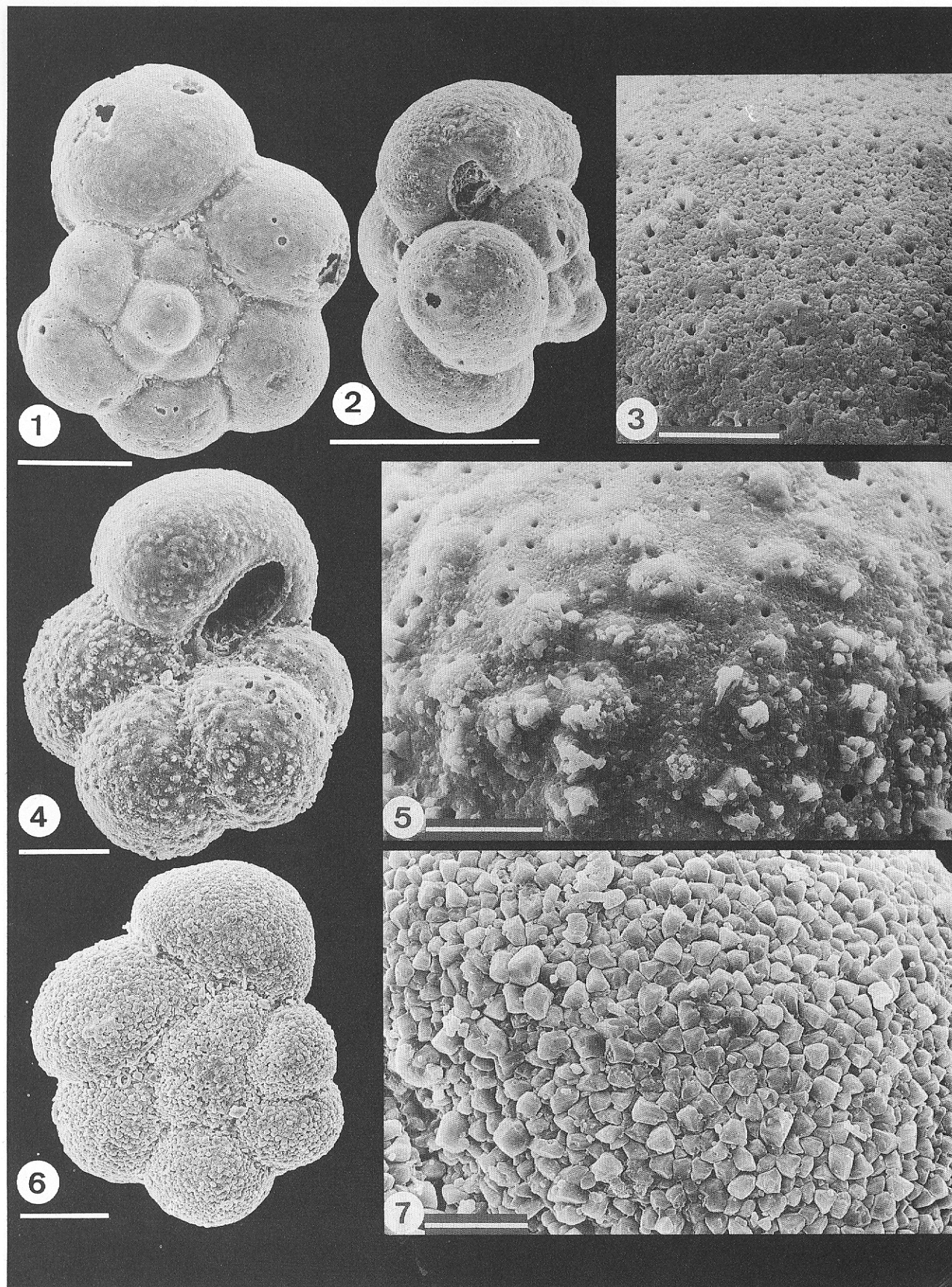


PLATE 8

Figs. 1-7 *Parvularugoglobigerina eugubina*, Early Danian, (Zone P α) from Clayton Basal Sands, Millers Ferry, Alabama (Figs. 1-5) and DSDP Site 577 (Figs. 6, 7). Fig. 1: bar = 40 μ m, Fig. 2: bar = 100 μ m, and Fig. 3: bar = 1 μ m show initial microperforate smooth wall of this species (Fig. 3 detail of prepenultimate chamber of Fig. 2); Fig. 4: bar = 40 μ m and Fig. 5: bar = 10 μ m show the development of pore mounded pustules of a later ontogenetic stage (Fig. 5 antepenultimate chamber of Fig. 4); note that pore mounded pustules develop on all chambers. Fig. 6: bar = 40 μ m and 7: bar = 10 μ m show the blunt pustule armor-like covering that develops by diagenetic calcite growth on the pore mounded pustules, thus altering the original wall texture and enhancing preservation.

to the previous chambers. The cancellate structure is weakly developed. The pores which average about 1 μm in diameter at the narrowest point lie at the base of the cancellate ridges. The walls are about 4 μm to 7 μm in thickness and the overall size of the test is up to 300 μm across.

The occurrence of this species at Millers Ferry is similar to that of *P. taurica* and the same is true of its preservation. The species was originally described (Blow, 1979) from Zones P α and P1 at DSDP Site 47 (Shatsky Rise). A paratype was also designated from the Pine Barren Member of the Clayton Formation in Alabama. The locality of this paratype is in Wilcox County, Alabama in the vicinity of the Millers Ferry section. Although there is no precise biostratigraphic data on the paratype locality, most probably it is either in Zones P α or P1 because the Pine Barren is early Danian in age (Mancini and others, 1989; Olsson and Liu, 1990).

SMOOTH-WALLED NORMAL PERFORATE

These forms are very low trochospiral with compressed tests. The walls are smooth and the pores are cylindrical and set normal to the chamber surface. Small pustules most commonly occur on the chamber surfaces immediately surrounding the umbilicus. The diameter of the pores is similar to the pores of the cancellate groups, averaging around 1 μm at the narrowest point. In their classification of Globigerinacea Steineck and Fleisher (1978) regarded smooth-walled species such as *Globorotalia menardii* as having finely perforate wall texture. The earliest Paleocene smooth-walled *Globanomalina* can not be differentiated on pore size from cancellate forms. The aperture is interior-marginal, umbilical to extraumbilical and forms a low slit that is bordered by a narrow lip. The test contains five to six ovate chambers in the ultimate whorl. The umbilicus is small and shallow but open to the previous chambers. These early Paleocene forms are nonspinose and belong to a single genus, *Globanomalina* (Banner, 1989). Three species are recognized in Zones P0 to P1, *G. archeocompressa*, *G. planocompressa*, and *G. compressa*. The first two are illustrated here.

Globanomalina

Globanomalina archeocompressa (Blow) 1979 is a very small-sized species, being less than 130 μm in greatest diameter (Pl. 7, Figs. 1–5). It has a flattened compressed test with the spiral side being nearly plane. Five to six, compressed oval-shaped chambers that increase very gradually in size make up the ultimate whorl. The umbilicus is shallow and broad and is open to the previous chambers. The aperture is a narrow slit which is bordered by a narrow lip. The pores which average 1 μm at the narrowest point are mostly confined to the chamber surfaces away from the periphery which is largely imperforate. The wall ranges from 4 μm to 7 μm in thickness.

This species occurs in Zones P0 and P α at Millers Ferry where it is very rare. Its rarity is due to its original population density which was sparse and not to a lack of preservation. Although it is small and has thin walls (less than 7 μm) it appears not to be readily susceptible to dissolution, perhaps due to few pores in the test walls.

Globanomalina planocompressa (Shutskaya) 1965—Although the original types are presumably lost, the meaning of this taxon seems clear from study of Russian collections and Blow's (1979) analysis of the species is followed here. This species (Pl. 7, Figs. 6–8) is larger than *G. archeocompressa*, being about 220 μm in greatest diameter. The five chambers in the ultimate whorl increase moderately in size. The chambers are more inflated than in *G. archeocompressa* and globular to ovoid in shape. The pores which average 1 μm at the narrowest point are evenly distributed in the chamber walls although some areas, especially on parts of the periphery, are imperforate. The wall ranges from 4 μm to 7 μm in thickness.

This species occurs very rarely but consistently in the upper part of Zone P α and in Zone P1 of Millers Ferry. Its original population density, like *G. archeocompressa*, was probably sparse.

MICROPERFORATE

This is a complex group in the earliest Paleocene and there is a great variety of usage of taxonomic names, including taxa from the genera discussed above, that are applied by various workers to morphologic forms within this group. The wall texture of this group is distinctly different from the other three groups of the earliest Paleocene planktonic foraminifera. The walls are penetrated by very small cylindrical pores which are 0.3 μm to 0.45 μm in diameter. The walls contain pustules which include in some types the characteristic pore mounds or pustules that grow around pores. There are a number of studies dealing with various members of this group (Boersma and Premoli Silva, 1988, 1989; d'Hondt, 1991; d'Hondt and Keller, 1991; Li and Radford, 1991; Liu and Olsson, in press). Genera that are placed in this group include *Guembelitria* Cushman, *Chiloguembelitria* Hofker, *Globoconusa* Khalilov, *Chiloguembelina* Loeblich and Tappan, *Woodringina* Loeblich and Tappan, and *Parvularugoglobigerina* Hofker. We do not intend to discuss here the details and evolutionary relationships of the various early Paleocene species of this group except to point out that most workers regard the species of this group to be linked phylogenetically, although they may differ in their interpretations. Nevertheless, it is important to point out that this group is not linked phylogenetically to the normal perforate cancellate spinose, normal cancellate nonspinose, and normal perforate smooth-walled groups. Furthermore, most of the members of the microperforate group do not survive beyond the early Danian. The majority of later planktonic foraminiferal species are derived from the three other groups whereas *Chiloguembelina* is the most important genus of the microperforate group to survive beyond the early Danian. Of the microperforate group *Parvularugoglobigerina* seems to be the most misunderstood.

Parvularugoglobigerina

Parvularugoglobigerina Hofker 1978 was erected with *Globigerina eugubina* Luterbacher and Premoli Silva as the type species. Hofker selected this name because he believed that this species had a rugose wall texture. Smit's study (1982) of this species from the Gredero section of Spain

indicated that *P. eugubina* has a smooth wall but he was uncertain whether the test walls were perforated. The rugose appearance of the type specimens, he determined, was due to recrystallization. Li and Radford (1991) also reported that *Parvularugoglobigerina* has a smooth wall with scattered microperforations but that the surface may have a rugose appearance due to dissolution or recrystallization. The SEM illustrations of this species from El Kef (Smit, 1982; Keller, 1988; Brinkhuis and Zachariasse, 1988) show the test wall to be covered with densely packed rounded blunt pustules. The same is true of specimens illustrated by d'Hondt and Keller (1991) from Deep Sea Drilling Site 577. Keller (1989a) figured two specimens of *P. eugubina* from Brazos River, Texas, one that shows the pustule covered surface and the other showing a smooth wall. The preservation of *P. eugubina* at Millers Ferry clearly shows the nature of the wall texture (Pl. 8, Figs. 1–7). The chamber surface in the early adult stage is smooth and penetrated by numerous tiny pores which are less than 0.45 μm in diameter (Pl. 8, Figs. 1–3). Then pustules grow on the surface (Pl. 8, Figs. 4–5), most of which build up around the pores forming pore mounds similar to those in *Guembelitra* (Olsson, 1970). Thus, the pustule covered surface observed in this species in the above studies partly results from the development of a pore mounded wall texture. Subsequently, the pore mounds become sites for overgrowths of calcite that in many specimens produce a dense armor-like coating (Pl. 8, Figs. 6, 7). This diagenetic overprint apparently enhances the resistance of specimens to dissolution. This species and possibly other microperforate species in the earliest Paleocene may be more resistant to dissolution than the cancellate and smooth-walled groups. This is certainly suggested in the Gredero and El Kef sections where specimens of the latter groups are either absent, rare, sporadic, and poorly preserved in Zones P0 and P α . In contrast, the microperforate *Parvularugoglobigerina* and *Guembelitra* are present in large numbers and persistently distributed stratigraphically. In addition to *P. eugubina* this genus also contains other forms which are perhaps valid species (see d'Hondt and Keller, 1991 and Li and Radford, 1991 for discussion).

Guembelitra, *Globoconusa*, *Chiloguembelina*, *Woodringina*

Guembelitra, *Globoconusa*, *Chiloguembelina*, *Woodringina* are other microperforate genera that occur in Zones P0 and P α . They have been treated in some detail by Boersma and Premoli Silva (1988, 1989), d'Hondt and Keller (1991), and Li and Radford (1991). Their surface textures vary from pore mounded pustules to blunt or sharp pustules with pores that are offset from the pustules. They and *Parvularugoglobigerina* appear to be related phylogenetically although there is not a complete consensus on their relationships among workers. We include all early Paleocene microperforate forms in the Heterohelicea.

PREVIOUS CLASSIFICATION

There have been several attempts at a suprageneric classification of the planktonic foraminifera. We review briefly here three of these (Blow, 1979; Banner, 1982; Loeblich

and Tappan, 1988) insofar as they pertain to the classification of the early Danian forms treated in this paper (Table 1).

Blow (1979:837) created a new suborder, the Globigerinida, for living forms formerly referred to the Rotaliina, characterized by a planktonic habit and fossil forms of presumed similar habit extending back to the mid-Jurassic (e.g., *Gubkinella*). Two superfamilies, the Globigerinacea (1979:839) and the Heterohelicea (1979:1379) were recognized, primary distinction being made by the presence in the former of a true umbilicus, and its absence, or modification as a "pseudoumbilicus" in the biserial-triserial tests of the latter. A further subdivision into the families Globigerinidae and Globorotaliidae, *i.al.*, was made (1979:841) with differentiation being based primarily on apertural character and position, and only secondarily on the presence/absence of "normal" spines (1979:842) "which are usually present" in the Globigerinidae and absent (by implication, but never specifically discussed by Blow) in the Globorotaliidae.

A similar classification scheme is that of Loeblich and Tappan (1988), although the Heterohelicea (1988:452), Globorotaliacea (1988:473) and Globigerinacea (1988:488), are maintained at equivalent rank as superfamilies. A clear-cut distinction was made between the latter two based on the presence (Globigerinacea) or absence (Globorotaliacea) of true spines.

Somewhat enigmatic is the classification of Banner

TABLE 1. A comparison of some features of the classification schemes of Banner (1982) and Loeblich and Tappan (1988).

Banner (1982)	Loeblich and Tappan (1984, 1988)
1. spinose/non-spinose criterion used at subfamily level and generic and in inconsistent manner	spinose/non-spinose criterion used at superfamily level
2. Globorotaliinae (incorrectly) identified as spinose	Globigerinacea (spinose), Globorotaliacea (non-spinose)
3. Forms identified as non-spinose which are actually spinose <i>Subbotina</i> <i>Dentoglobigerina</i> <i>Eoglobigerina</i>	<i>Subbotina</i> <i>Dentoglobigerina</i> <i>Paragloborotalia</i> <i>Eoglobigerina</i>
4. Forms identified as spinose which are actually non-spinose <i>Globoquadrina</i> <i>Turborotalia</i> <i>Neogloboquadrina</i> <i>Clavatorella</i> <i>Globorotalia</i> <i>Catapsydrax</i>	
5. Placement of certain genera	
a. <i>Parvularugoglobigerina</i> (<i>eugubina</i>) Tenuitellinae (Globigerinidae)	Eoglobigerinidae (Globorotaliacea)
b. <i>Eoglobigerina</i> (<i>ebulloides</i>) Eoglobigerininae (Globigerinidae)	Eoglobigerinidae (Globorotaliacea)
c. <i>Globoconusa</i> (<i>conusa</i>) Heterohelicea	Eoglobigerinidae (Globorotaliacea)
d. <i>Globanomalina</i> (<i>ovalis</i>) Eoglobigerininae (Globigerinidae)	Globanomalinidae (Hantkeninacea)

(1982) in which apertural character and modification are given primary, the presence of spines only secondary, importance in the hierarchy of discriminant characters (1982: 199; see discussion below).

Blow (1979:1206) recognized that the base of the Cenozoic is characterized by a "group of phylogenetically primitive highly morphologically variable, but seemingly already related forms which seem to have some semblance of valid genetic unity and biostratigraphic value within mainly the interval of (Zone P α -P2)". He denoted this group as the eoglobigerinids (*Eoglobigerina* Morozova, 1959) characterized by 1) weakly, but consistently developed porticus; 2) (almost) intraumbilical aperture; 3) normally distributed mural pores with distinct pore pits and associated inter-pore ridges (i.e., weakly cancellate texture). The wall texture differences between this group and *Globigerina* d'Orbigny and *Subbotina* Pozaryska and Brotzen were said to be allometric, i.e., those of scale rather than degree or kind, and it was the restricted stratigraphic distribution and small size that was used to delineate/distinguish the eoglobigerinids from the other two groups.

Blow (1979:1203) erected the family Eoglobigerinidae for trochospiral forms with intraumbilical or asymmetric umbilical-extraumbilical apertures and included in it *Eoglobigerina*, *Subbotina* and *Globastica* (as typified by *G. daubjergensis*). While considering that *Eoglobigerina* has a wall structure of "normal globigerinacean type" (Blow, 1979:1205), no mention was made of the presence of true spines in this group. Although it is clear that Blow (1979: 1290, pl. 238, fig. 5) recognized that *Subbotina* is spinose in drawing attention to the presence of "small, solid spines at the confluence of the inter-pore ridges" on a specimen of *S. triloculinoides*, he did not emphasize this fact in his classification of the Eoglobigerinidae. *Globastica* was specifically included in the Eoglobigerinidae on the basis of its umbilicate test, interiomarginal, intraumbilical aperture and pustule-like "spines" (Blow, 1979:1231). Blow (1979: 1203) considered that *Eoglobigerina* (ancestral to *Subbotina*) and *Globastica* were derived paedomorphically from latest Cretaceous rugoglobigerinids.

Blow (1979) also distinguished *Turborotalia* as a non-carinate subgenus of *Globorotalia* characterized by nonmucate walls with or without pore pits and inter-pore ridges, umbilical-extraumbilical aperture, and weakly developed/reduced portical (apertural) structures. Indeed, he distinguished eoglobigerinids and turborotaliids on the basis of the loss of the weakly developed portical structures and adaption of a stabilized umbilical-extraumbilical apertural system in the turborotaliids. *Turborotalia* was interpreted as derived on the one hand from *Eoglobigerina* (through the loss of weakly developed portical structures and adoption of stabilized umbilical-extraumbilical system); on the other hand some turborotaliids (as *pseudobulloid*) were considered to have evolved directly from a *Hedbergella* ancestor with a well developed portical structure and, indeed, Blow (1979:1047) suggested that *pseudobulloid* might be more appropriately assigned to *Hedbergella*.

Blow believed that the portical structure and the apertural lip were of major taxonomic significance and this is perhaps why he assigned little importance to the spinose condition. He considered that the porticus was a structure distinct from

the apertural lip. He interpreted the porticus as a late stage ontogenetic structure that was added to the chamber wall above the aperture. He demonstrated the porticus with species with cancellate walls to show that the cancellate texture was distinctly separated from the porticus. He used this observation to conclude that the porticus was a separate structure that was added to the chamber wall. In contrast, the apertural lip according to Blow was formed by an outer bending of the chamber wall and he illustrated it in non-cancellate species. It is now known from ontogenetic studies of planktonic foraminifera that the cancellate wall texture is built up ontogenetically on the outer test wall of chambers and is often further enhanced by gametogenetic calcification (Hemleben and others, 1989). Consequently, it is clear that the porticus as envisioned by Blow and the apertural lip are the same morphological structure and do not have major taxonomic significance.

Banner (1982) placed only secondary emphasis on spines in his classification of planktonic foraminifera. For example, mention of the presence of spines as a taxonomic character within the Globigerininae is made only midway through the diagnosis of various taxa in this subfamily which include such typical forms as *Globigerina*, *Beella*, *Globigerinoides*, (Banner, 1982:200, 201), while excluding such (spinose) forms as *Subbotina*, which he considered nonspinose. The Eoglobigerininae were incorporated within the Globigerinidae and considered nonspinose as well (Banner, 1982:202).

At the other extreme the Globorotaliinae were interpreted to include forms which had a "surface with true spines embedded in spine bases over all or part of the test" (Banner, 1982:203). Included here were such (nonspinose) forms as *Turborotalia* and *Neogloboquadrina*. The Eoglobigerininae were thought to have been derived from unknown Caucasellinae, or from small species of "*Hedbergella*" by way of loss of muricae and an intraumbilical-umbilical migration of the aperture (Banner, 1982:220). This hypothesis was subsequently modified (Banner and Desai, 1988) with the recognition of the "microperforate" genus *Blefuscuiana* (as distinct from the "macroperforate" *Hedbergella*) and the suggestion that forms referable to this group in the Late Cretaceous may have been ancestral to early Danian "microperforate" forms such as *Turborotalia archeocompressa* Blow.

An interesting feature of the different classification schemes discussed above is the fate of the taxon *eugubina* Luterbacher and Premoli Silva (= *longiapertura* Blow) variously ascribed to *Turborotalia* (Blow, 1979) or *Parvularugoglobigerina* (Banner, 1982; Loeblich and Tappan, 1988). Blow (1979:1085) considered *longiapertura* (= *eugubina*) a "primitive member of the *compressa* (sensu lato) evolutionary gens" and readily referable to *Turborotalia*. Banner (1982:202) included *Parvularugoglobigerina* in the (microperforate) Tenuitellinae (Globigerinidae), Loeblich and Tappan (1988:474) included *Parvularugoglobigerina* in the (supposedly nonspinose) Eoglobigerinidae (Globorotaliacea).

These schemes of classification (Table 1) illustrate a certain level of misunderstanding that exists on the wall texture and architecture of early Danian planktonic foraminifera. Our observations on wall texture and architecture and the

presence or absence of spines show that they are of major taxonomic significance in the classification of planktonic foraminifera.

DISCUSSION

Our studies show that four separate types of wall texture developed in the earliest Paleocene planktonic foraminifera. The evolution of genera and species in the early Danian occurred within each of these groups of planktonic foraminifera. Thus, in the study of the Cretaceous-Paleogene boundary it is essential to correctly define and identify species within these groups. Unfortunately, the taxonomy of the earliest Paleocene planktonic foraminifera is not well understood among workers on the K/P boundary sections. We attempt here to clarify some of the taxonomic misconceptions that have been published. We also present a phylogenetic scheme based on our studies of the early Paleocene and point out some of the remaining problems in early Paleocene phylogeny. Although the question of survivorship of Cretaceous species in the early Paleocene is not addressed in this study, it is important to point out that except for *Guembelitra cretacea* none of the Cretaceous species proposed as survivors by Keller (1989a, b) and Barrera and Keller (1990) belong in any of the four early Paleocene groups discussed above. Thus, even if some of the proposed Cretaceous survivorship species did survive the terminal Cretaceous event, they are not important to the phylogeny of the four groups of Paleocene planktonic foraminifera.

A common mistake that adds much confusion to the understanding of the impact of the K/P event on planktonic foraminifera is the assignment of various earliest Paleocene species and morphotypes to microperforate specimens of *Parvularugoglobigerina*. Although the taxonomy of many described early Paleocene species (particularly Russian species) is not clearly understood there are some which we describe and illustrate in this paper which are well known. The specimens identified by Keller (1988) from El Kef as *Globigerina* (*Eoglobigerina*) *hemisphaerica*, *G. (Eoglobigerina)* *taurica*, *Globigerina* cf. *edita*, and *Globigerina* *fringa* (Plate III, Figure 16) are all microperforate forms which belong to *Parvularugoglobigerina*. All of these species possess normal perforate cancellate wall texture (see above) and, thus, these species have been used incorrectly by Keller. *Parvularugoglobigerina eugubina*, the main species of this genus, exhibits a large range of morphologic variability which is expressed by several morphotypes such as those included in the studies of d'Hondt and Keller (1991) and Li and Radford (1991). Further study is needed to determine whether all or only some of these morphotypes are valid species. Brinkhuis and Zachariasse (1988) in their study on the El Kef section also identified forms which they correctly placed in the microperforate genus *Parvularugoglobigerina* but incorrectly placed in normal perforate cancellate species. These include their identifications given as *Parvularugoglobigerina edita edita*, *P. edita taurica*, and *P. fringa*. Also, generic names such as *Globigerina*, *Globorotalia*, and *Neogloboquadrina* (Brinkhuis and Zachariasse, 1988; Keller, 1988, 1989; Smit 1982) should not be used for early Paleocene taxa because these genera first

appear much later in the Cenozoic and are not directly related to the early Paleocene taxa. The misuse of early Paleocene normal perforate cancellate taxa in the El Kef section would appear to reflect the awareness of these workers of the importance of these taxa and their expectation that they should occur at El Kef. In fact, our studies of El Kef material from the basal Paleocene indicates that normal perforate cancellate species are present but are very rare and poorly preserved. As pointed out above, the microperforate group, especially *Parvularugoglobigerina*, tends to be more resistant to dissolution than the cancellate group. Consequently, preservational bias exists in the basal Paleocene section at El Kef which distorts the phylogenetic history of the planktonic foraminifera. It is not surprising, then, that Smit (1982) derived the normal perforate cancellate globigerinids from the microperforate *Parvularugoglobigerina* and that Brinkhuis and Zachariasse derived (1988) the first Paleocene planktonic taxa from a benthic foraminifera, *Caucasina*.

Our concept of the phylogeny of the early Paleocene planktonic foraminifera is given in Figure 1. Four main groups of planktonic foraminifera are involved in the evolution of early Paleocene species. These groups are separated on the basis of their wall texture as outlined in the discussion above. These are the microperforate (*Parvularugoglobigerina*, *Chiloguembelina*, *Globoconusa*, *Guembelitra*, *Woodringina*), normal perforate cancellate nonspinose (*Praemurica*), normal perforate cancellate spinose (*Eoglobigerina*, *Parasubbotina*, and *Subbotina*), and normal perforate smooth-walled nonspinose (*Globanomalina*). We include all the microperforate taxa in the Heterohelicea for the moment; the other three groups are included with the Globigerinacea with the spinose *Eoglobigerina*, *Parasubbotina*, and *Subbotina* included in the Globigerinidae, the nonspinose *Globanomalina* and *Praemurica* in the Globorotaliidae. The great bulk of the evolutionary radiation that led to the diversification of planktonic foraminifera in the Paleogene and the Neogene is derived from the three normal perforate walled groups. Except for *Chiloguembelina* the microperforate group does not play a significant role in these radiations. *Parvularugoglobigerina* is a short-lived guembelitriid genus of the early Danian.

The Cretaceous ancestor of the normal perforate groups is regarded as the *Hedbergella* plexus centered around the species *H. monmouthensis*. The first species of *Globanomalina*, *G. archeocompressa*, retains the general smooth-walled morphology of *Hedbergella holmdelensis* Olsson. Of the three normal perforate groups this appears to be the most conservative, giving rise to apparently only two other species in the early Paleocene. Even in the later Paleocene it is represented by only a few species. The cancellate nonspinose group, although represented by possibly three species in the early Paleocene is ancestral to the important radiations that occurred within the muricate (nonspinose) genera *Morozovella* and *Acarinina* in the later Paleocene and Eocene. The origin of the cancellate wall structure at the beginning of the Paleocene must lie in modification of the wall texture in response to a rapid ecological adaption to different habitats that became available at this time. In the nonspinose cancellate species the ridges supported rhizopods which were able to capture detritus but were not strong

Superfamily		HETEROHELICACEA				GLOBIGERINACEA			
Family		GUEMBELITRIIDAE				GLOBOROTALIIDAE		GLOBIGERINIDAE	
Generic Radiation		Tri-, biserial, trochospiral genera				Globanomalinids		Praemuricates	
Wall texture		non-spinose				non-spinose		spinose	
		microperforate				smooth wall, normal perforate		cancellate, normal perforate	
early Paleocene	P2								
	P1								
	P α								
	P0								
latest Cretaceous									

FIGURE 1. The suggested phylogeny of the early Paleocene planktonic foraminifera showing the four main groups of that are involved in the evolution during early Paleocene. These groups are separated on the basis of their wall texture as outlined in the text and include: the microperforate (*Parvularugoglobigerina*, *Chiloguembelina*, *Globoconusa*, *Guembelitria*, *Woodringina*), normal perforate smooth-walled nonspinose (*Globanomalina*), normal perforate cancellate nonspinose (*Praemurica*), normal perforate cancellate spinose (*Eoglobigerina*, *Parasubbotina*, *Subbotina*).

enough to capture actively moving organisms. Without the cancellate cover the nonspinose early Paleocene planktonic foraminifera have a basic hedbergellid design. Like the hedbergellids they possess a very low trochospiral test with five or more chambers in the final whorl and an umbilical-extraumbilical aperture that is bordered by an elongate narrow lip. The cancellate spinose group appears to have begun the earliest radiation of the normal perforate groups, giving rise to three genera and several species in the earliest Paleocene. The development of spines in the eoglobigerinids and the parasubbotinids allowed these groups to become more carnivorous since the spines were bases that supported long strands of rhizopods which allowed capture of actively moving organisms. In the spinose globigerinids the similarity to the hedbergellids is less distinct. As in the nonspinose planktonic foraminifera, without the cancellate cover the test is similar in that the aperture is bordered by an elongate lip. However, the aperture is not only extraumbilical (*P. pseudobulloides*) but also takes a more umbilical position which appears to be a result of a somewhat higher trochospiral test (*E. eobulloides*). Except for *E. edita* the rate of increase in size of chambers is greater than in *Hedbergella*.

In the spinose species the calcite deposited during the construction of the test supports spines which are set upon the initial primary organic layer. During chamber formation additional layers of calcite platelets build up around the spines as collar-like structures. In an architectural sense the modification of test morphology could be related to the development of more chamber surface area. The greater the surface area the greater the number of spines that can be accommodated on a chamber; thus, density of spines is an advantage in catching and holding actively moving organisms. Primitive pitted wall texture has been observed in specimens of *Hedbergella monmouthensis* Olsson from Zone P0 at Millers Ferry and is currently under study. There may be other species not shown in Figure 1 which can be placed in the early Paleocene phylogeny, but additional studies are needed to clarify their validity. The species shown on Figure 1 are the most common and characteristic species that are known to occur in the lower Danian sections. Consequently, it is these species which will provide the most important information on the nature of the recovery of planktonic foraminifera from the K/P boundary event. In addition, we believe that the classification pre-

sented here approaches more closely one which is biologically guided and evolutionarily based (Steineck and Fleisher, 1978) than previous classifications used in the early Paleocene planktonic foraminifera because the wall texture reflects directly the habitat of the species.

CONCLUSIONS

The following conclusions result from this study on wall texture of the earliest Danian planktonic foraminifera:

1. Four groups of planktonic foraminifera based on wall texture are recognized in the basal Danian sections. These groups are the microplicate (Guembelitriidae), the normal plicate smooth-walled nonspinose (*Globanomalina*), the normal plicate cancellate nonspinose (*Praemurica* gen. nov.), and the normal plicate cancellate spinose (*Eoglobigerina*, *Subbotina*, and *Parasubbotina* gen. nov.).

2. Two new genera, *Praemurica* (typified by *Globigerina taurica* Morozova 1961) and *Parasubbotina* (typified by *Globigerina pseudobulloides* Plummer 1926) are erected for the newly recognized cancellate nonspinose group and one of the cancellate spinose groups, respectively, in the Danian.

3. Other than *Guembelitria* sl. and *Hedbergella*, no Cretaceous planktonic genera are related to these four groups. Thus, in view of the rapid evolution of the earliest Paleocene groups (a radiation which points to radically changed and/or vacated niches), it is difficult to envision survivorship of the great mass of Cretaceous species. Survivorship of other Cretaceous taxa is difficult to prove in the lower Danian sections where reworking is evident. In any case, no other Cretaceous species are important to the radiation events that began immediately after the boundary event.

4. The classification proposed here should provide a biological basis for the study of the phylogeny of planktonic foraminifera in the Danian and later epochs of the Cenozoic.

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