

## Early Palaeocene *Parvularugoglobigerina* and late Eocene *Praetenuitella*: does evolutionary convergence imply similar habitat?

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**ABSTRACT** - The species of the earliest Palaeocene planktonic foraminiferal genus *Parvularugoglobigerina* are characterized by a small test with a smooth, microperforate wall and an elongate aperture. Pore-mound structures may occur on some specimens, while the coiling mode varies from high- to low-trochospiral. Four morphotypes are distinct enough to be recognized as species: *P. eugubina* (Luterbacher & Premoli Silva) is low spiral and multichambered and *P. perexigua* n. sp. is four-chambered; *P. fodina* (Blow) has a *Globigerina bulloides*-type morphology and *P. alticonusa* n. sp. has a high trochospire. With the exception of the high spire, this general morphology is repeated in late Eocene forms classified as *Praetenuitella*: *P. insolita* (Jenkins), *P. patefacta* Li, and other associated forms.

The two groups acquired their strong similarities – highly distinctive, peculiarly elongated aperture and microperforate walls – through evolutionary convergence, not by being directly related. Stratigraphically they each have a brief occurrence in a geologically significant slice of Palaeogene time: the one during the recovery of ecosystems in the earliest Palaeocene; the other immediately prior to the great cooling and in the time of rapid change known as the Terminal Eocene Event. This study shows that *Praetenuitella* flourished in eutrophic conditions and that their evolution might have been nutrient-driven. We suggest by morphological pattern analogy that forms of *Praetenuitella* and *Parvularugoglobigerina* reflect similar habitat in their similar form and especially in their aperture. *J. Micropalaeontol.* 14(2): 119–134, October 1995.

### INTRODUCTION

Hofker (1978) introduced the generic name *Parvularugoglobigerina* to include forms described as and related to *Globigerina eugubina* Luterbacher & Premoli Silva (1964), occurring immediately above the Cretaceous/Palaeogene (K/P) boundary. Using schematic drawings, Hofker referred forms with heavy pustules to the type species *eugubina*. Smit (1982), however, showed that *eugubina* is smooth and finely (rather than heavily) pustulate and microperforate, although the micropores are scattered and difficult to observe. *Globorotalia (Turborotalia) longiapertura* Blow (1979) falls within Smit's (1982) species concept for *Globigerina eugubina*: accordingly, we treat *longiapertura* as a junior synonym of *eugubina*. This view has been followed by several others including Boersma & Premoli Silva (1983), Toumarkine & Luterbacher (1985), Brinkhuis & Zachariasse (1988) and Keller (1988), but Canudo *et al.* (1991) considered *longiapertura* as a distinct species. Specimens of *P. eugubina* from the Millers Ferry section in Alabama have recently been found to possess pore-mounds on the wall surface (Olsson *et al.*, 1992), whereas most individuals are smooth with scattered micropores. Wall texture aside, the most conspicuous character of *P. eugubina* is the highly elongate aperture. *Praetenuitella* spp. from the late Eocene also possess an elongate aperture. Beginning with a comparison of the two groups, this study considers the implications of the strongly convergent development of the aperture, which is most unusual among the Cenozoic planktonic foraminifera in its form. Material from DSDP Holes 152 and 577, ODP Hole 749B and the Otway Basin in southern Australia was

examined and some typical specimens of selected species are illustrated.

### MORPHOLOGICAL CHARACTERISTICS OF *PARVULARUGOGLOBIGERINA*

#### 1. Test and coiling

The test in most species of *Parvularugoglobigerina* has 8–12 subglobular to globular chambers, with 4–7 in the final whorl. Chambers increase slowly in the inner whorl but rapidly in the outer, final whorl. The test diameter ranges commonly from 80–150  $\mu\text{m}$  (Pl. 1), although tests as large as 220  $\mu\text{m}$  have been found (Olsson, 1992, pers. comm.). Coiling is dominantly low trochospiral, as seen in the type species, *P. eugubina* (Pl. 1, figs 1–11), but intermediates are common between the low- and high-trochospiral forms (Pl. 2, figs 8, 9).

#### 2. Surface texture

The wall is smooth but may be slightly rugose due to the overgrowth of calcite particles on many specimens in our material. Unlike the true pustules, these calcite particles, or pseudopustules, are closely packed (see also Hemleben *et al.*, 1991; Olsson *et al.*, 1992). This can be easily observed when specimens have been poorly preserved or slightly dissolved (Pl. 1, fig. 7; Pl. 2, fig. 3). On the other hand, forms with typical pore-mounds (Pl. 1, figs 3–7) have similar, but less distinct, characters to those on the triserial *Guembelitra cretacea* Cushman. This has led Olsson *et al.* (1992) to propose their affinity, i.e. the parvularugoglobigerines may be the direct descendants of *G. cretacea*. This can be disputed because the pore-mound structure has been

observed independently on several forms which are phylogenetically unrelated: the early Cretaceous *Blefuscuiana* (see illustrations in Banner & Desai, 1988; Banner *et al.*, 1993), the late Cretaceous to early Palaeocene *G. cretacea* and Oligocene–Miocene *Cassigerinella chipolensis s.l.* Banner & Desai (1988) suggested that the origin of *P. eugubina* could be descended directly from late Cretaceous *Blefuscuiana* with minimal morphological change.

The perforations on *P. eugubina*, when observable, are extremely small, about 0.2–0.3  $\mu\text{m}$  in diameter, and irregularly distributed (Pl. 1, figs 2, 3, 6, 7). With about 5 micropores per 100  $\mu\text{m}^2$ , pore density of *P. eugubina* is the lowest among the Cenozoic microporate planktonic taxa, as is the porosity which is only 2% or less (Li, 1991).

### 3. Apertural features

As observed earlier by Blow (1979) on *Globorotalia* (*Turborotalia*) *longiapertura* (= *P. eugubina*), the aperture in most tests is high and elongate. In low trochospiral individuals (typical of *longiapertura*) the aperture is (umbilical-) extraumbilical and extends onto the apertural face (Pl. 1, figs 1, 2, 4–6, 8–10). It gradually moves towards the umbilicus when the test becomes high trochospiral (Pl. 2, figs 6–10). The apertural lip is absent from some specimens of *P. eugubina* (Pl. 1, figs 4–6, 10), but may be well developed in some others (Pl. 1, figs 1, 2, 8, 9). As reported by Gerstel *et al.* (1986) and D'Hondt & Keller (1991) and observed by us in DSDP Holes 465 and 577, many specimens of *P. eugubina* have aberrant and varying apertures, which may extend onto the spiral (dorsal) side.

## MORPHOTYPES OF

### PARVULARUGOLOBIGERINA

Four morphotypes here grouped within the genus *Parvularugoglobigerina* are considered to warrant taxonomic distinction. They are *P. eugubina* (Luterbacher & Premoli Silva), *P. fodina* (Blow), *P. perexigua* n. sp. and *P. alticonusa* n. sp. Specimens of the *eugubina*-type and *perexigua*-type are both characterized by a low trochospire, but they can be separated by 5 or more and only 4 chambers in the final whorl respectively. By contrast, *P. fodina* possesses a medium-high spire and an almost circular aperture, while *P. alticonusa* is high and has an elongate aperture similar to that of typical *eugubina*. Detailed taxonomic discussions on these and several related taxa are presented in Appendix A.

## EVOLUTION AND DISTRIBUTION OF

### PARVULARUGOLOBIGERINA

*Parvularugoglobigerina* is now known to be a microporate genus having various morphotypes. Changes in the spire

height from high to low or vice versa, accompanied by changes in the apertural location, are useful for differentiation of species (or morphotypes). Some morphotypes have been misidentified; those, for example, with four-chambered tests described by Brinkhuis & Zachariasse (1988) among others, as *Globigerina fringa* Subbotina should be the new species *P. perexigua*, because the types of *G. fringa* possess a cancellate wall and belong therefore in the eoglobigerines (Berggren, 1990, pers. comm.; Berggren, 1992). Similarly, the records of *P. minutula* from various K/P boundary sections (e.g. Smit, 1982; as *G. conusa*, 1989 in Keller, 1988) should be changed to *P. alticonusa*, for *Globigerina minutula* Luterbacher and Premoli Silva is in fact an early subbotinid with a distinct cancellate wall (Premoli Silva, 1990, pers. comm.), although the type material has recently been found to be so heavily recrystallized 'that the wall texture was completely uninterpretable' (Olsson, 1992, pers. comm.). From our present knowledge of this group, however, it became diverse shortly after the K/P boundary mass extinction (Premoli Silva, 1977; Boersma & Premoli Silva, 1991). Figure 1 shows the approximate ranges of *Parvularugoglobigerina* spp. and other genera in the early Palaeocene.

From the K/P boundary section at El Kef in NW Tunisia, Brinkhuis & Zachariasse (1988) suggested that both *Globoconusa minutula* (= *P. alticonusa*) and *P. fringa* (= *P. perexigua*) probably evolved from a benthic form *Caucasina*, simply by increasing chamber volumes to achieve buoyancy. This suggestion may confirm Hofker's (1978) view that *Parvularugoglobigerina* might have arisen from the larval stage of a benthic form. But alternative explanations are equally tenable. For example, Banner & Desai (1988) concluded that the Cretaceous *Blefuscuiana* was its likely ancestor, while we observed a complete transitional series between the triserial-biserial planktonic *Guembelitra*–*Woodringina* and *Parvularugoglobigerina* spp. from DSDP Hole 465A. On the other hand, Olsson *et al.* (1992) derived both *Parvularugoglobigerina* and *Globoconusa* from *Guembelitra*, on the evidence that early representatives of these genera are all similar to *Guembelitra* in having a microporate and mounded wall, although diagenetic calcite growth may alter this wall surface texture. Also like *Guembelitra*, many forms of *Parvularugoglobigerina* (referable to *P. alticonusa*) are high trochospired. From the El Kef section, Brinkhuis & Zachariasse (1988), Keller (1988) and D'Hondt & Keller (1991) reported that forms of the *alticonusa*-type (= *P. minutula*, or *P. morphotype* 1 of these authors) occurred together with the compressed *P. eugubina*. If *Guembelitra* is the ancestral form, then the immediate descendant to mark the establishment of the genus *Parvularugoglobigerina* must be *P. alticonusa*, from

### Explanation of Plate 1

*Parvularugoglobigerina eugubina* (Luterbacher & Premoli Silva) from the basal Palaeocene (Zone P $\alpha$ ). Scale bar = 50  $\mu\text{m}$  unless indicated otherwise. **Fig. 1.** Specimen from Sample 577-12-5, 113–114 cm. **Figs 2, 3.** Specimen from Sample 152-10-1, 140–143 cm. Note the pore-mound texture. **Figs 4, 5.** Single specimen with a lipless aperture form Sample 152-10-1, 140–143 cm. **Figs 6–8.** Specimens from Sample 152-10-1, 140–143 cm. Note the pseudopustules and scattered micropores with less distinct pore-mounds. **Fig. 9.** Specimen with a well developed apertural lip from Sample 577-12-5, 113–114 cm. **Figs 10, 11.** Two specimens with a low trochospire from Sample 152-10-1, 140–143 cm.

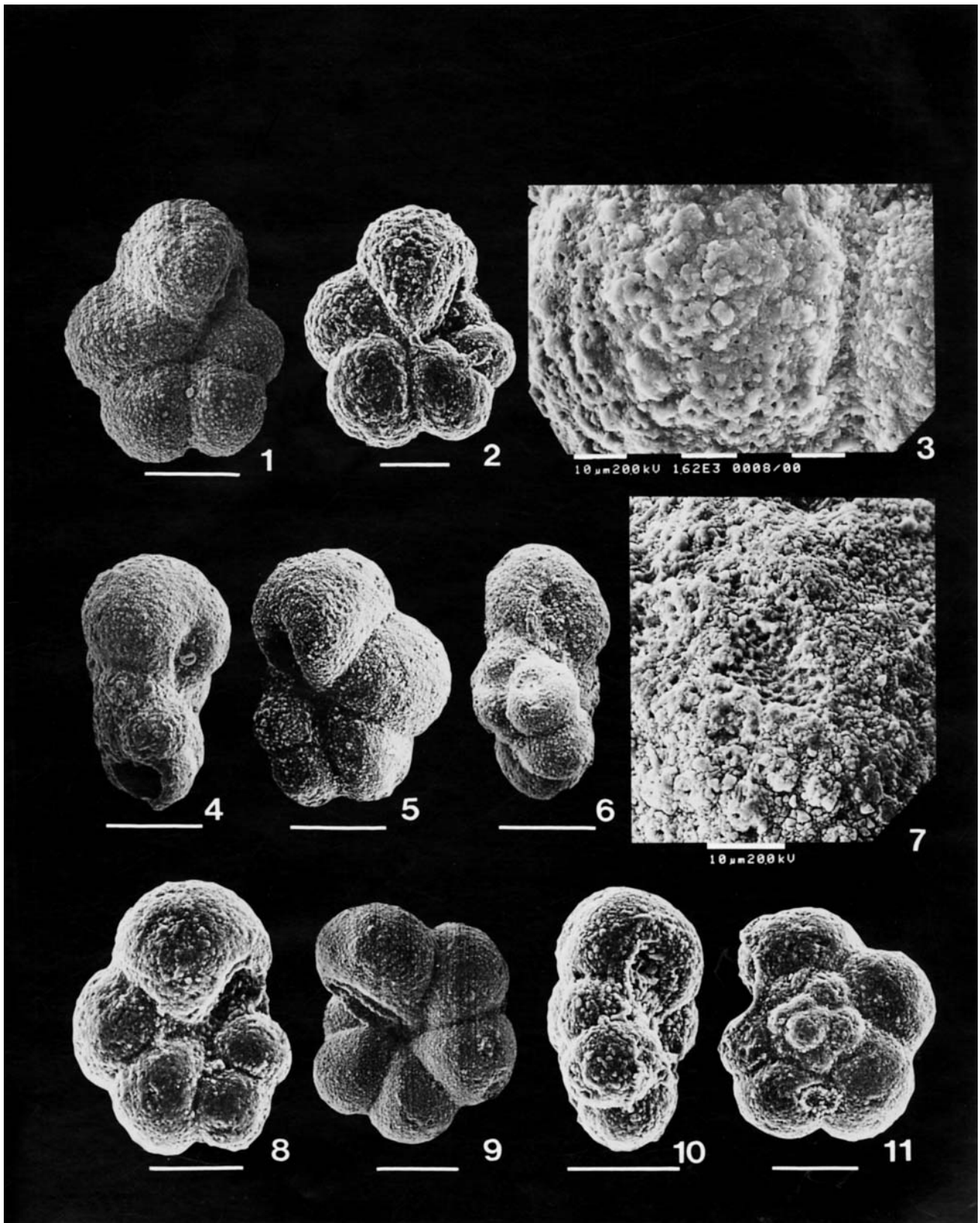


Plate 1

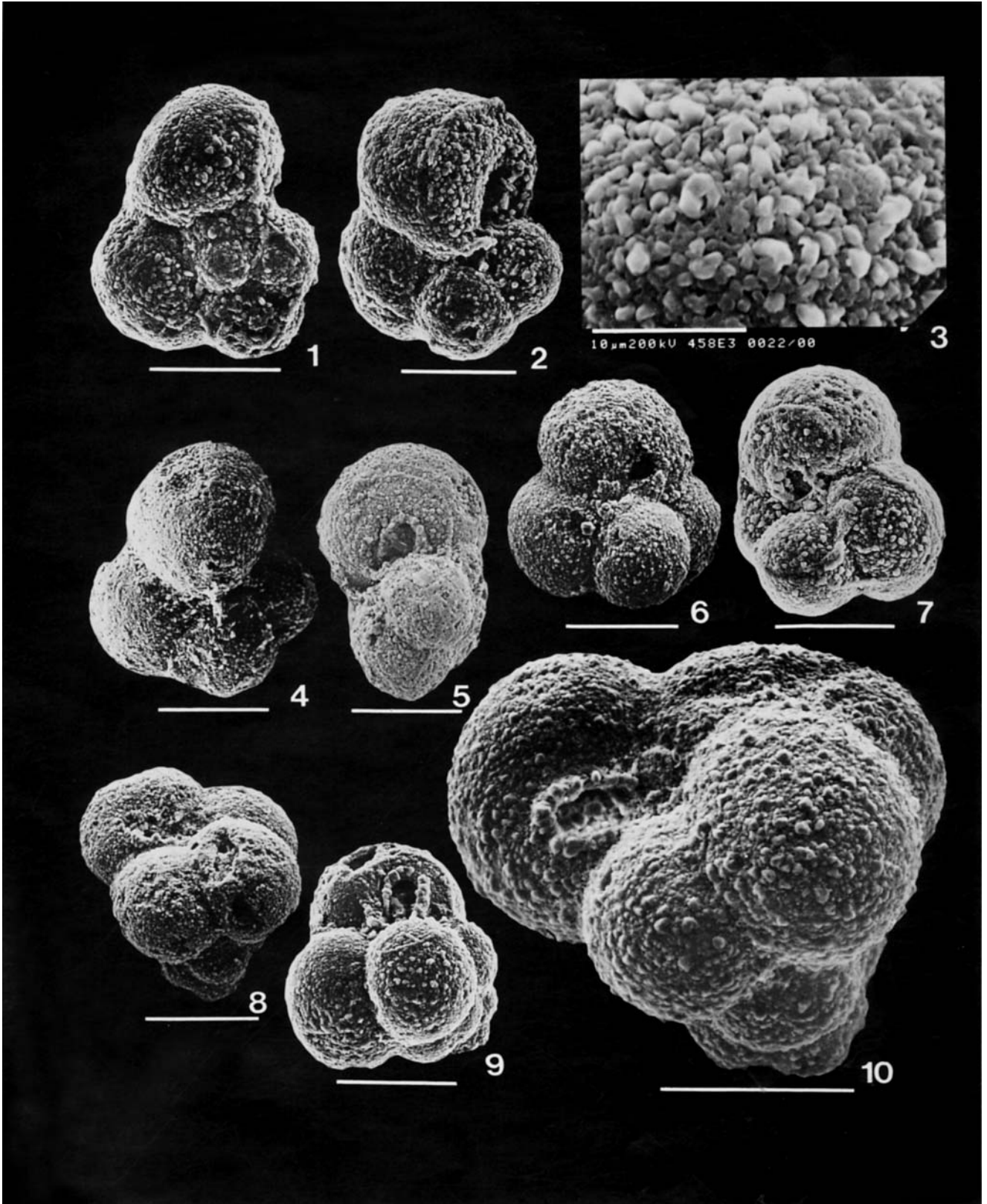
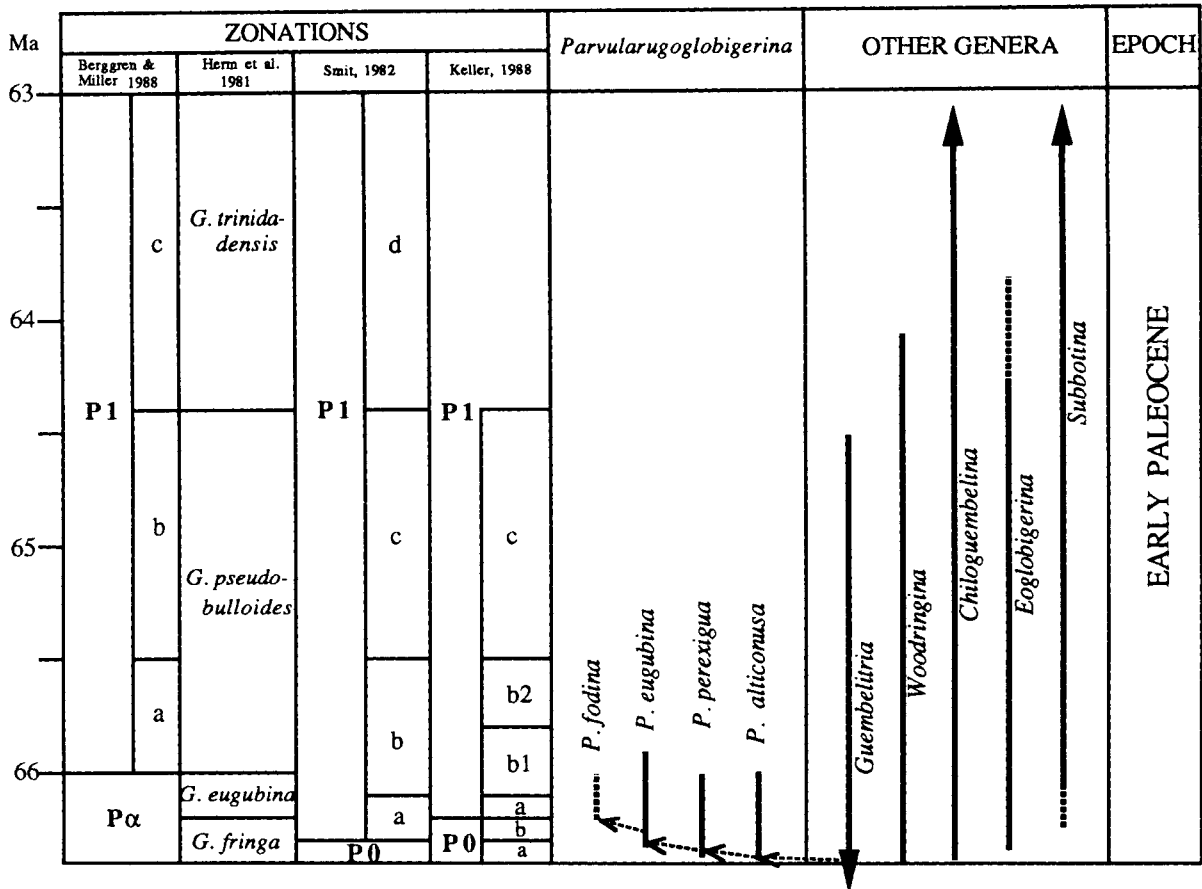


Plate 2



**Fig. 1.** Ranges of *Parvularugoglobigerina* spp. and related genera in the early Palaeocene. Chronology from Berggren *et al.* (1985). Several planktonic foraminiferal zonations are shown.

which all other parvularugoglobigerine morphotypes evolved in succession. We therefore suggest the evolutionary bioseries to be likely from *P. alticonusa* to *perexigua* (and *fodina*) to *eugubina*, where *P. fodina* may only represent a short branching from the main stock (Fig. 1). After a short period of proliferation, all species of *Parvularugoglobigerina* became extinct within Zone P1, leaving no direct descendants. (In contrast, Blow (1979) and Banner (1989) suggested that this lineage might lead to the appearance of several early Palaeocene groups, including *Globanomalina*.)

Species of *Parvularugoglobigerina* occur immediately above the K/P boundary in the earliest Palaeocene and indicate an age older than 65 Ma in the early part of Zone Pα of Blow (1979) (Berggren *et al.*, 1985), a level now recognized as Zone P0 (Smit, 1982; Olsson *et al.*, 1992). A recent discovery by Montgomery *et al.* (1992) that a clastic

event bed at the Brazos River K/P boundary section previously attributed to the latest Cretaceous is in fact the earliest Palaeocene. The presence of several Cretaceous species in that layer is due to reworking which had occurred several times during earliest Palaeocene time.

A reconstruction of the spatial distribution of *P. eugubina* (Fig. 2) shows that this species is widely distributed, with high abundances inferred in upwelling regions during the earliest Palaeocene. It may reach 50% in samples from the *eugubina* zone from many localities, including Spain (Smit, 1982), Denmark (Boersma & Premoli Silva, 1983, 1991), Shatsky Rise (Gerstel *et al.*, 1986) and Tunisia (Keller, 1988). In polar areas it is rare or absent, and the planktonic foraminiferal fauna there is dominated by *fringa*-type, macroperforate forms (Stott & Kennett, 1990, Weddell Sea, Antarctica; Berggren, 1992, Kerguelen Plateau).

#### Explanation of Plate 2

*Parvularugoglobigerina* spp. from the basal Palaeocene (Zone Pα). Scale bar = 50 μm unless indicated otherwise. **Figs 1–5.** *Parvularugoglobigerina perexigua* n. sp. from Sample 152-10-1, 140–143 cm; figs 1–3, holotype, with fig. 3 enlarged to show pseudopustules due to dissolution; figs 4 and 5 are two views of paratype. **Figs 6, 7.** *Parvularugoglobigerina fodina* (Blow). Two specimens with a semicircular, axiointraumbilical aperture from Sample 152-10-1, 140–143 cm **Figs 8–10.** *Parvularugoglobigerina alticonusa* n. sp., with a high trochospiral coiling from Sample 152-10-1, 140–143 cm (fig. 8, paratype; fig. 9, holotype) and Sample 577-12-5, 113–114 cm (fig. 10, paratype).

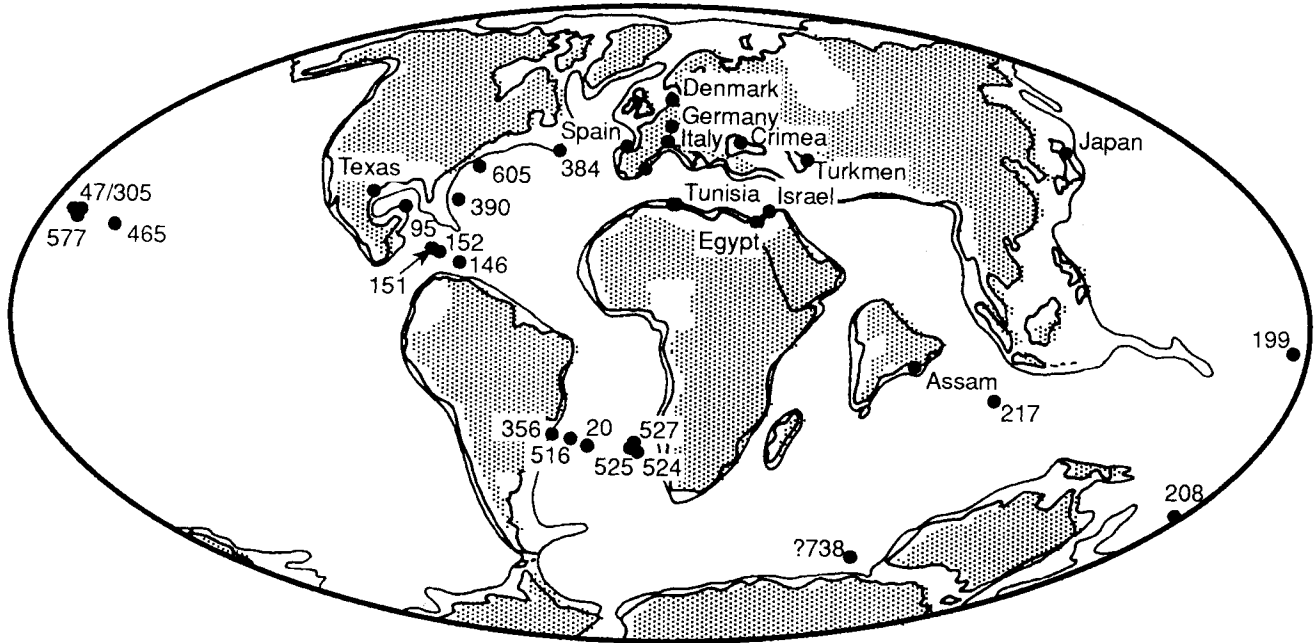


Fig. 2. Distribution of *Parvularugoglobigerina eugubina* in the earliest Palaeocene, as modified from Li & Radford (1991), on a base map adapted from Haq & Van Eysinga (1987) for the middle Palaeocene, at 60 Ma.

Another species commonly encountered is *P. alticonusa*. Smit (1982) and Brinkhuis & Zachariasse (1988) demonstrated that this species (as *G. conusa*) is the second most common microperforate species in Palaeocene sections in Spain and Tunisia. It was also recorded in this study from DSDP Hole 152 in the Caribbean and DSDP Hole 577 on Shatsky Rise. On the other hand, the geographic distributions of both *P. fodina* and *P. fringa* are poorly known, although the former was found in its type locality in DSDP Hole 47.2 on Shatsky Rise by Blow (1979) and in Hole 152 in this study.

#### THE LATE EOCENE PRAETENUITELLA, AN ANALOGUE OF PARVULARUGOGLOBIGERINA?

The genus *Praetenuitella*, erected by Li (1987) and discussed further by Li *et al.* (1992), includes the late Eocene tenuitellids with a small maximum test size (about 150  $\mu\text{m}$ ) characterized by a smooth, microperforate wall and by an elongate aperture (Pls 3 and 4). Represented by *P. insolita* (Pl. 3, figs 1–12; Pl. 4, figs 7–9) and *P. patefacta* (Pl. 4, figs

1–4), *Praetenuitella* is believed to have originated from *Pseudohastigerina* and subsequently given rise to *Tenuitella* spp. close to the Eocene/Oligocene boundary. Uncertainty remains because *Pseudohastigerina* is planispiral and smooth-walled, whereas *Tenuitella* is trochospiral and pustulate-walled. Although the trochospiral coiling is constantly low, *Praetenuitella* mimics the apertural character of *Parvularugoglobigerina* and these two taxa, as shown in Plates 1–4, are extremely similar in overall test morphology, thus representing one of the strongest convergent developments among Cenozoic planktonic foraminifera. The late Eocene *Praetenuitella* is a homeomorph of, but phylogenetically unrelated to, the early Palaeocene *Parvularugoglobigerina*. Unlike the parvularugoglobigerines, *Praetenuitella* had issue, giving rise to *Tenuitella* close to the Eocene–Oligocene boundary in an evolutionary transformation recorded in many localities (Li, 1991). Brief notes on *Praetenuitella* species are given in Appendix B.

*Praetenuitella insolita* was described from a short interval in the Port Elizabeth section in New Zealand, where it extends from just below the highest *Acarinina collectae*

#### Explanation of Plate 3

*Praetenuitella* spp. from the late Eocene of the Browns Creek Formation, Otway Basin, southern Australia (see McGowran *et al.*, 1992 for discussions on stratigraphy and palaeoenvironment). Scale bar = 50  $\mu\text{m}$ . Figs 1–7, 9, 10. *Praetenuitella insolita* (Jenkins). This species is characterized by 4–5 oval chambers in the final whorl, a smooth wall surface and a rather convex dorsal (spiral) side. Fig. 8. Intermediate form between *P. insolita* and *P. patefacta* (see Pl. 4). Figs 11, 12. Intermediate specimens between *P. insolita* and *P. praegemma* (see Pl. 4) with more than 5 chambers in the final whorl.

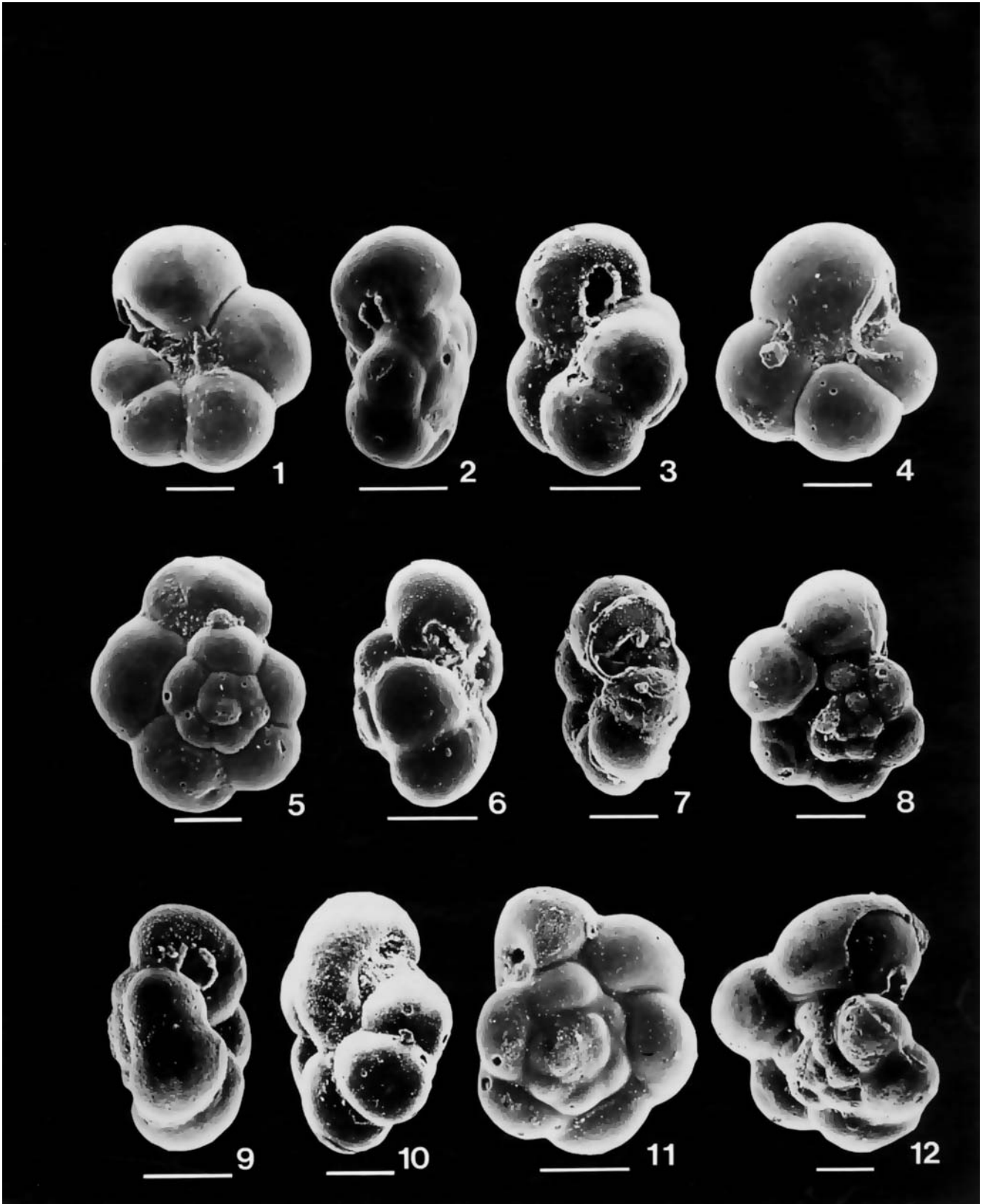
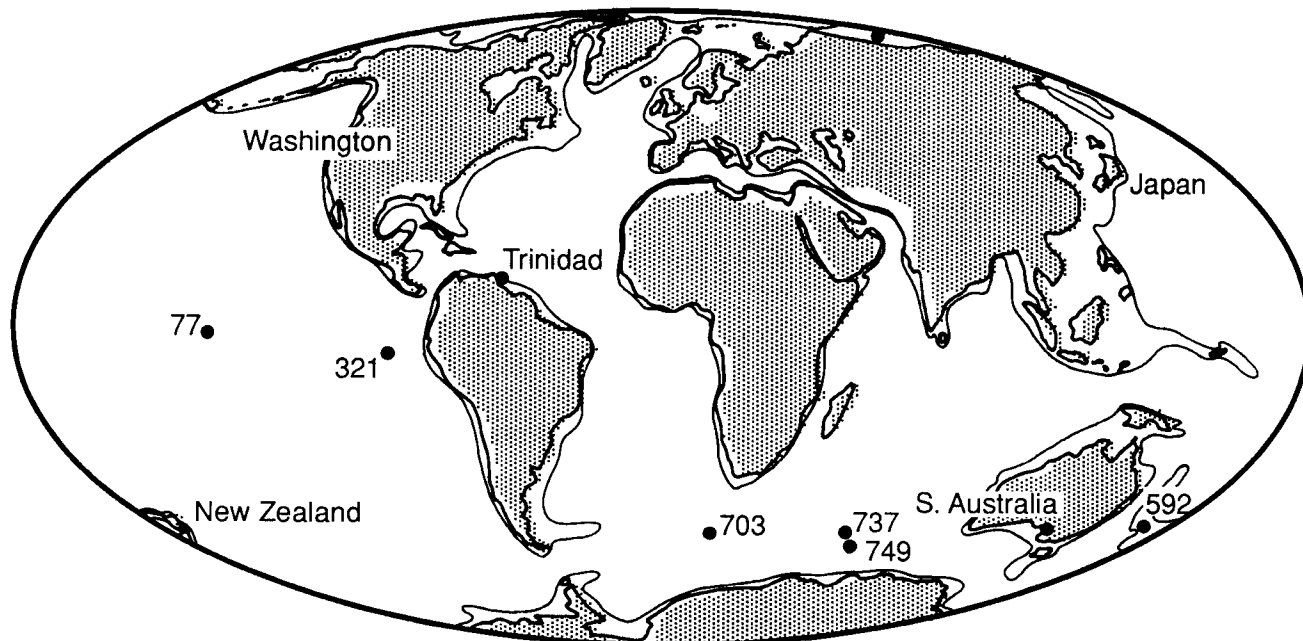


Plate 3





**Fig. 3.** Distribution of *Praetenuitella insolita* in the late Eocene on a base map adapted from Haq & Van Eysinga (1987) for the middle Oligocene at 30 Ma. Data sources are cited in the text.

(Finlay) to just below the highest *Globigerinatheka* spp. (Jenkins, 1966). The composite range in southern Australia is very similar or even identical, extending as it does from one recorded co-occurrence with *Acarinina primitiva* (Finlay) at the base (correlated approximately with the P14/P15 boundary), to the topmost records which are with the last *Globigerinatheka* (McGowran, 1991). The brief range of *P. insolita* coupled with their sometimes high frequency encouraged the establishment and recognition of a *P. insolita* zone (= *Globorotalia insolita* zone of Jenkins & Orr, 1972) in the southern hemisphere (Nocchi *et al.*, 1991; Li *et al.*, 1992). The zone is distinctive and easily recognized particularly at high southern latitudes, as at ODP Hole 749B on the Kerguelen Plateau (Fig. 4). Kaiho (1984) found similar forms in Japan but most records are from the southern hemisphere (Fig. 3; see also Quilty, 1976; Jenkins & Srinivasan, 1985).

The occurrence of *P. insolita* in neritic sediments in southern Australia gives us some insight into the species'

preferences. Figure 5 shows the relative abundances of '*Tenuitella gemma/munda/insolita*' (which is mostly *P. insolita* in the late Eocene). Visual inspection shows a distinct tendency to associate with *Chiloguembelina cubensis* and *Pseudohastigeria micra*. This group of species collectively is high in its relative abundance when *Globigerinatheka* is low and vice versa. That suggests fluctuations in nutrient, *Globigerinatheka* being the more oligotrophic. But the Blanche Point Formation as a whole is grey-green to black with high carbon content and very rich in opaline silica, and its benthic foraminiferal faunas are rich in uvigerinids and bolivinids (McGowran & Beecroft, 1986). The combined foraminiferal (benthic and planktonic), organic geochemical, microfossil and sedimentary evidence suggests a brief time of high productivity on the southern Australian margin in both open and restricted environments. That brief time essentially is confined to third-order cycles 4.2–(lowermost) 4.3 or, approximately, to planktonic foraminiferal zones upper P15–P16 (Fig. 6).

#### Explanation of Plate 4

*Praetenuitella* spp. from the late Eocene in ODP Hole 749B, southern Indian Ocean. Scale bar = 50  $\mu$ m unless indicated otherwise. **Figs 1-4.** *Praetenuitella patefacta* Li from Sample 749B-3-1, 36–38 cm having an almost planispiral test (figs 1 and 2 are different views of a single specimen). **Figs 5, 6.** Intermediate specimens between *P. patefacta* and *P. insolita*, from Sample 749B-3-1, 36–38 cm, showing the oval, rather than spherical, chambers and an aperture migrating away from the periphery. **Figs 7-9.** Two specimens of *P. insolita* with a slightly convex dorsal side from Sample 749B-3-1, 36–38 cm. Also note that the microporiferate wall on fig. 9, enlarged from fig. 8, has been obscured by diagenesis. **Figs 10, 11.** *Praetenuitella praegemma* Li, two specimens from Samples 749B-3-1, 36–38 cm and 749B-3-2, 50–53 cm respectively, with an umbilical–extraumbilical aperture. **Fig. 12.** Part of the population of *Praetenuitella* spp. from Sample 749B-3-1, 36–38 cm.



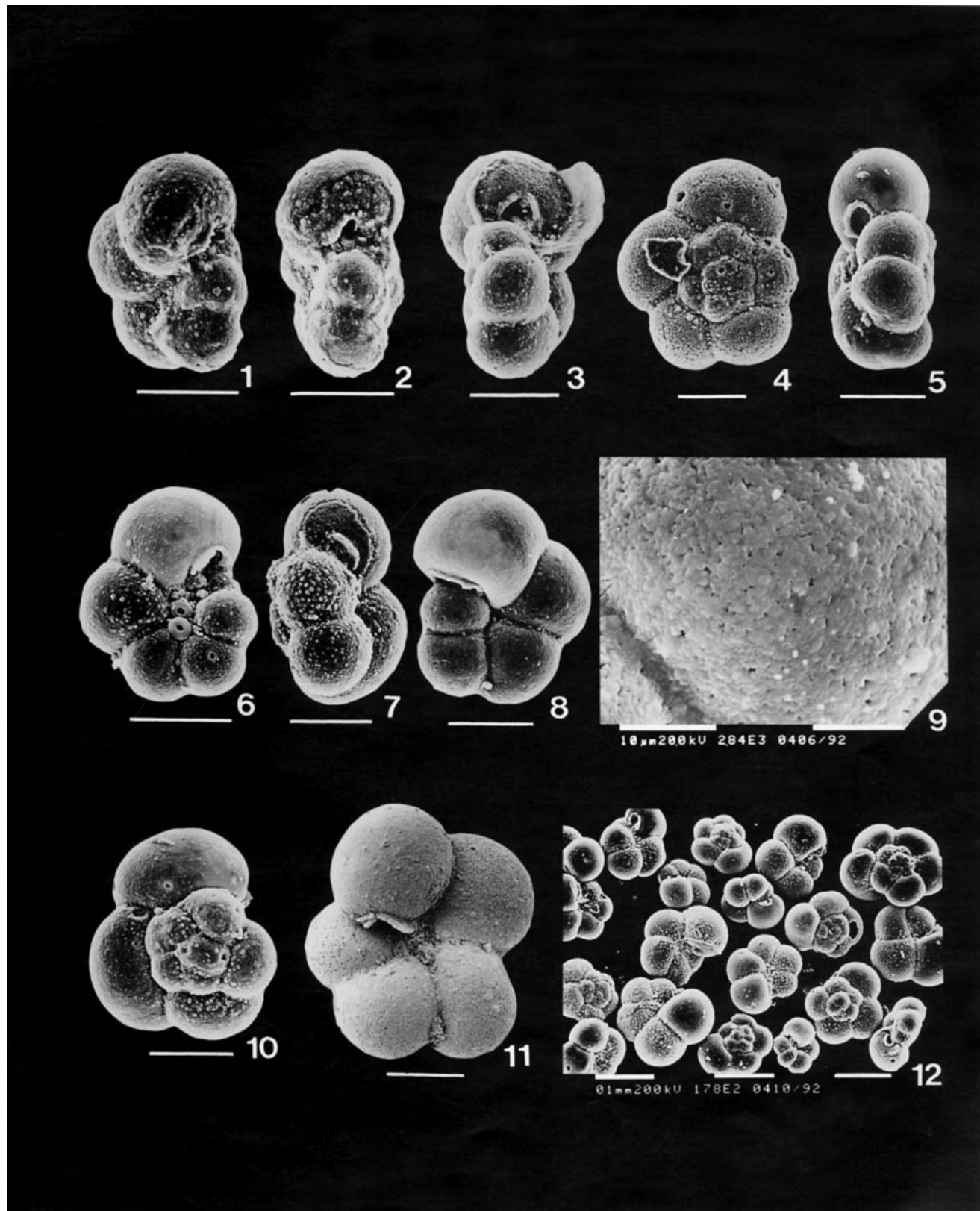
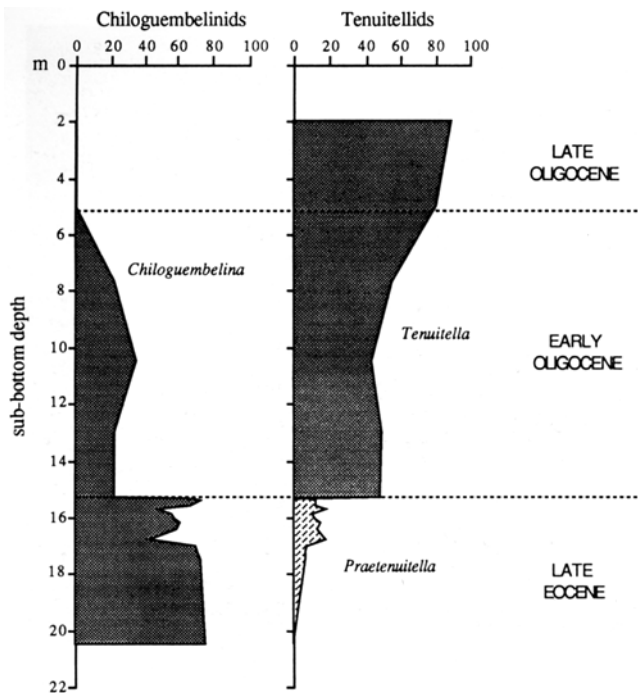


Plate 4



**Fig. 4.** Abundance of microperforate planktonic foraminifera in the  $<150\ \mu\text{m}$  fractions from the ODP Hole 749B (data from Li, 1991). Note that the relative richness of the chiloguembelinids in the late Eocene is coincident with the occurrence of *Praetenuitella* spp., while typical tenuitellids become predominant in the Oligocene.

The narrow band of high productivity signalled especially by the accumulation of opaline silica, organic carbon and benthic foraminiferal biofacies is neither a localized nor only a neritic phenomenon. The Oamaru Diatomite in New Zealand and the diatomite at Fundo Desbarrancado in Peru are in the same silica window, which in Peru is constrained by the radiolarian *Calocyclus bandyca* subzone (McGowran, Marty *et al.*, 1989). The silica window thus is trans-Pacific at least, and is sandwiched between a significant warming event early in the late Eocene and the great cooling at the end. We believe that it signifies a brief time of intensified upwelling. Be that as it may, though, the close parallel in time of the silica window and the common and morphologically distinctive *P. insolita* is significant. It is significant too that *Praetenuitella* appears first at the time of a pronounced spike in abundances of chiloguembelinids at the zone P14/P15 boundary at higher latitudes in the Atlantic Ocean, and that its peak in abundance in the silica window is at the next chiloguembelinid spike in zone P16 (spikes are in Boersma & Premoli Silva, 1989; Li & Radford, 1991). The P16 spike in the ocean thus is coeval with the neritic spike in *C. cubensis* shown below the maximum flooding surface of cycle TA4.2 (Fig. 5).

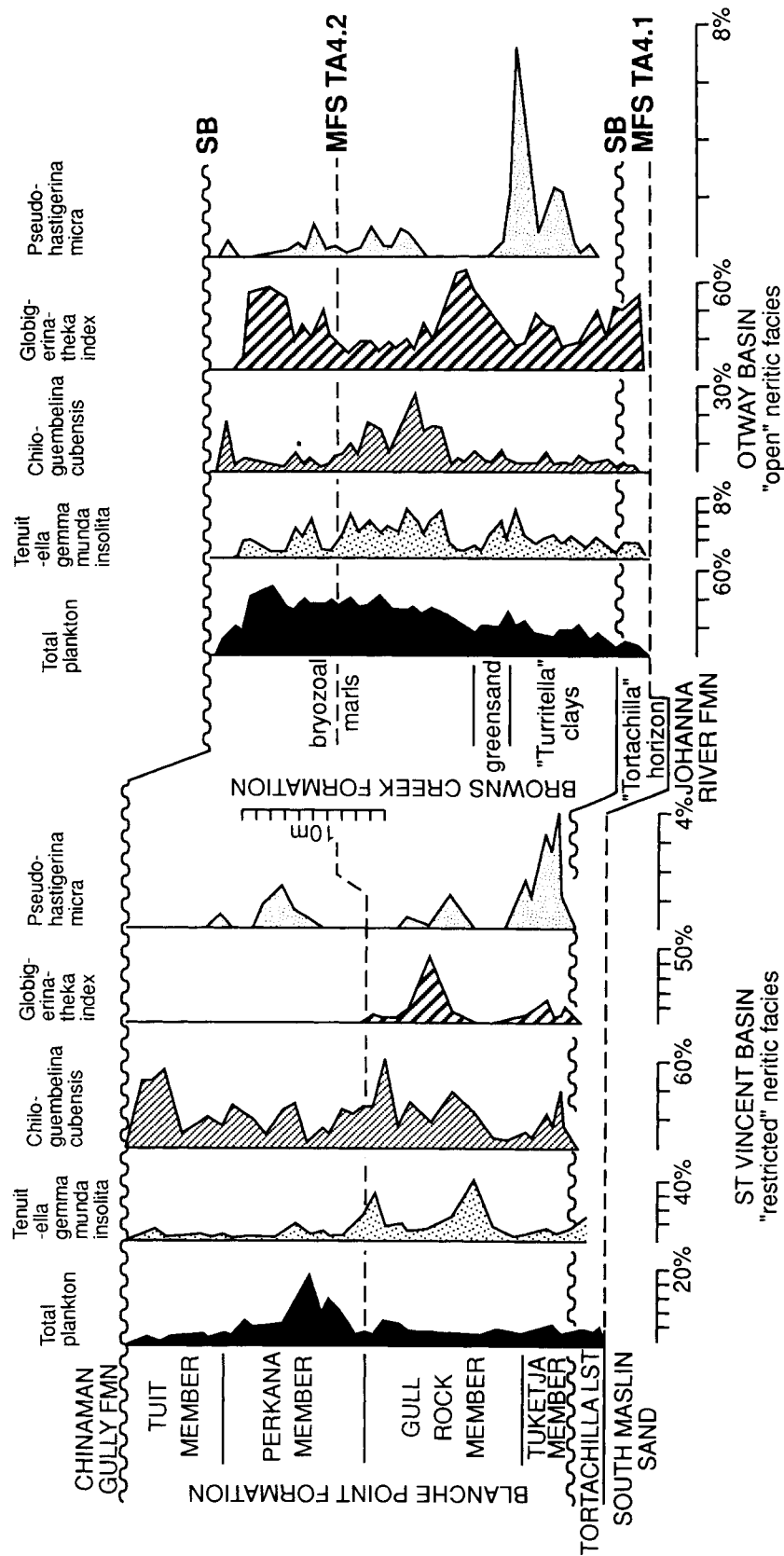
## DISCUSSION AND CONCLUSION

It has been suggested that the evolutionary recovery of planktonic foraminifera after the Cretaceous/Palaeogene

boundary event was due to the re-establishment of temperate to warm climate and a new ecosystem in the water column of the global ocean in the earliest Palaeocene. The evidence for that conclusion is rapid colonization and speciation at all latitudes (Boersma & Premoli Silva, 1991). The most conspicuous evolutionary response is the diversification among the triserial guembeliniids and biserial chiloguembelinids (Boersma & Premoli Silva, 1989). Although they did not attain the levels of the chiloguembelinids, species of *Parvularugoglobigerina* commonly constituted 20–50% of the total fauna. Predominating in mid-latitudes and upwelling regions, the parvularugoglobigerines may have been opportunists seeking nutrient-rich waters in the earliest Palaeocene (Boersma & Premoli Silva, 1991). The small maximum test size and the typical elongate aperture might relate to rapid reproduction and large populations with a range of phenotypes. Eutrophic to highly eutrophic conditions, as depicted by Hallock *et al.* (1991), are commonly occupied by r-mode opportunists which in this case included the chiloguembelinids and globigerinids. Because opportunistic species can inhabit a broad range of conditions and respond to physical instability they are usually long-lived, in the mode of generalists. Unlike opportunists, however, parvularugoglobigerines occurred only in the earliest Palaeocene for a time span of about half a million years, indicating that they speciated as eutrophic colonizers (Table 1). A record of rare *P. eugubina* in some early Palaeocene sections, such as the Brazos River Section in Texas (Keller, 1989), may indicate a relatively warm, nutrient-poor environment there, unless it had been obscured by hiatuses (Montgomery *et al.*, 1992).

We can use the ecological notions of r- and K-selection related to the trophic resource continuum (TRC) in the photic zone (Hallock *et al.*, 1991; Boersma & Premoli Silva, 1991) and relate the fluctuating fortunes of neritic and planktonic communities to the palaeoceanographic events of the Palaeogene at geological, not ecological, time scales. Perhaps reduced oceanic mixing enhances a tendency toward stratification, both oligotrophy and eutrophy at the respective extremes of the TRC and niche specialization, whereas cooling stimulates mixing and promotes opportunism. In broad terms, the diverse communities in K-mode develop in the latest Cretaceous, late Palaeocene–early Eocene, and middle to late Eocene. Following the perturbations at the Cretaceous/Palaeogene, early/middle Eocene and Eocene/Oligocene boundaries respectively, we find survivors or opportunists (see also McGowran, 1991, McGowran *et al.*, 1992).

Populations of *Praetenuitella* occurred most commonly within the late Eocene which broadly was a time of partial restoration of K-mode communities following the Khirthar transgression (shown on Fig. 6). But the sum of evidence suggests high productivity at the actual times of common *Praetenuitella*, as discussed above. This may well be due to a pronounced leakage of nutrients into what becomes the silica window at one end of an expanded TRC, still at a time of general warmth (at least at the surface, although bottom waters never warmed greatly again after the global cooling in the early middle Eocene). A cooling spike is shown in



**Fig. 5.** Profiles of relative abundance, selected planktonic taxa and groups, late Eocene neritic facies, southern Australia (adapted from McGowan, 1987). SB, sequence boundary; MFS, maximum flooding surface for third-order cycles TA4.2 and 4.2 (4.3 has been truncated by erosion). Note how 'Tenuitella spp.' - mostly *Tenuitella insolita* - together with *Chiloguembelina* and *Pseudohastigerina* alternates with *Globigerinatheka*.

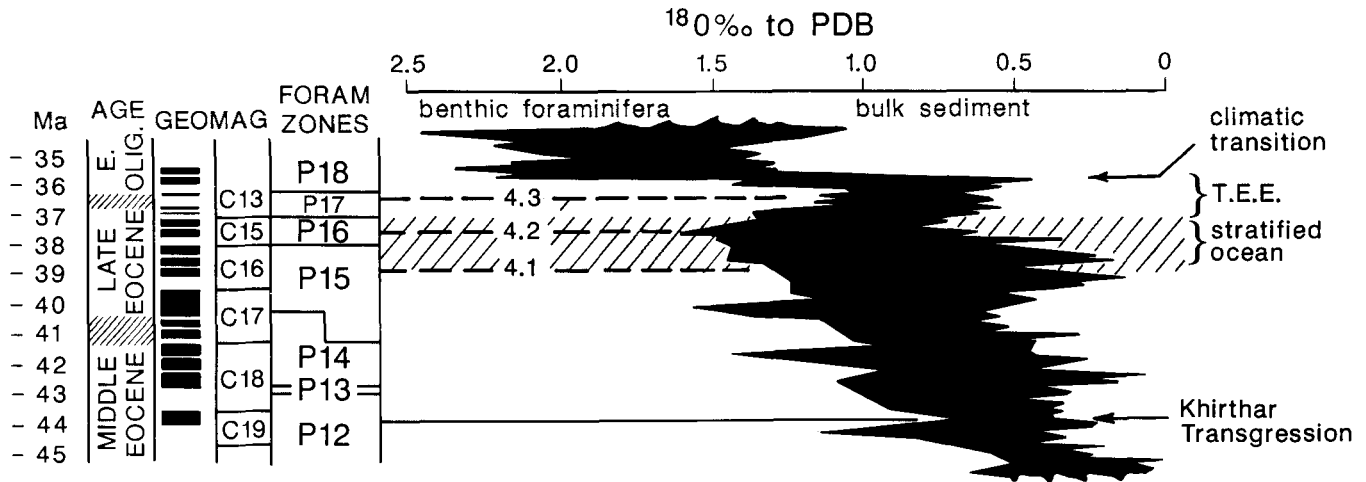


Fig. 6. A Late Eocene scenario, from McGowran (1987, 1989). Time scales, third-order sequences and Shackleton's (1986) isotopic curves, correlated using the Berggren *et al.* (1985) scales. Wilson Bluff to Aldinga: marine transgressions in southern Australia; Wilson Bluff is but part of the Indo-Pacific Khirthar transgression. It is suggested that the Khirthar transgression and the great cooling in the earliest Oligocene bound the partial restoration of a stratified ocean. Within that time span there is the narrow 'silica window' based on the occurrence of the Fundo Desbarracando, Blanche Point and Oamaru siliceous deposits. Note that the neritic-oceanic silica window spans the neritic record of common 'Tenuitella spp.' (mostly *Praetenuitella isolita*) in Fig. 5.

Fig. 6 in Zone P16, although it is premature to take correlations at this resolution too seriously in the late Eocene. At present we cannot say whether that event was the stimulus for high productivity or its very opposite, the preceding warming at the Tuketja transgression. The most recent evidence for that comes from the deep sea in the Southern Ocean (Miller, 1992).

The essential point here is not the mechanism but the association of test morphology and facies.

The similar wall in *Parvularugoglobigerina* and *Praetenuitella* may reflect similar conditions where slightly corrosive waters are prevailing because, like modern high-latitude forms such as *Neogloboquadrina pachyderma* and *Tenuitellinata uvula* (Hemleben *et al.*, 1989), they show a similar pattern in the test morphology, the test became smooth and the porosity decreased. But physiochemical variables were balanced and dissolution was rare. The small, delicate test would otherwise have been dissolved and the variation of various morphotypes eliminated. The growth of calcite crystals on the test wall of *P. eugubina*, according to Olsson *et al.* (1992), is evidence that the species might be well resistant to dissolution.

The subsequent oceanographic developments in both the Palaeocene and the latest Eocene to early Oligocene may have generated and enhanced competition between the new and surviving species. Warming in the early Palaeocene gave oligotrophic forms, such as the subbotinids and acarininid-morozovellids, opportunities to diversify, whilst forcing *Parvularugoglobigerina* to extinction in Zone P1. By contrast, the pronounced cooling with steepening thermal gradients close to the Eocene-Oligocene boundary stimulated the replacement of *Praetenuitella* by the typical tenuitellids (Li, 1991). Unlike their Palaeocene counterparts which left no distinct morphotypes, *Praetenuitella* spp. were able to change to *Tenuitella gemma* (Jenkins) and related

forms with a pustulate wall and a low aperture in the earliest Oligocene. Some of their descendants, including *Tenuitellinata juvenilis* (Bolli) and *Globigerinita glutinata* (Egger) show typical characters of opportunists: little morphological variability and long ranges (Table 1).

In summary, *Parvularugoglobigerina* and *Praetenuitella* are unique in possessing a microperforate, smooth test with an elongate aperture. There are variations, particularly in the details of the microperforate wall texture and the trochospiral coiling. Morphotypes of *Parvularugoglobigerina* exhibit a wall sometimes with pore-mounds and a coiling mode from high to low, while *Praetenuitella* spp. are constantly smooth and rather low trochospiral. Their respective radiations coincided with two short but significant

characters	opportunists	eutrophic indices	eutrophic colonizers
test size	small-medium	small	small
population	small to larger	larger	larger
reproduction	rapid	rapid	rapid
morphological variability	low-high	low	high
aperture	short/low	long	long
surface	pustulate	smooth-pustulate	pustulate
distribution	cosmopolitan	temperate belts	cosmopolitan
life strategy	radiation/little evolution	evolution	radiation
life span	longest lived	longer lived	short lived
example	<i>T. juvenilis</i> , <i>G. glutinata</i> (Oligocene-Recent)	<i>P. insolita</i> (late Eocene)	<i>P. eugubina</i> (earliest Palaeocene)

Table 1. Microperforate species differentiated by habitat preferences.

events in the Cenozoic: the initial return of a normal planktonic ecosystem in the earliest Palaeocene and the climatic fluctuations in the late Eocene. We suggest by morphological pattern analogy, in our ignorance of morphological function, that these forms reflect similar habitat in their similar form and especially in their aperture. The mechanism producing their peculiar morphology may lie in a similar life style in nutrient-rich, oxygen-poor upper waters. This study thus partially supports the suggestion of Banner & Desai (1988) that all microperforate, non-spinose and non-muricate globigerines preferred such eutrophic conditions where the particle-size of the seston was smallest.

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#### APPENDIX A. TAXONOMIC NOTES ON PARVULARUGLOBIGERINA AND RELATED TAXA

Apart from the four morphotypes of *Parvularugoglobigerina* – *P. eugubina*, *P. fodina*, *P. perexigua* and *P. alticonusa* – several taxa which commonly occur together with or have been referred to as having affinities with the parvularugoglobigerines are discussed here.

*alticonusa*, *Parvularugoglobigerina* n. sp. Pl. 2, figs 8–10. This species is proposed for the high-spined parvularugoglobigerines that have been identified as *Globigerina minutula* by Smit (1982), as *Globoconusa conusa* by Keller (1988), as *Globoconusa minutula* by Brinkhuis & Zachariasse (1988), and as *Parvularugoglobigerina* morphotype 1 by D'Hondt & Keller (1991). It is, however, not identical to *Globigerina minutula* Luterbacher & Premoli Silva which typically bears a weakly cancellate wall and represents an ancestral form of *Subbotina triloculinoidea* (Boersma & Premoli Silva, 1983; Premoli Silva, 1990, pers. comm.). Neither is it *Globoconusa conusa* Khalilov, which is heavily pustulate and has affinity with *Globoconusa daubjergensis* Brönnimann (Hansen, 1970; Stainforth *et al.*, 1975; Toumarkine & Luterbacher, 1985). On the other hand, *P. alticonusa* may represent the early and high trochospiral morphotype from which all other species of *Parvularugoglobigerina* developed.

*edita*, *Globigerina Subbotina*, 1953. Brinkhuis & Zachariasse (1988) assigned some medium-spined microperforate forms to *Globigerina edita*. Although showing transitional morphology between *P. alticonusa* and *P. eugubina*, the specimens illustrated by these authors may not truly represent Subbotina's species. With a mean size of 250  $\mu\text{m}$ , the type of *G. edita* is almost twice as large as the specimens

assigned to it by these authors. In his work, Blow (1979) did not recognize this species in any small-sized groups but regarded it as a large-sized *Eoglobigerina*. Blow also described a subspecies *E. edita praedita*, and both *edita* and *praedita* are distinctly cancellate. Olsson *et al.* (1992) clarify the matter by confirming that *edita* is a cancellate *Eoglobigerina*.

*eugubina*, *Globigerina* Luterbacher & Premoli Silva, 1964. Pl. 1, figs 1–11. This form is characterized by a slightly to strongly flattened test commonly with 5 or more chambers in the final whorl. The test size, commonly <150  $\mu\text{m}$ , is variable, as forms as large as 220  $\mu\text{m}$  have been measured (Olsson, 1992, pers. comm.). Chambers are subtriangular to oval in strongly compressed tests but become subglobular to globular in tests with increasing spire height. The aperture is constantly elongate, with or without a thin lip. Smit (1982) first clarified the species concept of *P. eugubina* but retained it in the genus *Globigerina*. The typically mounded to microperforate wall, however, indicates that it is not a *Globigerina*. The specimens with heavy pustules as drawn by Hofker (1978) might have been mistaken for those with overgrowth of calcite due to dissolution when viewed with light microscopes. The massive calcite crystals are now interpreted by Olsson *et al.* (1992) to signal its dissolution-resistant capacity. In contrast to these views, Canudo *et al.* (1991) used *longiapertura* for those compressed morphotypes.

*extensa*, *Globigerina* Blow, 1979. Similar to *Parvularugoglobigerina* spp. in having a smooth, microperforate wall and an elongate aperture, this taxon may represent a morphotype of this group. Its medium-high trochospiral test and the oblique extraumbilical aperture explicitly show transitional features between those in *P. alticonusa* and *P. eugubina* (see Pls. 1–2). It is thus considered to be an intermediate form between the latter two.

*fodina*, *Eoglobigerina* Blow, 1979. Pl. 2, figs 6, 7. This is a rare but typically smooth-walled morphotype of *Parvularugoglobigerina*. Unlike *P. eugubina*, *P. fodina* has a medium-high trochospire with an aperture which is almost circular on the umbilical side. Chambers are inflated or globular, with 3–4 constituting the final whorl. Bordered with a thin lip, its circular aperture represents an extreme variation to the *Globigerina bulloides*-type morphology. As *Globobastica* Blow possesses a densely pustulate wall and is probably a junior synonym of *Globoconusa* Khalilov (Li, 1991), it should not embrace this smooth-walled species, as suggested by Canudo *et al.* (1991).

*fringa*, *Globigerina* Subbotina, 1953. Stainforth *et al.* (1975), Smit (1982) and Berggren (1992) all considered *Globigerina fringa* to be densely perforate to weakly cancellate, so that *G. fringa* should be considered as typical *Eoglobigerina* and probably synonymous with *E. eobulloides*, as in Stainforth *et al.* (1975) and Toumarkine & Luterbacher (1985). Material from Russia did show *G. fringa* to be cancellate (Olsson, 1992, pers. comm.). For this reason, any proposals that *G. fringa* might be a parvularugoglobigerine could not be upheld, and all the previous records of *P. fringa* by authors should be

considered to represent those of the new species *P. perexigua*.

*hariana*, *Postrugoglobigerina* Salaj, 1986 (*vide* Loeblich & Tappan, 1988). This is a trochospiral form with pore-mounds found in the lowermost Palaeocene of Tunisia. The overall morphology overlaps with that observed in some *Parvularugoglobigerina eugubina* and *P. fringa*. It appears to us that the type specimens of this taxon probably represent an immediate descendant from *Guembelitra*.

*hillebrandti*, *Globigerina* Orue-Etxebarria, 1985. The medioperforate to weakly cancellate wall in this taxon is similar, if not identical, to that in *Globigerina fringa* of Stainforth *et al.* (1975) and Smit (1982), although its chamber enlargement in the final whorl is slow. Whether *G. hillebrandti* and *G. fringa* of authors represents a single species is not clear, but the cancellate wall suggests that *G. hillebrandti* belongs to neither *Globigerina* nor *Parvularugoglobigerina*, but to *Eoglobigerina*.

*longiapertura*, *Globorotalia (Turborotalia)* Blow, 1979. This work follows the conventional view that this species is a junior synonym of *P. eugubina* (Smit, 1982; Li & Radford, 1991; Olsson *et al.*, 1992). By contrast, Canudo *et al.* (1991) recognized this species for forms with a compressed, multichambered test and a narrow elongate aperture, some extreme variants of *P. eugubina* (above). Further work is necessary to resolve this.

*minutula*, *Globigerina* Luterbacher & Premoli Silva, 1964. According to Krasheninnikov & Hoskins (1973) and Boersma & Premoli Silva (1983), this is a weakly cancellate form having affinity with *Subbotina triloculinoides*, although Stainforth *et al.* (1975) regarded it as a junior synonym of *Globigerina fringa*. In contrast, Smit (1982) illustrated a smooth, microperforate form as representing this taxon. Smit's species concept was followed by Brinkhuis & Zachariasse (1988) but as *Globoconusa minutula*. This study, however, identifies all high trochospiral forms with a smooth and microperforate wall as *P. alticonusa* (see below), for the same reason as indicated by Premoli Silva (1990, pers. comm.), that typical *minutula* represents an early *Subbotina* because it bears a weakly cancellate wall.

*perexigua*, *Parvularugoglobigerina* n. sp. Pl. 2, figs 1–5. This is a tiny form (about 80  $\mu$ m) with only 4 chambers in the last whorl but possessing a microperforate, smooth wall as in the majority of *P. eugubina*. Otherwise it is similar to equally small but weakly cancellate *Eoglobigerina fringa* (*Subbotina*). As *E. fringa* is not a parvularugoglobigerine, this species is proposed to include those described previously under *P. fringa* in Brinkhuis & Zachariasse (1988) and Li & Radford (1991), among others. The concept of *Parvularugoglobigerina* morphotype 2 of D'Hondt & Keller (1991) falls within this new species. See systematic description below.

#### SYSTEMATICS

Genus *Parvularugoglobigerina* Hofker, 1978

(Type species: *Globigerina eugubina* Luterbacher & Premoli Silva, 1964)

*Parvularugoglobigerina alticonusa* sp. nov.

(Pl. 2, figs 8–10)

**Holotype.** DSDP Hole 152, Caribbean. Sample 152-10-1, 140–143 cm, *P. eugubina* Zone. Pl. 2, fig. 9.

**Description.** Test small, high trochospiral, chambers subglobular, four in the final whorl, wall smooth to weakly pustulate, early part sometimes with pore mounds, aperture elongate, extending obliquely from the base of last chamber near the umbilicus to the apertural face, with a distinct lip.

**Remarks.** This species is proposed to include forms described by authors as *Globigerina minutula* (Luterbacher & Premoli Silva) which, however, is a medium-spined, cancellate form. See above for notes on these two species.

*Parvularugoglobigerina perexigua* sp. nov.

(Pl. 2, figs 1–5)

**Holotype.** DSDP Hole 152, Caribbean. Sample 152-10-1, 140–143 cm, *P. eugubina* Zone. Pl. 2, figs 1–3.

**Description.** Test small, about 80  $\mu$ m, low trochospiral, chamber subglobular, increasing rapidly, four chambers in the final whorl, wall smooth to weakly pustulate, rarely with pore mounds, aperture elongate, extraumbilical-peripheral, or extending to the upper part of the apertural face, with or without a thin lip.

**Remarks.** This species is proposed to include forms which have been widely misidentified as *Globigerina fringa* by several workers. Studies of Russian material by the Palaeogene Planktonic Foraminiferal Working Group, however, indicate that *G. fringa* belongs to the cancellate group (Olsson, 1992, pers. comm.) and should be considered a species of *Eoglobigerina* (Berggren, 1992). See above for notes on these two species.

#### APPENDIX B. TAXONOMIC NOTES ON

##### *PRÆTENUITELLA* spp.

*impariapertura*, *Praetenuitella* Li, 1987. Although the apertures in both *impariapertura* and *insolita* (below) are similarly high and peripheral to extraumbilical, this taxon can be distinguished from the latter by its rather high elliptical test outline, concave dorsal side and a wide umbilicus. It appears to be a low latitude representative of that genus.

*insolita*, *Globorotalia* Jenkins, 1966. Pl. 3, figs 1–12; Pl. 4, figs 7–9. This species is characterized by a smooth wall and a highly arched aperture. It differs from *P. impariapertura* by its almost circular test outline, a convex dorsal side and a narrow umbilicus. It has been recorded in the late Eocene of New Zealand (Jenkins, 1966), equatorial Pacific (Jenkins & Orr, 1972, DSDP Hole 77), East Pacific (Quilty, 1976, DSDP Hole 321), Tasman Sea (Jenkins & Srinivasan, 1985, DSDP Hole 592), southern Australia (Lindsay, 1985; McGowran, 1987), Japan (Kaiho, 1984), Washington State (Jenkins & Srinivasan, 1985), southern Atlantic Ocean (Nocchi *et al.*, 1991, ODP Hole 703), and southern Indian Ocean (Li *et al.*, 1992).

*patefecta*, *Praetenuitella* Li, 1987. Pl. 4, figs 1–4. Similar to *P. impariapertura*, this taxon has a high elliptical test outline with more than 5 chambers in the final whorl, a flat dorsal side and a wide umbilicus, but can be identified by its more distinct trochospiral coiling with a flat spiral side and an

aperture being peripheral–extraumbilical–umbilical, rather than only peripheral-(short) extraumbilical.

*praegemma*, *Praetenuitella* Li, 1987. Pl. 4, figs 10, 11. This form is recognized by its four- or five-chambered, biconvex test and an extraumbilical aperture. It differs from the immediate early Oligocene descendant *Tenuitella gemma* (Jenkins) in having a smooth to weakly pustulate (rather than heavily pustulate) microperforate wall.

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