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# Stability and change in Tethyan planktic foraminifera across the Paleocene–Eocene transition

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## Abstract

Examination of planktic foraminifera in the Tethys basin during the Paleocene–Eocene transition reveals two stasis intervals that are separated by a major saltation event coincident with the P–E short-term perturbation in global climate and oceanography. Changes occurred at many spatial and temporal scales as well as many taxonomic and ecologic hierarchical levels, though with various rates and magnitudes. The stasis intervals are marked by slow changes at the species level and account for 50% of the observed first and last appearances during a 2.5 Myr interval. The saltation event is marked by rapid changes at the species and morpho-guild levels and accounts for the remaining 50% of first and last appearances during an interval of about 100–200 kyr. Despite these changes, many taxonomic and ecologic units, such as the depth assemblages and genera, and faunal parameters, such as species richness and turnover rates, are stable with respect to the P–E perturbation. This coexistence of change and stability marks the crisis of Tethyan planktic foraminifera across the P–E transition and reveals the possible dynamics of ecological evolution. © 1998 Elsevier Science B.V. All rights reserved.

*Keywords:* foraminifera; Paleocene; Eocene; Tethys; population dynamics; stability; change

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## 1. Introduction

Whether ecological communities are associations of interdependent and coevolving species, or merely a collection of species that happen to inhabit the same environment has been a central issue since the early 1900 (Clements, 1916; Gleason, 1926). Recent studies of fossil records have extended this debate to a new level. By examining the Paleozoic benthic communities in the Appalachian region, Boucot (1983) and Brett and Baird (1995) observed that the main features of communities, including richness, diversity, guild structure and species composition,

persist with relatively little change for several million years. These ‘coordinated stasis’ intervals are disrupted by brief (<100 kyr), but significant periods of reorganization, usually associated with climatic changes, sea-level fluctuations, or other environmental crises (Brett and Baird, 1995). Once the reorganization is completed, communities are back to their equilibrium states. This pattern of alternation between long stasis and brief saltation leads to the view that stability is the internal feature of ecological communities and, thus takes the central stage in the community evolution (see also Boucot, 1990a,b; Brett et al., 1990).

Other fossil records, however, promote a different view. By examining the Cenozoic benthic communities, Valentine and Jablonski (1993) and Buzas and

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Culver (1994) observed that changes exist throughout the fossil records. It appears that removal, addition, and substitution of species is natural and common in benthic communities, whether their environment is steady or fluctuating. Therefore, change rather than stability is the normal lot of communities over ecological as well as evolutionary time (Valentine and Jablonski, 1993). These different views on the nature of ecological communities are directly linked to the early debate where those arguing for tightly integrated communities see stability, whereas those arguing for loosely integrated communities see change (Boucot, 1990a,b; Valentine and Jablonski, 1993; Buzas and Culver, 1994; Jackson, 1994; DiMichele, 1994; Brett and Baird, 1995).

Microplankton have long been excluded from this debate because of their unique ecological characteristics (Lipps, 1970; Lazarus, 1983). Marine microplankton are commonly considered so sensitive to changes in ambient waters that they form essentially a passive component of the water environment. Many ecologists, therefore, prefer to study marine microplankton within the concept of ecosystems in which they are characterized as biomass, rather than communities in which they appear naturally as species and individuals. This passive view of marine microplankton was recently questioned by studies of planktic foraminifera across the Paleocene–Eocene transition which suggest that there is no consistent correlation between the nature and tempo of faunal turnovers and major changes in climate and oceanography (Lu and Keller, 1995b).

The Paleocene–Eocene (P–E) transition provides a unique test case to examine the ecologic structure and nature of planktic foraminifera because of the characteristic short-term changes in global climate and oceanography. The long-term changes in the oceanic environment across the P–E transition are marked by a warming trend and a gradual decrease in carbonate  $\delta^{13}\text{C}$  values (Shackleton, 1986). Superimposed on this long-term trend is a short-term event marked by a 6–8°C warming in the deep ocean and high-latitude surface ocean and a global negative excursion in carbonate  $\delta^{13}\text{C}$  values (Kennett and Stott, 1991; Stott, 1992; Lu and Keller, 1993; Canudo et al., 1995; Lu et al., 1996; Pardo et al., 1997). During this global change, ecosystems underwent significant reorganization that included a mass

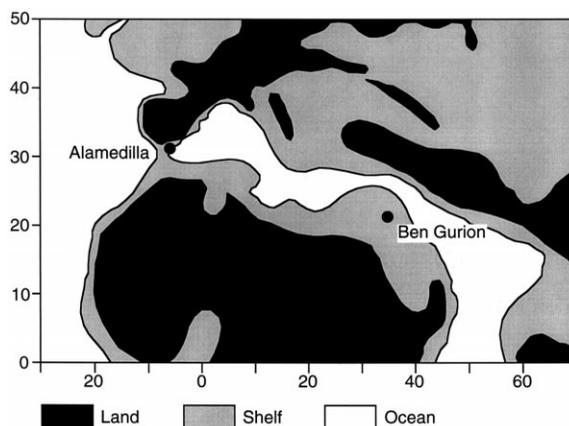


Fig. 1. Paleogeographic map of the Tethys during the Paleocene–Eocene transition with the localities of the *Ben Gurion* section in the Negev of Israel and the *Alamedilla* section of southern Spain.

extinction in benthic foraminifera, speciation in land mammals, and proliferation of thermophilic species in marine plankton and terrestrial plants (Gingerich, 1986; Wing et al., 1991; Thomas, 1990; Lu and Keller, 1993). After the short-term perturbation, major environmental parameters were restored to their previous states, rather than shifting to new states. In this study we examine the planktic foraminiferal turnover across the P–E transition in the western and eastern Tethys (Fig. 1) and probe the stability of these marine microplankton communities with respect to major global environmental changes.

## 2. Long-term speciation patterns

To place the P–E planktic foraminiferal turnover in the Tethys into perspective, it is necessary to discuss the long-term patterns in the open ocean. In a previous study, Lu and Keller (1995b) show that in the tropical–subtropical Pacific planktic foraminifera (DSDP Site 577), changes at the species level occurred throughout a 12 Myr interval spanning the Late Paleocene to Early Eocene. However, the rates and magnitudes of these changes varied dramatically and hence differentiate stasis intervals from saltation events. Species richness and species turnover rates show stasis intervals characterized by: (1) low species turnover rates (0.6–1.8 species/100 kyr); (2) relatively constant species richness (vari-

ation of  $\pm 1.4$ – $3.3$  species); and (3) long durations (2.56–5.21 Myr). Separating long-term stasis intervals are short-term saltation events, as marked by: (1) high species turnover rates (4–12 species/100 kyr); (2) major replacement of species (49–56%) and populations (49–78%); and (3) short durations (200–400 kyr). These stasis and saltation intervals reveal the first order pattern of the ecological evolution of the tropical–subtropical planktic foraminifera during the Late Paleocene to Early Eocene. Such a pattern is similar to the community evolution model by Brett et al. (1990) and Brett and Baird (1995).

Stasis intervals are also distinguished from saltation events in the relationships among species and between the fauna and its environment. For the relationship among species, the stasis intervals emphasize dynamic equilibria. Changes at the species level were observed throughout stasis intervals. However, because these changes occurred slowly and in most cases randomly, species richness and diversity remain largely steady. Species were more likely to show individualistic features during stasis intervals than during saltation events. For instance, during stasis intervals, changes in one species usually had little impact on other species (Lu and Keller, 1995b). Moreover, a preliminary study suggests that species in stasis intervals are more readily separated by their shell  $\delta^{13}\text{C}$  signals — a measure of physiological diversity — than during saltation events (Lu and Keller, 1996).

For the relationship between fauna and environment, the stasis intervals emphasize biotic stability. During the Paleocene–Eocene stasis intervals, the oceanic environment changed gradually, including water temperature, ocean chemistry and, possibly, surface wind intensity (Lu and Keller, 1995b). However, species richness and species turnover rates of planktic foraminifera remained steady. This faunal stability at times of environmental change suggests an active environment–biota interaction.

It is not surprising though that planktic foraminiferal faunas are stable during intervals of little or only gradual environmental changes. A more vigorous test of faunal stability occurs during major environmental changes, such as the P–E global change which induced a major saltation event (Zones P5–P6a). In the tropical–subtropical Pacific, the P–E event has a mean turnover rate of 12 species/kyr, a major increase

in species richness and results in the replacement of 53% of the species and 49% of the population over an interval of about 100–200 kyr as shown by Lu and Keller (1995b) for the equatorial Pacific Site 577. In this study, we show that planktic foraminiferal faunas retain a strong community organization and relative stability during the major global changes across the P–E event throughout the Tethys region.

### 3. Materials and methods

Sedimentary samples spanning 2.5 Myr across the P–E transition were collected from the Alamedilla section in southern Spain and the Ben Gurion section in Israel (Fig. 1). The Alamedilla section is located near the village of Alamedilla in the Province of Granada, Spain, and is geologically in the Subbetic Zone (Betic Cordillera). Several hundred meters of Paleocene through Eocene marls, shales and clays are exposed along a valley (Fig. 2a). About 30 m of this section spanning planktic foraminiferal zones P5–P7, or about 2.5 Myr, were sampled at 35 cm intervals (about 30 kyr) as shown in Fig. 3b. Closely spaced samples at 5 cm intervals were collected across the 2 m thick clay interval that represents the global change across the P–E transition (Fig. 2b). Benthic foraminiferal analysis indicates that the paleodepth of deposition was 1000–2000 m for the Alamedilla basin (Ortiz, unpubl. data). Stable isotopic and mineralogical analyses of this section were published in Lu et al., 1996, 1998). A biostratigraphic and planktic foraminiferal quantitative study was published by Arenillas and Molina (1996) and will be discussed below. The current study documents the planktic foraminiferal turnover with special emphasis on intervals of stability and rapid change.

The Ben Gurion section is located near the town of Sde Boqer in the Negev. Paleocene and Eocene sediments are well exposed on the upper part of a hillside that spans from early Maastrichtian limestones at the base through late Maastrichtian marls, Danian clays and shales to the shales and clays of the Paleocene–Eocene transition (Fig. 3). Samples were collected at 40 cm intervals (about 80 kyr) and additional samples (10 cm spacing) were added for a higher resolution isotopic analysis across the  $\delta^{13}\text{C}$  shift interval. The paleodepth is estimated at 500 m

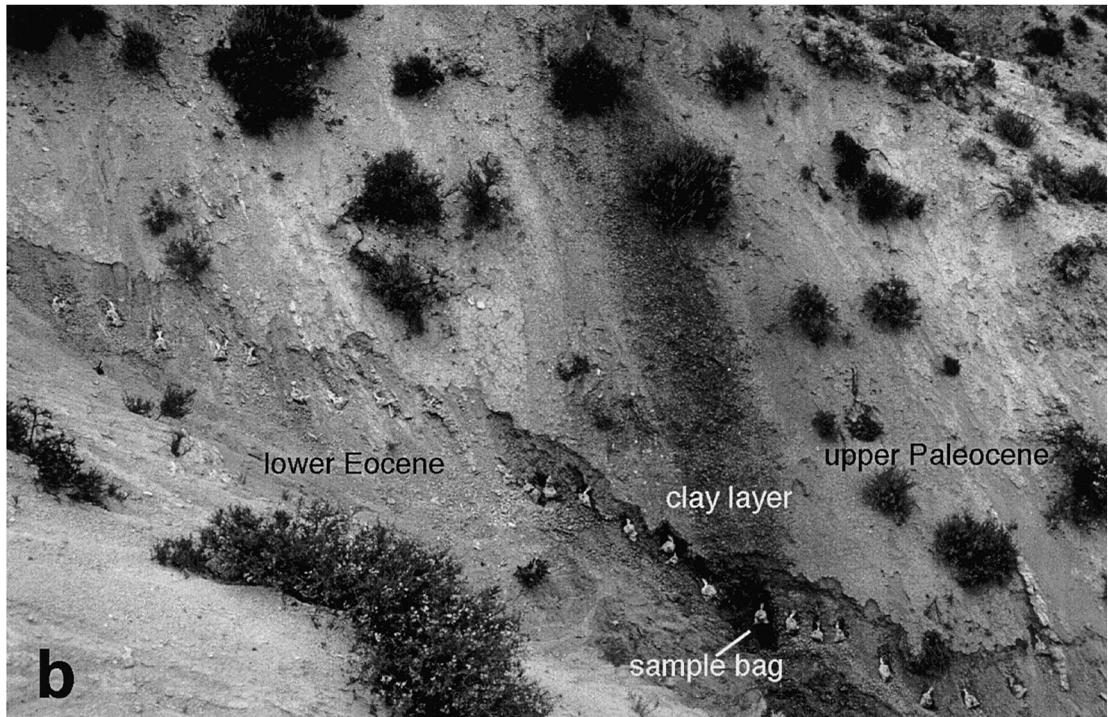




Fig. 3. View of the Ben Gurion Paleocene–Eocene section in the Negev, Israel, trenched for sampling along the ridge with sample bags in position.

(Speijer, 1994) and deposition occurred at the continental margin outside the late Cretaceous–Eocene phosphatogenic zone (Lu et al., 1995; Benjamini and Eisenshtein, 1995). The stable isotope study was published in Lu et al. (1996) and clay mineralogical analysis was done by Bolle et al. (in prep.). The current study concentrates on the planktic foraminiferal turnover.

Samples were processed by standard micropaleontological techniques as outlined in Lu and Keller (1993). First and last appearances, species richness

and relative abundances were based on counts in random sample splits of approximately 300 individuals from the  $>106\ \mu\text{m}$  size fraction. Justification for choosing this sample size and size fraction for low-latitude planktic foraminifera during the P–E interval is given by Buzas (1990) and Lu and Keller (1995a). About 50 planktic foraminiferal species were encountered. Their classification was discussed in Lu and Keller (1995a) for the tropical Pacific and by Arenillas and Molina (1996) for the Alamedilla section and is further discussed in Appendix A. Relative species abundance data from the Alamedilla and Ben Gurion sections are given in Appendix B (Tables B1, B2). Age estimates are based on the benthic foraminiferal extinction, planktic foraminifera datum events and  $\delta^{13}\text{C}$  stratigraphy calibrated to the Geomagnetic Polarity Time Scale by Cande and Kent (1992).

#### 4. Biostratigraphy

The biostratigraphy of the Alamedilla and Ben Gurion sections is based on the revised zonation by Berggren et al. (1995) with Zone P5 modified by Pardo (1998) and Pardo et al. (in press) (Fig. 4). Note that this updated biozonation differs from that in our earlier publications. There are significant differences between this study and that of Arenillas and Molina (1996) which are caused either by their use of different defining criteria for the biozones or by differing taxonomic concepts. The authors have collaborated with Arenillas to determine where species concepts differ in order to explain differences between our studies which were done on substantially the same data set. The results of this collaboration are noted below wherever differences in the biozonation are evident and taxonomic differences are noted for all species in Appendix A along with explanatory notes.

##### 4.1. Zone P4

This zone is defined by the total range of *Planorotalites pseudomenardii* (Berggren et al., 1995) and is

Fig. 2. (a) View of the valley with the exposure of the Alamedilla section, located near the town of Alamedilla. The total outcrop shown spans about 50 m. (b) Close-up view of the exposure of the Alamedilla section. The clay layer spans 2 m. Note the color change from light gray marls to dark (red colored) clay.

TIME (Ma)	POLARITY	CHRON	EPOCH	PLANKTIC FORAMINIFERAL BIOZONATIONS				
				DATUM EVENTS	Pardo, 1998 this study	Berggren et al., 1995	Berggren & Miller, 1988	Arenillas & Molina, 1996
52		C23	EOCENE		P6b	P6b	P6c	M. formosa
53				M. formosa ▲				
					P6a	P6a	P6b	M. subbotinae
54		C24						
				M. velascoensis ▼	P5b			M. velascoensis
				A. africana A. sibaiaensis BFEI ▼ I. laevigata		P5	P6a	
55			PALEOCENE		P5a			I. laevigata
				M. subbotinae L. pseudomenardii ▼			P5	
56		C25						
				M. soldadoensis ▲	P4	P4	P4	P. pseudomenardii
57								
58		C26						

Fig. 4. Comparison of commonly used planktic foraminiferal zonations across the Paleocene/Eocene boundary along with their datum events (after Pardo, 1998; Pardo et al., in press). The magnetostratigraphy and absolute age chronology correlated with planktic foraminiferal datum events are based on studies by Cande and Kent (1992) and Berggren et al. (1995). We have marked the P/E boundary with a stippled pattern since it has not been officially defined.

present in both Ben Gurion and Alamedilla sections where it spans about 4 and 8 m, respectively. Although Arenillas and Molina (1996) use the same species for their P4 equivalent *Luterbacteria pseudomenardii* Zone (synonymous with *Planorotalites pseudomenardii*; Fig. 4) at Alamedilla, their biozone spans only 6.5 m. The 1.5 m difference in the range of this zone is most likely due to the difficulties in separating early morphotypes of *P. pseudomenardii* from *P. troelseni*.

#### 4.2. Zone P5

This concurrent range zone is defined by the last appearance (LA) of *P. pseudomenardii* at the base and the LA of *M. velascoensis* at the top (Berggren et al., 1995). Zone P5 coincides with the *Igorina laevigata* and *Morozovella velascoensis* biozones of Arenillas and Molina (1996) who separate these two zones based on the LA of *I. laevigata*, a species rarely present and difficult to identify unambigu-

ously. For this reason we subdivide Zone P5 into two subzones based on the first occurrence of *Acarinina sibaiaensis* and/or *A. africana*, as proposed by Pardo (1998) and Pardo et al. (in press).

**Subzone P5a.** This subzone is defined by the LA of *P. pseudomenardii* at the base and the first appearance (FA) of *A. sibaiaensis* and/or *A. africana* at the top (Pardo, 1998; Pardo et al., in press). At Alamedilla the range of P5a virtually coincides with that of the *Igorina laevigata* biozone of Arenillas and Molina (1996) because the FA of *A. sibaiaensis* and the LA of *I. laevigata* occur at the same stratigraphic interval (Fig. 4). In the Ben Gurion section the uppermost part of P5a is missing due to a hiatus (Lu et al., 1995; Arenillas, 1996; Schmitz et al., 1996).

**Subzone P5b.** This concurrent range subzone is defined by the FA of *A. sibaiaensis* and/or *A. africana* at the base and the LA of *M. velascoensis* at the top (Pardo, 1998; Pardo et al., in press). The  $\delta^{13}\text{C}$  excursion and the rapid planktic foraminiferal diversification occurs within this subzone. P5b coincides with the *Morozovella velascoensis* Zone of Arenillas and Molina (1996) since their study also uses the LA of *M. velascoensis* datum event. In this study, subzone P5b at Alamedilla spans from 14 to 17 m, but according to Arenillas and Molina (1996) the LA of *M. velascoensis* occurs at 19.55 m. Their longer range is most likely due to different taxonomic concept for transitional morphotypes of *M. velascoensis* and *M. occlusa*, and possibly early specimens of *M. formosa*.

#### 4.3. Zone P6

Zone P6 is defined by the LA of *M. velascoensis* at the base and the FA of *M. aragonensis* at the top (Berggren et al., 1995) and is divided into two subzones.

**Subzone P6a.** Subzone P6a is defined by the LA of *M. velascoensis* at the base and the FA of *M. formosa* at the top (Berggren et al., 1995) and is equivalent to the *Morozovella subbotinae* biozone of Arenillas and Molina (1996) (Fig. 4). At Alamedilla, P6a ranges from 17 to 22 m in this study, and from 19.55 to 27.5 m in Arenillas and Molina's study. As noted above, this difference is due to the use of different taxonomic concepts of transitional morphotypes of *M. velascoensis* and of *M. formosa*. In the Ben Gurion

section the FA of *M. formosa* occurs only 50 cm above the LA of *M. velascoensis* and suggests a hiatus or very condensed subzone P6a.

**Subzone P6b.** This partial range subzone is defined by the FA of *Morozovella formosa* at the base and the FA of *Morozovella aragonensis* at the top (Berggren et al., 1995). At Alamedilla, P6b spans from 22 m to the top of the section and no *M. aragonensis* were observed. Similarly, Arenillas and Molina (1996) did not report *M. aragonensis*. However, both studies report the presence of *Morozovella crater* from the sample 31.0 m (Arenillas and Molina, 1996) and 28.0 m (this study). *Morozovella crater* predates *M. aragonensis* and differs from this morphotype only by its lower number of chambers (4 to 5). It is therefore possible that some of the reported *M. crater* are early morphotypes of *M. aragonensis*. The difference in the observed presence is likely due to the rare occurrence.

### 5. P–E faunal changes in the Tethys

P–E planktic foraminiferal changes in the Tethys can be examined on the basis of geographic, taxonomic and ecologic variations. Geographic variations are illustrated in this study by a comparison between Alamedilla, Spain, and Ben Gurion, Israel. However, variations at different taxonomic and ecologic levels will be discussed only for the Alamedilla section because of its higher resolution sampling as compared with the Ben Gurion section.

#### 5.1. Geographic variations

Ranges of planktic foraminiferal species at the Alamedilla and Ben Gurion sections are shown in Figs. 5 and 6, respectively. Of all the species encountered, 85% appear in both sections and have similar ranges. 10% of the species which appear at only one of the two sections are rare taxa with relative abundances less than 2%. Their absences at one of the two sections may be due to: (1) different environmental conditions; (2) small sample sizes; or (3) errors in identification. The remaining 5% include three taxa of compressed acarininids, e.g. *A. africana*, *A. sabaiaensis* (Plate I, 14–21) and *A. berggreni*. These three taxa are present in

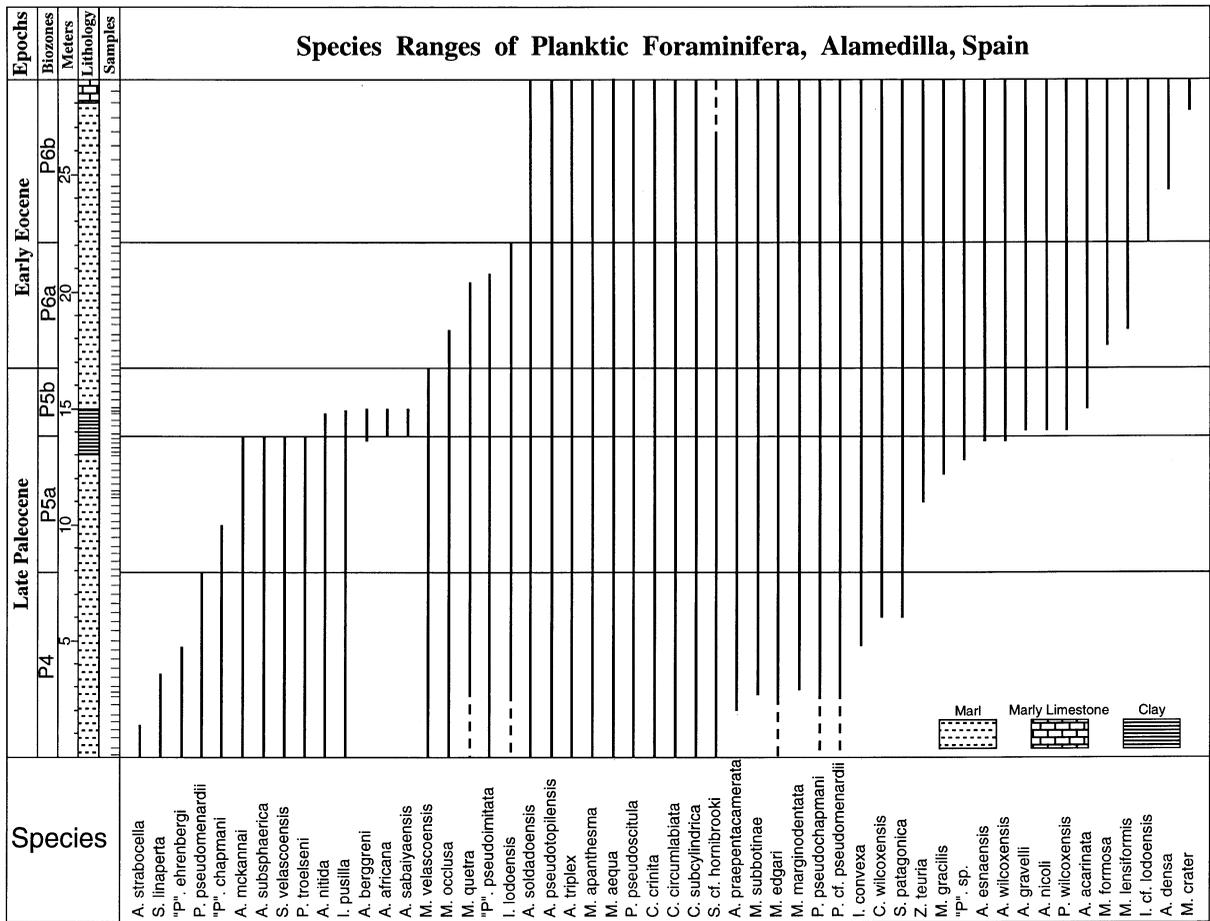


Fig. 5. Species ranges of planktic foraminifera across the P–E transition at Alamedilla, Spain. The presence and short ranges of three compressed acariniid species within the clay layer near the end of the late Paleocene mark the major global crisis within the P–E transition. ‘P’ marks the genus *Planorotalites*.

the Alamedilla section with very short ranges, but we have not found them in the Ben Gurion samples studied. However, these taxa were described from the Esna–Idfu region in Egypt (El-Naggar, 1966), not far from Ben Gurion as well as in the west equatorial Pacific Site 865 (Kelly et al., 1996). Their absence at the Ben Gurion section may suggest a short hiatus, possibly at the lithologic transition between the clay and marl (Fig. 6; Arenillas, 1996; Schmitz et al., 1996).

P–E faunal changes at the Alamedilla and Ben Gurion sections are shown in Figs. 7 and 8, respectively. To facilitate comparison of faunal parameters between these two sections, samples are plotted against time (time scale of Cande and Kent, 1992).

The age model for the Ben Gurion section was developed in Lu et al. (1995) and for the Alamedilla section in Lu et al. (1996) based on correlation of the  $\delta^{13}\text{C}$  shift and biozones (see Lu et al., 1995, 1996 for details). A major difference is apparent in the microfaunal composition of the size fraction ( $>106\ \mu\text{m}$ ). Microfaunas at the Alamedilla section are composed almost exclusively of planktic foraminifera; significant abundances of benthic foraminifera occur only in one sample. The absolute abundance of planktic foraminifera is stable for most of the sampled section, except within a 50 cm interval at the base of the P–E faunal change, where it drops by 2–3 orders of magnitude. In contrast, at the Ben Gurion section, the P–E faunal change is marked by a ma-

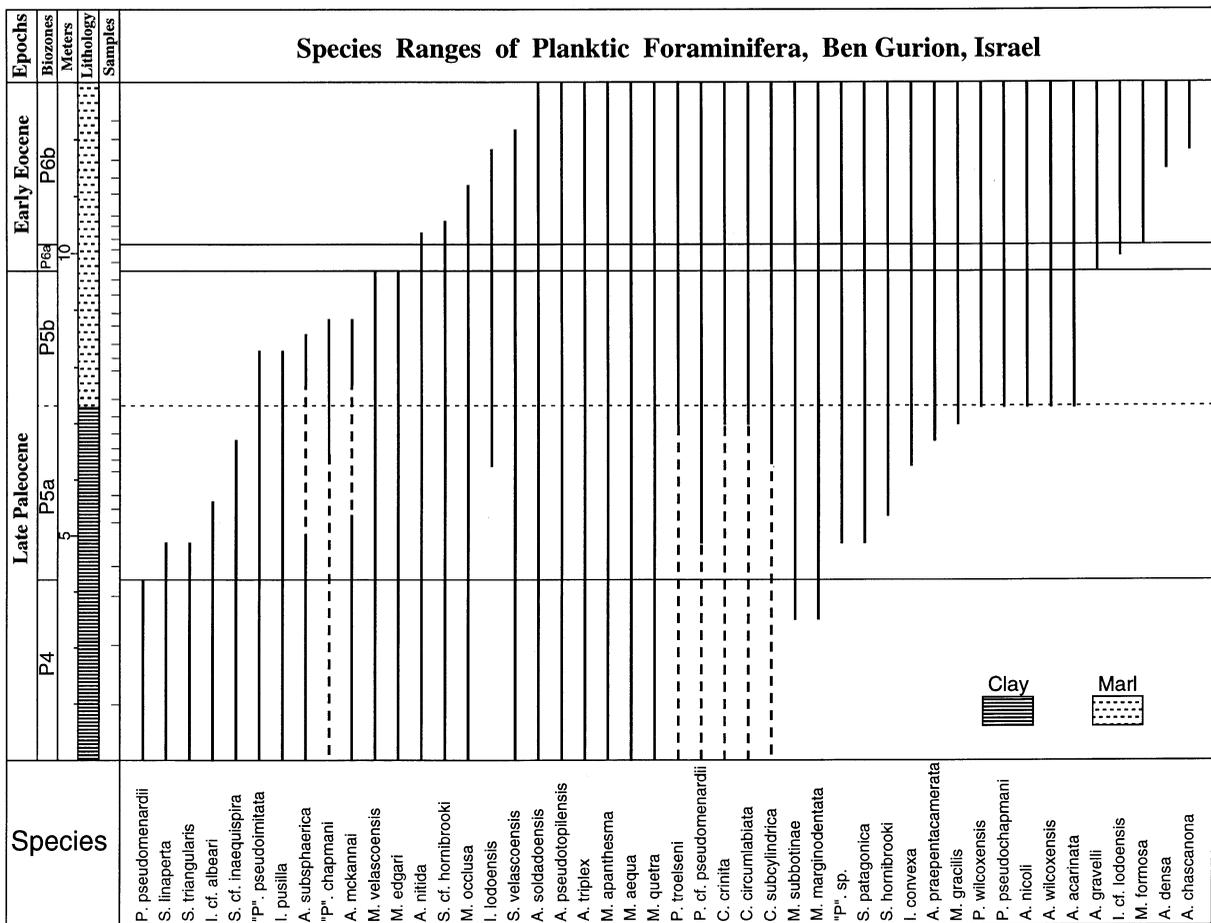


Fig. 6. Species ranges of planktic foraminifera across the P–E transition at the Ben Gurion section in the Negev of Israel. Note that the absence of compressed acarininid species near the end of the late Paleocene in this section may indicate a short hiatus coincident with the global crisis interval. ‘P’ marks the genus *Planorotalites*.

major shift in microfaunal composition (Fig. 8). Below the P–E event, the absolute abundance of microfossils is low. Benthic foraminifera are the dominant component and radiolaria are commonly present. Planktic foraminifera account for only 25%. Above the P–E event, the absolute abundance of microfossils increased by 2–3 orders of magnitude. Planktic foraminifera increased to 90% in relative abundance, while benthic foraminifera decreased to 10% and radiolaria disappeared. Changes in coastal upwelling at Ben Gurion associated with the P–E global warming may be the reason for this change in the microfaunal composition (Lu et al., 1995).

Other faunal parameters show similar patterns of change between the two sections, except that at Ben

Gurion faunal changes appear to occur over a longer time interval. This difference in duration may be real or due to errors in correlation and age calibration. Moreover, the P–E spike in species turnover rates is lower in the Ben Gurion section, though if the turnover rate is adjusted for the absence of the three compressed acarininid taxa (their absence may be due to a short hiatus), a spike similar to the Alamedilla section is present (see dotted line in Fig. 8). Species indices suggest that this turnover occurred rapidly over a period of about 100–200 kyr. The population turnover, however, appears to have occurred slowly through several major steps and varied geographically. The overall results of this turnover for the Tethyan planktic foraminifera is the

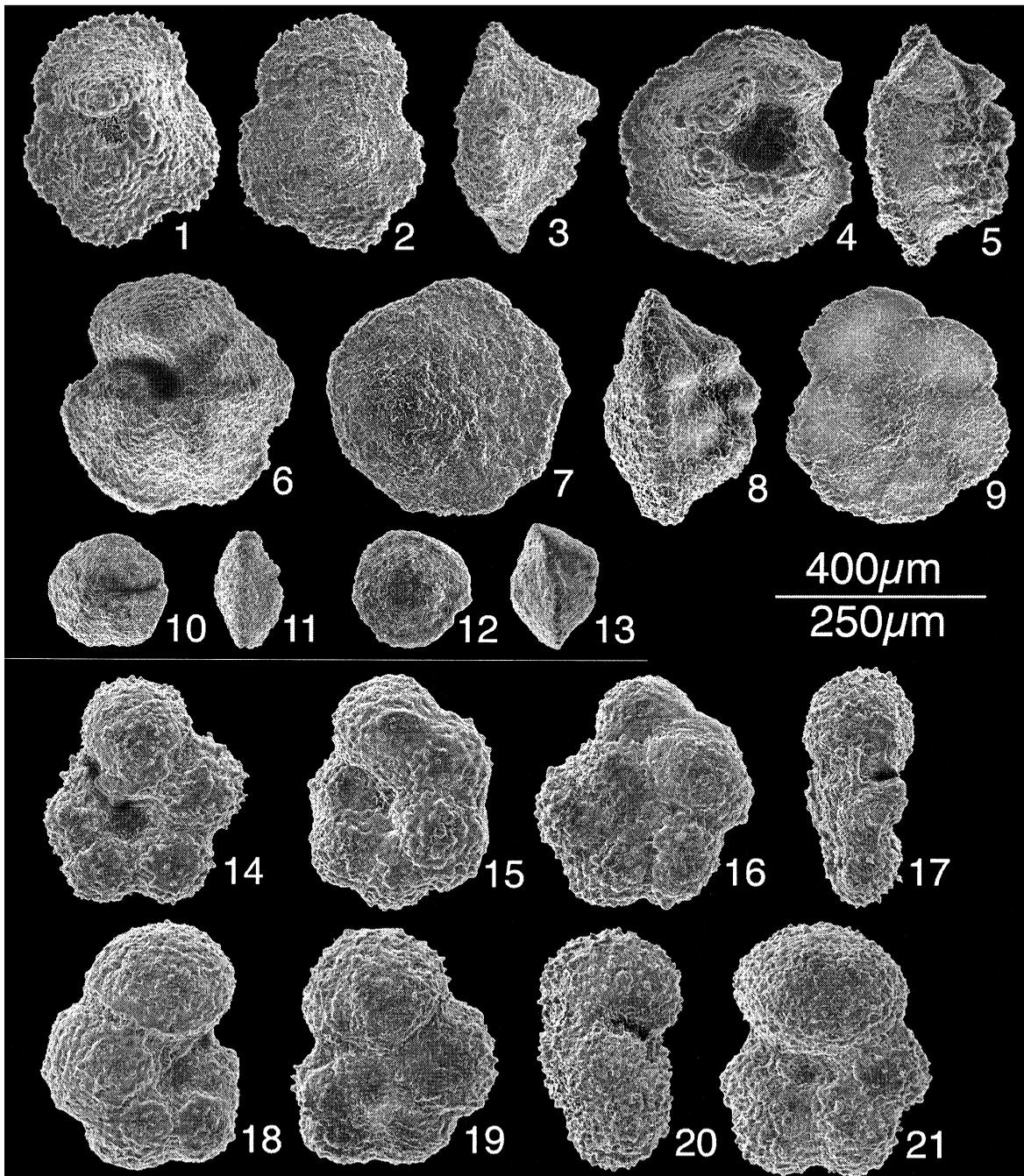


Plate I

Selected Late Paleocene and Early Eocene planktic foraminifera (i.e., morozovellids, igorinids and acarininids) along with benthic *Nuttallides truempyi* specimen from the Alamedilla section of Spain. Above the white line, scale bar indicates that all specimens are at 400 microns; below the white line the specimens are at 250 microns.

- 1–3. *Morozovella subbotinae* (Morozova), sample 14.8 m.  
 4, 5, 9. *Morozovella velascoensis* (Cushman), sample 13.9 m.  
 6, 7, 8. *Movorzovella formosa* (Bolli), sample 28.0 m.  
 10–11. *Igorina lodoensis* (Mallory), sample 15.7 m.  
 12–13. *Nuttallides truempyi* (Nuttall), sample 15.7 m.  
 14–17. *Acarinina africana* (El Nagggar), sample 14.5 m.  
 18–21. *Acarinina sibaiyaensis* (El Nagggar), sample 14.5 m.

## Alamedilla, Spain

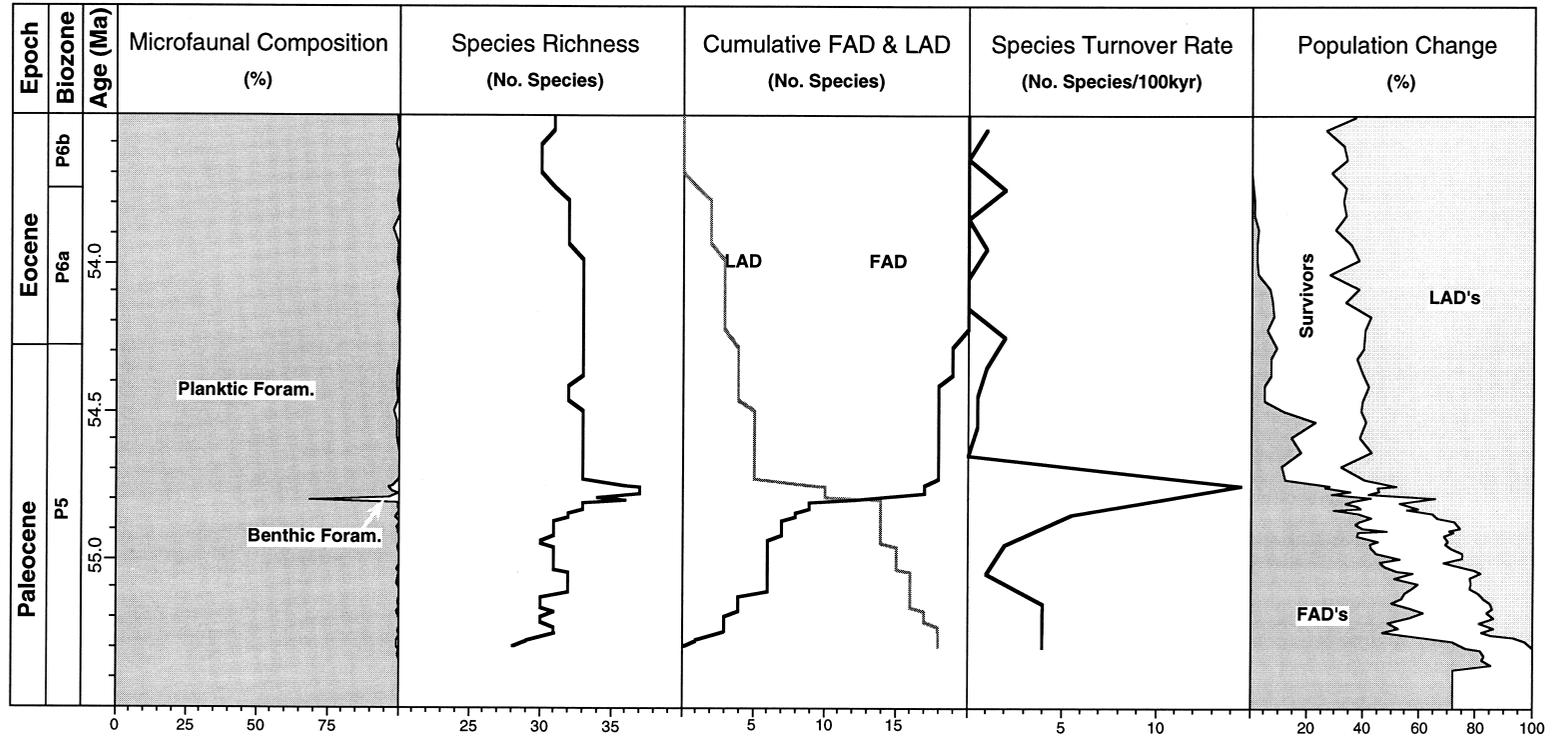


Fig. 7. Planktic foraminiferal changes across the P-E transition at Alamedilla, Spain. Note the contrast between the P-E short-term turnover event, as indicated by a spike in species turnover rates and the high number of first and last appearances, and the slow changes above and below this turnover event. Absolute ages from Lu et al. (1996).

### Ben Gurion, Israel

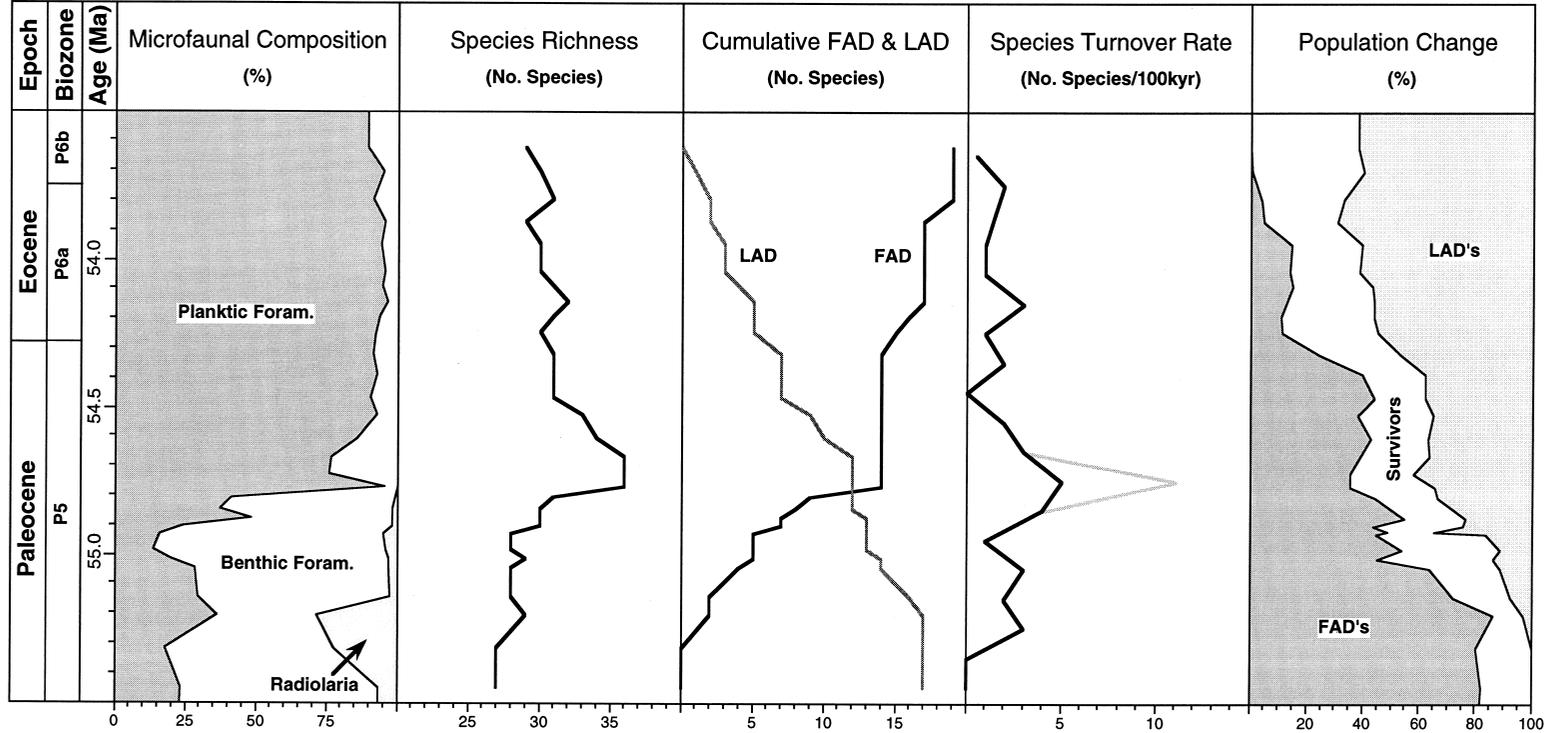


Fig. 8. Planktic foraminiferal changes across the P–E transition at Ben Gurion, Israel. Note the major change in the microfaunal composition coincides with the major P–E crisis. The apparent slower rate of change during the crisis, compared with the Alamedilla section, may be due to errors in correlation and age calibration. The lower species turnover rate during the crisis interval is due to the absence of the compressed acarininids possibly due to a short hiatus; the dotted line marks the species turnover rate if compressed acarininids are included. Absolute ages from Lu et al. (1995).

replacement of nearly 50% of the species and 60% of the population, a magnitude comparable with the P–E turnover in the equatorial Pacific (Lu and Keller, 1995a).

### 5.2. Depth assemblages

Living planktic foraminifera can be grouped into assemblages based on their dwelling depth (Bé, 1977; Hemleben et al., 1989). Oxygen and carbon stable isotope analysis enables reconstruction of relative dwelling depths of fossil planktic foraminifera and tracing their physiologic activities (Shackleton et al., 1985; Pearson et al., 1993; D'Hondt et al., 1994; Lu and Keller, 1996). During the Late Paleocene to Early Eocene, planktic foraminifera can be separated into three depth assemblages (e.g., surface, sub-surface and deep assemblages, based on their shell  $\delta^{18}\text{O}$  values as discussed in Lu and Keller, 1996). This separation is consistent with the grouping of genera based on morphologic characteristics, particularly wall-texture.

At the Alamedilla section, the surface assemblage is the dominant component and accounts for 60% of the species and 60–90% of the population (Fig. 9). The P–E faunal change is marked by a short-term high in species richness and relative abundance in this assemblage. The sub-surface assemblage accounts for 35% of the species and 10–35% of the population. Its relative abundance reached a minimum during the P–E faunal change, whereas species richness remained unaffected. The deep assemblage accounts for 5% of the species and less than 5% of the population. Its species richness and relative abundance were not affected by the P–E faunal change. The short-term increase in species richness and relative abundance in the surface assemblage is likely the result of a reduction in the vertical thermal gradient because of the P–E deep ocean warming (Kennett and Stott, 1991). Such a reduced vertical thermal gradient may have affected habitats for the sub-surface (thermocline) assemblage and thus reduced its relative abundance (Fig. 9).

### 5.3. Genera

Faunal changes at the genus level are illustrated in Fig. 10. At Alamedilla, the surface assemblage in-

cludes three genera with pustulate wall-texture (e.g., *Morozovella*, *Acarinina* and *Igorina*, Plate I). Examination of species richness indicates that the P–E faunal change resulted in a short-term increase in the number of species (from 7 to 12) in *Acarinina*, whereas *Morozovella* and *Igorina* remained relatively unaffected (Fig. 10). Relative generic abundances indicate that at this time *Acarinina* increased from 15–20% to nearly 70%, whereas *Igorina* and *Morozovella* decreased. These short-term changes are superimposed on the gradual transition from a *Morozovella*-dominated to an *Acarinina*-dominated surface assemblage (Fig. 10; Pardo et al., 1997; Pardo, in press).

The sub-surface assemblage includes four genera with cancellate wall texture (e.g., *Subbotina*) and smooth wall textures (e.g., *Chiloguembelina*, *Planorotalites* (*Luterbacheria*) and *Pseudohastigerina*). Across the P–E transition, species richness increased in *Chiloguembelina*, decreased in *Subbotina* and *Planorotalites* (*Luterbacheria*), and decreased briefly in *Pseudohastigerina*. However, few of these species richness changes were associated with the short-term P–E faunal turnover (Fig. 10). Though relative abundances between these four genera changed significantly during the P–E faunal event as marked by a major increase in *Pseudohastigerina* accompanied by decreases in *Chiloguembelina* and *Planorotalites* (*Luterbacheria*). These short-term changes in relative abundances are superimposed on the long-term and gradual transition from a *Subbotina*-dominated to a *Chiloguembelina*-dominated sub-surface assemblage, which has been interpreted as an increase in the hypoxic conditions in the subsurface layer (Pardo, 1998; Fig. 10).

The deep assemblage includes one genus with pitted wall-texture, e.g., '*Planorotalites*'. It is a minor component of this planktic foraminiferal fauna and its number of species and relative abundance was not affected by the short-term P–E faunal change, though changes occurred gradually over a long time period (Fig. 10).

### 5.4. Morpho-guilds

Based on chamber shape, arrangement and coiling style, species in the genera *Acarinina* and *Morozovella* can be grouped into morpho-guilds. A

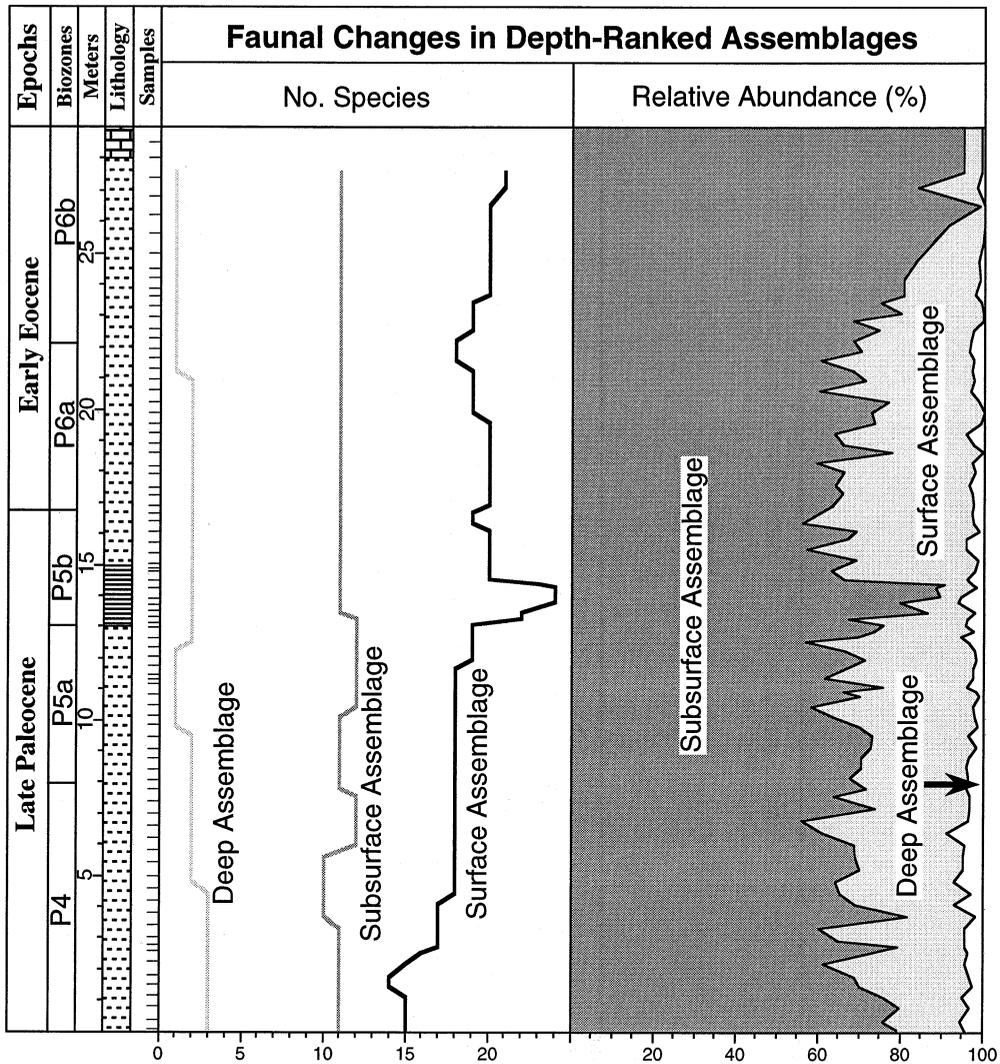


Fig. 9. Faunal changes in depth-ranked assemblages at Alamedilla, Spain. The short-term maxima in species richness and subsurface assemblage and the coincident decrease in the surface assemblage mark the interval of the P–E crisis.

morpho-guild is defined as a group of species with similar morphologic characteristics that lived in a similar habitat (i.e. depth, temperature) inferred from stable isotope ranking (e.g., Lu and Keller, 1996). Species in each morpho-guild may or may not have a close affinity. Each morpho-guild demonstrates a unique pattern in species and relative abundance changes across the P–E transition. Faunal changes in other genera, which are too small to be separated into morpho-guilds, can only be observed at the species level.

The genus *Acarinina* can be separated into four morpho-guilds (e.g., conicate, compressed, rounded and angulate acarininids, Fig. 11). The conicate morpho-guild appeared with the first occurrence of the genus *Acarinina* and represents the primary form of acarininids (Lu and Keller, 1995a). This morpho-guild was an important component in planktic foraminifera during the Late Paleocene, but became extinct during the P–E faunal change (Fig. 11). The compressed acarininids represent a unique and opportunistic morpho-guild (Plate I, 14–21). They have

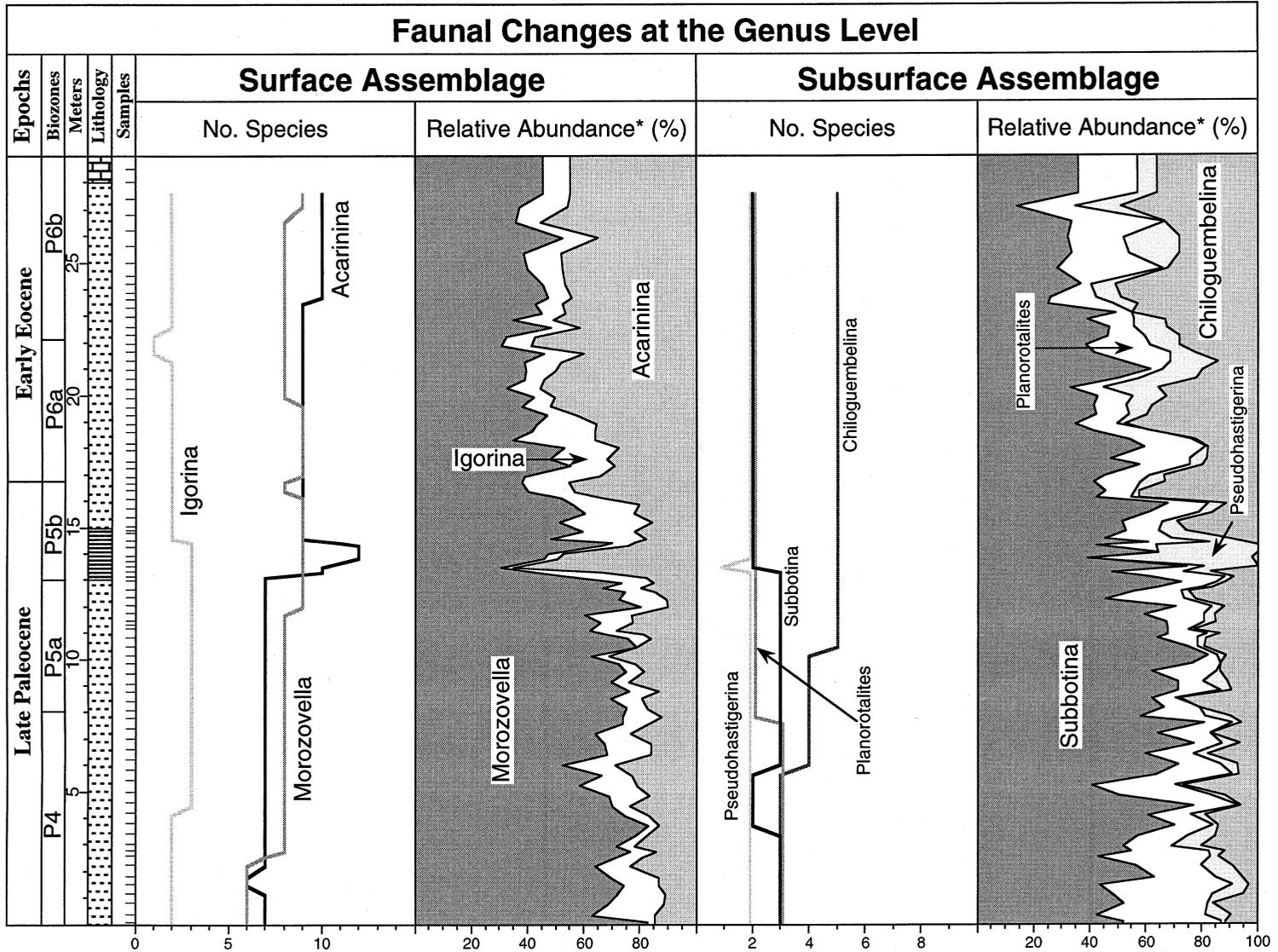


Fig. 10. Faunal changes at the genus level at Alamedilla, Spain. The short-term maxima in species richness, *Acarinina* and *Pseudohastigerina* mark the interval of the P-E crisis.



been observed in the Tethys region (Arenillas and Molina, 1996; Arenillas, 1996; Pardo, 1998; Pardo et al., in press) and the equatorial Pacific (Kelly et al., 1996) and existed in high relative abundances only during the P–E faunal change interval (Fig. 11). The rounded acarininids first appeared in the middle part of the Late Paleocene and significantly increased their species richness and relative abundances during the P–E faunal change. This morpho-guild dominated planktic foraminifera during the Early Eocene global warming. Angulate acarininids represent a minor morpho-guild that appeared during the Early Eocene global warming. Thus, the pattern of the P–E faunal turnover in *Acarinina* is illustrated by species and relative abundance changes in these four morpho-guilds which may be characterized by extinct, opportunistic, carry-over and emergent units, respectively (Fig. 11).

The genus *Morozovella* can also be separated into four morpho-guilds (e.g., discoidal, coniccate, hispid and muricate morozovellids, Fig. 11). The discoidal morpho-guild dominated *Morozovella* during the Late Paleocene (Plate I, 4, 5, 9). It was severely affected by the P–E faunal change and became extinct shortly thereafter. The coniccate morpho-guild represents one of the primary morozovellid morphotypes and has been a major component during the early evolution of *Morozovella*. By the Late Paleocene to Early Eocene, this morpho-guild included a few long ranging species which survived through the P–E faunal change (Fig. 11). The hispid morpho-guild is another carry-over unit. It first appeared during the Late Paleocene, increased its species richness and relative abundance during the P–E faunal change, and became the dominant component during the Early Eocene. The muricate morpho-guild, which includes *M. aragonensis* (Plate I, 6–8), appeared after the P–E faunal change and became the only morozovellid survivor during the global cooling that followed the Early Eocene global warming (Lu and Keller, 1995a).

*Acarinina* and *Morozovella* are the two dominant genera during the P–E transition. Both were severely affected by the P–E faunal change, particularly at the morpho-guild level (Fig. 11). The patterns of changes, however, seem to be different between the two genera. While the changes appear to be abrupt in *Acarinina*, they are gradual and sequential in

*Morozovella*. Evolution may be an important factor, among others, in causing this difference. During the P–E transition, the genus *Acarinina* was still in its early stage, but became the leading genus in terms of species richness and relative abundance in the Early Eocene. The P–E faunal event marks its first major change as noted in the increased species richness and relative abundance. In contrast, *Morozovella* was already well developed at this time and dominated the Late Paleocene in species richness and relative abundance. The P–E faunal change represents its last, though not very successful attempt to adjust to changing environmental conditions. Its failure is evident in the decreased abundance and replacement by *Acarinina* during the Early Eocene.

### 5.5. Species

Relative abundance changes in all planktic foraminiferal species are shown in Figs. 11 and 12. Major features of faunal changes at the species level include: (1) first and last appearances occur throughout the entire studied interval; (2) many first and last appearances concentrate at the P–E faunal change; and (3) there are stronger species turnovers in some taxonomic and ecologic units (e.g., morpho-guilds, genera, and depth assemblages) than in others.

Of over forty first and last appearances in the studied interval, nearly 50% occurred over a period of about 100–200 kyr during the P–E faunal change. The other 50% are distributed over about 2 Myr. The distribution of first and last appearances grouped into taxonomic and ecologic units shows significant variations. In the surface assemblage, 57% of the first and last appearances occurred during the P–E faunal change (Fig. 11), in contrast to 33% in the sub-surface and deep assemblages (Fig. 12). Among eight genera, *Acarinina* demonstrates the strongest P–E turnover as indicated by 82% of the total first and last appearances that occurred within the P–E faunal change interval as compared with an average 28% in the other genera. The compressed, coniccate and rounded acarininids show abrupt turnovers with over 75% of their first and last appearances within the P–E faunal change interval. Species turnovers in other morpho-guilds are relatively gradual.

With an average of 30 species over the entire studied interval, a relative abundance of 3% can be



and 6 are rare. These data seem to suggest that common species have their first or last appearances associated with major faunal changes, whereas rare species may be less bonded by community changes.

## 6. Community and environment

Planktic foraminifera, like other marine plankton, are sensitive to changes in water environments and community structures because of their passive life-style (Lipps, 1970; Lazarus, 1983). An understanding of associated environmental conditions and community evolution is thus essential for proper recognition of turnover patterns at different taxonomic and ecologic hierarchical levels for the Tethyan planktic foraminifera.

A correlation between faunal indices of planktic foraminifera and indices of the oceanic and sedimentary environment at Alamedilla is shown in Fig. 13. The sample turnover rates (e.g., the number of first and last appearances per sample calibrated to the time scale), rather than mean turnover rates (e.g., the number of first and last appearances in many samples per unit time) as in Figs. 7 and 8, are computed to show the abrupt nature of the P–E turnover and its correlation with environmental and sedimentary parameters. This correlation reveals three major features of the P–E event: (1) Both faunal and environmental parameters show little or only gradual changes before and after the P–E event; (2) Most parameters change abruptly during the event; and (3) all parameters re-establish their previous states after the event.

Reconstruction of the P–E plankton community in the Tethys basin is hampered by taphonomic alteration. Remains of planktic organisms sink slowly to the bottom of the ocean in the form of ‘particle rain’. During this journey, most organic remains are degraded. For the inorganic remains, most siliceous particles are dissolved because of the undersaturation of silica in sea waters, whereas calcareous particles may be preserved or dissolved depending on whether they are above or below the carbonate compensation depth. After settling on the sea floor, degradation of organic remains and dissolution of inorganic matter continue. At the Alamedilla section, the total organic carbon content is approximately 0.05% with

some samples as high as 0.7%. No biogenic silica is detected. Dissolution of biogenic carbonate is insignificant except possibly within a 25 cm interval from 13.50 m to 13.75 m that is correlated with the lowest calcite content (Fig. 13). Figs. 7 and 8 show that, for the >106  $\mu\text{m}$  size fraction, planktic foraminiferal tests are the predominant component of the sediments. These calcite tests, however, account for less than 20% of the biogenic calcite at the Alamedilla section. Most of the fine fraction calcite consists of coccoliths. Studies of living species show that the diet of planktic foraminifera includes various zooplankton (such as copepods, ciliates and tintinids) and phytoplankton (such as dinoflagellates and diatoms). None of these have been studied at the Alamedilla section. Nevertheless, these organisms could be important in shaping the turnover patterns in planktic foraminifera during the P–E transition.

The decrease in calcite content during the P–E event marks a major perturbation in planktic foraminifera in the Tethys region. This perturbation reduced the absolute abundance of planktic foraminiferal tests by 2–3 orders of magnitude within a 50 cm interval (between 13.50 and 14.00 m). In particular, biogenic calcite is reduced to trace amounts within a 25 cm interval (between 13.50 and 13.75 m) that coincides with the base of the P–E faunal change (Fig. 13). The rapid bounce-back in calcite content at the end of the P–E event marks the reappearance of calcareous plankton and, possibly, the re-establishment of the entire plankton community. The short-term excursion in  $\delta^{13}\text{C}$  values may also be an indication of the P–E perturbation in this plankton community (Fig. 13).  $\delta^{13}\text{C}$  measurements from planktic and benthic foraminifera show that, in the Antarctic oceans, the vertical  $\delta^{13}\text{C}$  gradient was eliminated during the P–E  $\delta^{13}\text{C}$  excursion, which was interpreted as a possible cessation in surface productivity (Kennett and Stott, 1991).

## 7. Discussion

### 7.1. Stable vs. unstable equilibrium

The Tethyan plankton community experienced a major perturbation during the P–E crisis, as suggested by short-term changes in calcite contents,

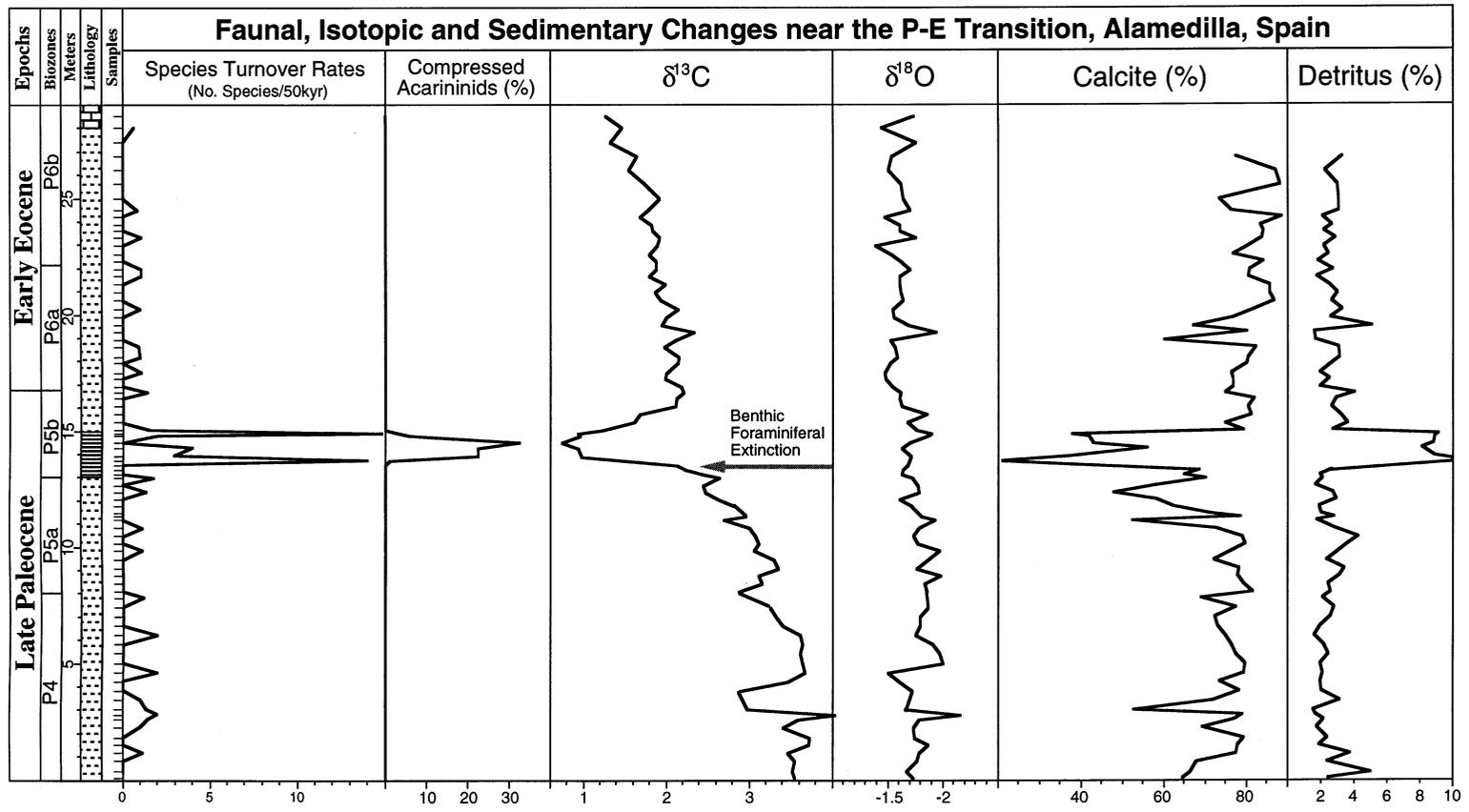


Fig. 13. Faunal, isotopic and sedimentary changes across the P–E transition at Alamedilla (after Lu et al., 1996). The species turnover rate per sample is used in this figure to show the abrupt nature of the faunal changes. Note the correlation between the rapid changes in faunal, isotopic and mineralogical parameters during the P–E crisis.

$\delta^{13}\text{C}$  values and planktic foraminifera. The perturbation started and ended abruptly. The crisis persisted for only a short time interval. This short-term perturbation provides an opportunity to test the stability of the Tethyan plankton community with respect to major global changes. Theoretically, a vigorous way of testing the stability of an ecologically defined system is to subject the system, usually in one of its equilibrium states, to a perturbation (Murray, 1990). The equilibrium is considered stable if the system can re-establish its previous equilibrium after the perturbation. If, on the other hand, the system responds to a perturbation by establishing a new equilibrium or becoming chaotic, the equilibrium is considered unstable with respect to this perturbation.

Stability, however, is relative to the parameters and taxonomic or ecologic hierarchical levels examined. At the community level, the rapid recovery in calcite content suggests that biogenic carbonate production was stable with respect to the P–E perturbation. In contrast, the species composition changed after the crisis, suggesting an unstable aspect of the community. For planktic foraminifera, typical stable parameters during the P–E transition include the species turnover rate, relative abundance of compressed acarininids (Fig. 13), and possibly species richness (Fig. 7), which re-established to levels preceding the P–E crisis. Typically unstable parameters include significantly changed species and population compositions after the P–E faunal change (Figs. 5–7). This study suggests that both ecologic (e.g., depth assemblages) and taxonomic units are stable with respect to the P–E perturbation (Figs. 9 and 10), whereas morpho-guilds are generally unstable (Figs. 11 and 12). Species and their relative abundances change constantly, with or without major perturbation, and represent the most unstable parameters.

Stability is also relative to the spatial and temporal scales of the study. For planktic foraminifera, the major spatial boundaries are the latitudinal bands that are determined mainly by surface water temperatures (Bé, 1977; Hemleben et al., 1989). During the P–E transition, the depth assemblages appear to have been stable units at low latitudes (Fig. 9). At high latitudes, however, significant changes occurred as marked by a major increase in the species richness and relative abundance in the surface assemblage (Lu and Keller, 1993; Pardo, 1998). This spatial differ-

ence in the faunal changes of planktic foraminifera may have been caused by the reduction in meridional thermal gradients due to the P–E high-latitude warming (Kennett and Stott, 1991; Lu and Keller, 1993, 1995b; Pardo, 1998). At a time scale of millions of years, the species richness of planktic foraminifera is an unstable parameter. In fact, the major increase in species richness coincides with the P–E faunal change. At a time scale of hundreds of thousand years, however, species richness appears stable as it re-establishes the previous equilibrium after the P–E faunal change (Figs. 7 and 8). Though species richness increased, it was gradual over more than one million years. Thus, the Tethys sections suggest that the increase in species richness in planktic foraminifera during the P–E transition is a long-term process.

## 7.2. Open system

For the P–E planktic foraminifera, species are the only taxonomic unit that changed constantly at a time scale of a few hundreds of thousand years. The rate of the change, however, could vary by an order of magnitude between stasis intervals and saltation events. This dramatic change between stasis intervals and saltation events provides a background to examine the relationships between foraminiferal species and enhances our understanding of the nature of ecological communities with particular regard to the renewed controversies between the views of tightly or loosely integrated communities (Boucot, 1990a,b; Valentine and Jablonski, 1993; DiMichele, 1994; Jackson, 1994; Brett and Baird, 1995).

The stasis intervals are marked by slow changes at the species level. As the result of the dynamic equilibrium between the first and last appearances, species richness may remain steady over a few million years. An example of these slow changes is shown in Fig. 12 by species and their relative abundance changes in the sub-surface and deep assemblages. Each first or last appearance seems to be individualistic with little immediate effect on other species or the entire community. However, the cumulative effects of such slow changes over a long period may alter the composition of major taxonomic or ecologic units. For instance, slow changes during the stasis intervals account for 50% of the total

first and last appearances observed at the Alamedilla section (Fig. 7). In the equatorial Pacific, Lu and Keller (1995b) observed that slow changes during the stasis interval following the P–E event changed the species ratio between the two dominant genera, *Morozovella* versus *Acarinina*, from 1:1 to 1:5. It thus appears that macro-patterns may be generated through individualistic, random-like changes.

The P–E saltation event is distinguished by rapid changes at the species and morpho-guild levels. The turnover is characterized by: (1) the sudden increase in species turnover rates at the onset and end of the event (Fig. 13); (2) the similar behavior patterns, such as first appearance, last appearance or survival, among species within a morpho-guild (Fig. 11); (3) the interaction between changes in one depth assemblage or genus and other depth assemblages or genera (Figs. 9 and 10); and (4), the unsuccessful invasion (in the long-term) of the three opportunistic species (e.g., the compressed acarininids, Figs. 11 and 13).

The compressed acarininid morpho-guild has not been detected below or above the P–E turnover event. Though during the crisis interval the relative abundance of this morpho-guild suddenly reached a high of 30% (Fig. 13). After the P–E crisis, rounded acarininids dominate, whereas compressed acarininids disappeared. The reason for this faunal change may be environmental (e.g., the restored environment prevented compressed acarininids from keeping their relative abundance) or biological (e.g., the more competitive taxa under normal environmental conditions excluded compressed acarininids from the community). Compressed acarininids appear to represent the failure of opportunistic species in adjusting to normal environmental conditions.

Observations from planktic foraminifera thus suggest that the P–E Tethyan plankton community was an open system. Species were able to join and leave the community without affecting other species. This open exchange was, however, limited to slow changes with small magnitudes, similar to changes occurring in the stasis intervals. Sudden and large-magnitude invasions appeared to be unwelcome and may be rejected, which appears to be the case for compressed acarininids. This suggests that marine plankton of communities are generally characterized by overall stability and that this inherent stability

prevails in the long-term, though short-term perturbations may temporarily alter the system.

## 8. Summary

Examination of planktic foraminifera in the Tethys basin during the P–E transition reveals two stasis intervals that are separated by a major saltation event which coincided with the P–E short-term change in global climate and oceanography. The stasis intervals are characterized by changes at the species level at a time scale of a few million years, whereas the saltation event is marked by changes at the species and morpho-guild levels at a time scale of a few hundred-thousand years. This alternation between persistent stasis and brief saltation forms the long-term pattern in faunal changes of planktic foraminifera.

The slow changes within the stasis intervals account for 50% of the total first and last appearances observed during a 2.5 Myr period across the P–E transition. These changes are more likely to involve rare than abundant taxa. Immediate effects on other species or the entire planktic foraminiferal community are minor after each first or last appearance. However, the cumulative effects of these slow, random-like changes can be significant in altering the species and population composition. The rapid changes within the saltation interval account for the remaining 50% of first and last appearances. These changes involved the more abundant rather than rare taxa. The saltation event had an immediate impact on Tethyan planktic foraminifera by replacing 30% of the species and population, and possibly on the entire plankton community by reducing biogenic calcite production by 60–70% as suggested by data from the Alamedilla section.

The global climatic and oceanographic perturbation across the P–E transition offers a chance to test the stability of the Tethyan plankton community. Short-term changes occurred at all ecologic and taxonomic hierarchical levels though with various magnitudes. This study suggests that many parameters for planktic foraminifera are stable with respect to the P–E perturbation including species richness, turnover rates, relative abundance of compressed acarininids, and calcite content in sediments. All of

these parameters were restored to pre-perturbation values after the P–E event. For various ecologic and taxonomic units, the depth assemblages and genera of planktic foraminifera are also stable with respect to the P–E perturbation. However, species and morpho-guilds appear to be inherently unstable.

Data from Tethyan planktic foraminifera indicate that changes occur at all spatial and temporal scales, though with various rates and magnitudes. While changes occur at some taxonomic and ecologic hierarchical levels and are measured by some parameters, other hierarchical levels and parameters are stable. This coexistence of change and stability may provide the possible dynamics for the evolution of the Tethyan plankton community, whether during the long-term intervals with relatively stable environments, or during the P–E short-term environmental perturbation.

### Acknowledgements

We are grateful to I. Arenillas for discussions of taxonomic concepts where our studies differ for the planktic foraminiferal species in the Alamedilla section. We thank E. Molina and C. Benjamini for help in collecting samples, T. Adatte for mineralogical analysis, and N. Ortiz for data on the benthic foraminiferal extinction event at Alamedilla. This study was supported by NSF grant OCE-9021338.

### Appendix A. Taxonomic remarks

The identification of paleontologic species is perhaps the least objective aspect of Paleontology. There is a saying that if you bring five paleontologists together in a room and show them the same specimen, you may get five different species names. While this is certainly a gross exaggeration, it makes the point. There is usually little problem in identifying the index species as long as they are fully adult and not end members of the population. However, it is extremely difficult to quantify morphological characteristics that are often gradational from one species to another, vary between gerontic and adult organisms within a species, and in quantitative studies must also include end members of each species population. As a result, the work of different investigators on either the same or different sections is often difficult to integrate, whereas the work of the same investigator on widely dispersed geographic locations can be easily integrated and compared.

The current study and that of Arenillas and Molina (1996) is a case in point. Though we have collaborated on field work and communicated on faunal analyses, it was not possible to reconcile our differing taxonomic concepts. Basically, our taxonomic approaches are rather different and simply put Arenillas and Molina are splitters whereas we are lumpers. Though by using these terms we do not intend to convey any derogative meaning, or to imply that one approach is better than another. However, since these taxonomic approaches are fundamentally different (one differentiates species based on relatively minor morphologic variations, whereas the other uses a population concept where morphologic variations are the norm in end-members), our species lists are also different. To enable the reader to compare these two studies, we provide comments on species names either not used in this study or where our taxonomic concepts differ.

Table A1  
Species names used in Arenillas and Molina (1996) but not in this study

Arenillas and Molina	This study	Comments
<i>M. acuta</i>	<i>M. acuta</i> lumped with <i>M. velascoensis</i>	In higher latitude sections dwarfed <i>M. velascoensis</i> look very similar to <i>M. acuta</i> morphotype and are difficult to differentiate.
<i>M. lacerti</i>	<i>M. lacerti</i> lumped with <i>M. subbotinae</i>	This morphotype differs from <i>M. subbotinae</i> only by having a more flattened dorsal side.
<i>M. tholiformis</i>	<i>M. tholiformis</i> lumped with <i>M. aequa</i>	This morphotype differs from <i>M. aequa</i> only by having a more flattened dorsal side.
<i>A. primitiva</i>	<i>A. primitiva</i> lumped with <i>A. acarinata</i>	<i>A. primitiva</i> and <i>A. acarinata</i> are very similar morphotypes and difficult to differentiate.
<i>A. berggreni</i>	<i>A. berggreni</i> included in <i>A. triplex</i>	Different species concepts of <i>A. berggreni</i> .
Muricoglobigerinids	labelled as 'rounded' acarininids	We retained the genus <i>Acarinina</i> for the morphoguild with rounded chambers.
<i>M. aquiensis</i>	<i>A. nitida</i> <i>A. soldadoensis</i>	<i>M. aquiensis</i> included in <i>A. nitida</i> or <i>A. soldadoensis</i> in this study. We retained the genus <i>Acarinina</i> .
<i>M. soldadoensis</i>	<i>A. soldadoensis</i>	
<i>S. eocaenica</i>	<i>S. patagonica</i>	These two taxa are synonyms. Arenillas and Molina (1996) prefer the name <i>S. eocaenica</i> since it was the first species defined with this morphology. They restrict the name <i>S. patagonica</i> for similar morphotypes in the middle Eocene. In this study we use <i>S. patagonica</i> because the holotype of <i>S. eocaenica</i> was lost and thus this name could be a nomen dubium.
<i>S. pseudoecaena</i> and <i>S. finlayi</i>	lumped with <i>S. hornibrookii</i>	This morphotypes are difficult to differentiate and therefore lumped in this study under <i>S. hornibrookii</i> .
<i>G. ovalis</i>	<i>P. pseudochapmani</i>	These morphotypes are very similar and we include them in the planorotaliid group.
<i>C. midwayensis</i> , <i>C. subtriangularis</i> and <i>C. trinitatensis</i>	lumped with <i>C. wilcoxensis</i>	Apart from the small size and similar morphology, the most relevant difference between chiloguembelinid taxa is the shape of the aperture, which is not clearly visible in most specimens. Our study includes 5 biserial species as compared to 10 by Arenillas and Molina. The 5 additional taxa are likely lumped in <i>C. wilcoxensis</i> and <i>C. subcylindrica</i> in this study.
<i>C. multicellaris</i> and <i>C. parallela</i>	lumped with <i>C. subcylindrica</i>	(see explanation above).

Table A2  
Different taxonomic concepts and species used in this study and by Arenillas and Molina (1996)

This study	Arenillas and Molina	Comments
<i>A. nitida</i>	<i>A. acarinata</i> / <i>M. aquiensis</i>	<i>A. nitida</i> may be lumped with either one of these two taxa depending on the position of the aperture.
<i>A. praepentacamerata</i>	<i>A. strabocella</i> and <i>A. sibiyaensis</i>	<i>A. praepentacamerata</i> may include Arenillas and Molina concepts of <i>A. strabocella</i> and <i>A. sibiyaensis</i> .
<i>A. esnaensis</i>	<i>A. pseudotopilensis</i>	<i>A. esnaensis</i> lumped with <i>A. pseudotopilensis</i> .
<i>M. quetra</i>	<i>A. wilcoxensis</i>	<i>M. quetra</i> is lumped with <i>A. wilcoxensis</i> .
<i>M. formosa</i>	<i>M. velascoensis</i> and <i>M. gracilis</i>	<i>M. formosa</i> may be lumped with <i>M. velascoensis</i> in the lower part and with <i>M. gracilis</i> in the middle part of its range.
<i>M. apantesma</i>	<i>A. apantesma</i>	Same species but different genera, since the holotype and paratypes do not clearly show a keel.
<i>M. occlusa</i>	<i>M. velascoensis</i>	Different species concepts for <i>M. velascoensis</i> , as suggested by the different biozone ranges in both studies.
Igorinids	Igorinids	Differences are likely due to problems in differentiating juvenile morozovellids from igorinids.

Appendix B

Table B1  
Relative percent abundances of planktic foraminifera across the P–E transition at Alamedilla, Spain

Sample (cm)	2850	2800	2740	2680	2620	2560	2500	2450	2420	2385	2360	2330	2295	2260	2230	2195	2165	2130	2095	2060	2025	1990	1955	1925	1890	1860	1815	1790	1750	1725		
Acarinina (coniccate)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. mckennai	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. niitida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. strabocella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. subsphaerica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Acarinina (rounded)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. acarinata	9	13	21	9	13	14	11	10	11	11	6	11	6	13	8	8	8	7	15	9	9	10	6	8	4	4	5	4	7	7		
A. csnaensis	2	1	1	2	4	1	3	2	2	4	4	4	3	2	3	3	3	1	2	1	1	1	1	2	2	.	1	1	1	2		
A. gravelli	2	.	2	.	1	.	1	.	1	1	1	1	2	2	.	1	.	1	2	.	1	1	.	1	.	1	.	.	.	2		
A. praepentacamerata	3	.	1	1	2	1	.	2	.	1	1	1	.	1	.	1	1	1	2	1	.	1	.	.	.	.	.	1	1	1		
A. pseudotopilensis	5	3	4	4	2	6	3	4	3	4	2	2	7	1	1	3	3	3	6	4	7	5	4	3	2	2	2	2	2	2		
A. soldadoensis	9	11	10	8	12	10	9	8	9	6	8	7	10	9	4	5	8	8	8	8	8	4	6	6	6	5	5	5	2	5		
A. triplex	6	4	5	4	4	4	5	5	5	7	8	2	6	9	4	7	7	7	6	9	9	4	7	5	5	4	5	5	6	7		
A. wilcoxensis	5	1	2	1	1	2	2	2	3	1	2	2	3	2	1	2	1	2	3	1	2	1	1	1	1	.	1	1	2	1		
Acarinina (angulate)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. densa	.	.	3	1	1	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. nicoli	3	4	6	2	4	2	1	3	2	2	3	1	2	2	3	2	4	2	1	3	1	1	.	1	1	2	1	2	.	1		
Acarinina (compressed)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. africana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. berggreni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. sibaiyaensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Chiloguembelina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
C. circumlabiata	.	1	.	.	.	.	2	1	2	1	1	.	.	1	1	.	.	1	.	1	1	1	1	.	1	1	1	1	2	1		
C. crinita	.	.	.	.	.	.	1	1	.	.	1	1	.	1	1	.	1	1	1	1	2	1	1	1	2	1	1	1	4	4		
C. subcylindrica	.	.	.	.	.	.	1	.	1	1	1	1	1	.	1	.	1	1	.	.	.	1	2	.	1	1	1	2	1	2		
C. wilcoxensis	2	5	.	1	2	4	5	6	6	5	8	5	6	6	6	3	3	5	7	6	7	9	9	6	5	2	2	3	4	5		
Z. teuria	.	1	.	1	.	1	1	2	1	.	1	1	.	.	.	.	1	.	.	.	1	1	2	1	1	1	1	1	.	1	.	
Igorina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
I. cf. lodoensis	4	4	1	3	4	2	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
I. convexa	6	10	8	9	8	8	6	7	7	6	10	6	7	7	8	8	7	4	5	2	3	3	5	2	3	1	2	2	7	4		
I. lodoensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	4	4	4	4	4	9	15	14	12	11	8	9	7	.	
I. pusilla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Morozovella (coniccate)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. apenthesma	1	8	3	10	8	8	6	6	10	4	6	7	2	5	4	5	6	3	3	3	3	5	3	3	3	7	3	3	4	5	4	
M. edgari	5	6	5	10	6	6	5	2	7	7	5	5	5	3	4	7	3	4	5	4	3	5	3	3	2	4	3	5	6	3		
Morozovella (discoidal)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. oclusa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	1	.
M. velascoensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Morozovella (hispid)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. aequa	1	.	.	1	.	1	.	.	1	1	2	2	1	.	1	3	2	2	1	1	2	1	2	1	3	5	4	3	1	4		
M. formosa	5	1	6	1	3	3	2	5	0	1	2	2	1	1	2	2	1	1	.	1	1	3	4	7	3	6	4	4	.	.		
M. gracilis	15	6	12	13	11	7	10	12	6	9	2	5	6	4	3	2	4	7	6	8	7	8	5	4	2	5	3	6	2	3		
M. marginodentata	1	.	2	1	.	1	.	1	.	1	.	.	.	1	2	1	1	1	5	2	1	1	5	3	2	2	2	3	1	2		
M. quetra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. subbotinae	13	6	6	11	4	8	10	10	8	11	5	13	6	7	8	6	10	6	5	11	9	8	6	8	2	7	10	8	7	7		
Morozovella (muricate)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. crater	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. lensiformis	1	3	2	3	1	.	3	2	1	1	1	1	1	1	3	2	1	.	.	1	1	1	.	1	.	2	.	.	.	.		
Planorotalites	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
P. cf. pseudomenardii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	1	
P. pseudomenardii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
P. pseudoscutula	1	3	.	2	2	6	1	2	5	1	5	2	4	6	10	5	1	3	2	3	3	3	5	4	8	6	8	6	4	5		
"Planorotalites"	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
"P". chrenbergi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
"P". hansbolli	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
"P". pseudoimitata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	2	.	1	.	.	.	2	1	1	.	
"P". sp.	1	2	.	.	.	1	1	2	1	.	.	2	3	3	2	3	1	3	1	.	1	3	1	.	2	2	1	2	2	2		
Pseudohastigerina	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
P. pseudochapmani	.	2	.	.	1	.	1	1	2	.	2	1	3	2	2	3	2	3	2	3	2	1	1	.	1	.	1	1	1	2		
P. troelseni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
P. wilcoxensis	.	.	.	1	1	.	.	1	1	.	1	2	1	1	2																	

Table B1 (continued).

Sample (cm)	1690	1665	1640	1605	1570	1535	1505	1490	1480	1450	1425	1390	1370	1350	1330	1310	1295	1265	1235	1205	1175	1145	1130	1115	1080	1045	1015	985	945	905	
Acarinina (coniccate)																															
A. mckannai	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	1	1	1	.	1	.	1	.	1	.	.	1	.	1	.	.
A. nitida	.	.	.	.	.	.	.	.	1	.	1	4	4	2	3	4	2	0	1	4	3	4	4	3	2	9	4	4	6	3	
A. strabocella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. subsphaerica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	1	1	.	1	1	
Acarinina (rounded)																															
A. acarinata	7	6	4	2	2	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. esnaensis	1	2	1	1	.	1	.	3	1	.	3	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. gravelli	1	2	2	.	.	1	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. praepentacamerata	1	1	1	1	.	1	.	1	2	1	3	4	4	2	1	1	1	1	.	1	1	2	1	1	1	2	2	2	1	.	
A. pseudotopilensis	3	3	.	1	2	2	3	3	3	1	2	4	3	2	2	5	2	3	3	2	4	3	2	3	3	4	3	3	4	2	
A. soldadoensis	4	3	2	3	2	2	4	5	3	2	2	7	4	3	3	2	2	1	1	3	.	2	1	1	2	2	2	2	3	2	
A. triplex	4	3	3	2	2	3	1	3	3	1	2	9	1	2	1	1	.	1	2	3	3	8	4	3	4	3	3	1	2	2	
A. wilcoxensis	.	2	1	1	2	2	.	1	1	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Acarinina (angulate)																															
A. densa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
A. nicoli	2	1	1	2	1	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Acarinina (compressed)																															
A. africana	.	.	.	.	.	.	.	1	1	16	10	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. bergreni	.	.	.	.	.	.	.	2	3	8	9	9	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. sibaiyaensis	.	.	.	.	.	.	.	1	2	9	3	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Chiloguembelina																															
C. circumlabiata	2	3	1	2	2	1	1	.	.	.	.	.	1	.	.	.	1	1	.	1	.	.	1	1	1	1	1	.	1	1	
C. crinta	6	3	1	2	4	3	1	.	.	.	.	.	2	1	1	2	7	5	2	3	3	2	2	5	2	3	2	2	2	2	
C. subcylindrica	2	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	1	1	1	.	.	.	.	
C. wilcoxensis	5	3	1	2	1	2	1	.	.	.	.	.	1	.	1	1	.	1	1	.	1	1	1	1	1	1	.	1	.	.	
Z. teuria	2	1	.	1	1	1	1	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	.	1	.	1	.	.	.	.	
Igorina																															
I. cf. Iodoensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
I. convexa	4	4	6	6	11	8	16	5	3	3	2	1	4	7	3	2	2	2	4	4	3	3	2	2	.	1	1	1	1	1	
I. Iodoensis	5	6	10	4	12	4	6	1	5	2	1	.	6	7	5	5	3	8	2	4	2	3	4	1	.	1	1	2	1	5	
I. pusilla	.	.	.	.	.	.	.	1	1	.	1	3	7	3	1	3	1	1	1	3	2	1	3	2	.	2	2	2	3	2	
Morozovella (coniccate)																															
M. apenthesma	3	4	3	2	6	2	7	7	5	4	2	.	2	2	3	2	3	4	8	10	12	6	5	14	8	6	10	14	8	8	
M. edgari	2	1	4	8	6	7	6	11	13	14	9	3	8	13	13	10	9	7	9	4	3	3	6	4	3	4	7	3	3	3	
Morozovella (discoidal)																															
M. ocellata	2	8	15	10	8	5	6	8	11	3	2	4	9	12	14	17	8	13	14	10	3	7	11	7	8	10	9	11	6	10	
M. velascoensis	.	.	.	1	3	3	1	17	9	13	13	19	5	8	12	5	12	12	14	7	10	11	13	12	8	4	11	12	13	18	
Morozovella (hispid)																															
M. aqua	5	1	2	3	1	2	3	4	3	1	4	.	1	1	3	3	2	3	3	4	5	9	2	5	4	4	3	1	8	3	
M. formosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M. gracilis	2	6	3	.	4	6	1	4	3	1	.	.	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	
M. marginodentata	1	6	3	3	1	2	.	1	2	.	.	.	.	1	3	4	3	1	2	1	5	3	1	1	2	2	.	.	1	1	
M. quetra	1	1	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	
M. subbotinae	7	8	8	7	6	11	7	11	12	5	5	.	3	6	5	5	5	7	7	5	3	7	10	8	12	11	13	11	10	10	
Morozovella (muricate)																															
M. crater	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M. lensiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Planorotalites																															
P. cf. pseudomenardii	.	.	.	1	1	2	1	.	.	.	.	.	1	.	.	1	1	2	1	1	1	.	1	1	1	0	0	1	1	1	
P. pseudomenardii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
P. pseudoscitula	4	3	4	6	4	2	6	2	2	.	.	1	7	5	3	3	5	7	3	5	4	2	3	3	1	1	3	4	2	3	
"Planorotalites"																															
"P". ehrenbergi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
"P". hansbolli	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
"P". pseudomitata	.	1	2	1	1	1	2	.	.	1	.	1	3	2	3	3	1	2	2	2	2	4	2	1	3	2	1	2	2	3	
"P". sp.	2	.	2	3	.	1	2	3	2	4	6	1	1	3	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	
Pseudohastigerina																															
P. pseudochapmani	.	1	1	1	1	2	6	.	3	2	7	2	2	1	1	.	1	1	1	.	1	.	1	.	1	.	1	.	1	1	
P. troelseni	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	1	1	1	1	1	.	1	1	1	.	.	.	2	.
P. wilcoxensis	.	.	1	1	.	1	.	1	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Subbotina																															
S. cf. hornibrooki	1	1	2	3	1	2	3	.	.	1	.	1	2	2	1	1	3	2	2	2	3	.	2	2	3	2	1	.	2	1	
S. linaperta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S. patagonica	18	12	17	20	14	16	10	4	4	3	5	7	11	9	14	12	16	8	7	9	7	5	7	5	12	9	9	5	6	5	
S. velascoensis	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	3	3	5	10	8	14	9	13	11	15	17	12	9	11	13	
<b>Total Counts</b>	<b>340</b>	<b>324</b>	<b>336</b>	<b>380</b>	<b>345</b>	<b>326</b>	<b>344</b>	<b>331</b>	<b>322</b>	<b>324</b>	<b>329</b>	<b>271</b>	<b>246</b>	<b>296</b>	<b>348</b>	<b>344</b>	<b>337</b>	<b>366</b>	<b>313</b>	<b>346</b>	<b>347</b>	<b>315</b>	<b>320</b>	<b>337</b>	<b>320</b>	<b>341</b>	<b>307</b>	<b>321</b>	<b>318</b>	<b>321</b>	
<b>No. Species</b>	<b>32</b>	<b>33</b>	<b>33</b>	<b>33</b>	<b>33</b>	<b>33</b>	<b>33</b>	<b>36</b>	<b>37</b>	<b>37</b>	<b>37</b>	<b>34</b>	<b>36</b>	<b>33</b>	<b>33</b>	<b>33</b>	<b>32</b>	<b>32</b>	<b>31</b>	<b>31</b>	<b>31</b>	<b>31</b>	<b>31</b>	<b>31</b>	<b>30</b>	<b>30</b>	<b>31</b>	<b>31</b>	<b>31</b>		
<b>No. FAD</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>3</b>	<b>2</b>	<b>3</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>		
<b>No. LAD</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>4</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>4</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>														

Table B1 (continued).

Sample (cm)	875	840	805	780	740	700	660	620	580	540	500	460	420	380	340	300	280	260	225	180	150	115	80	35	10		
Acarinina (coniccate)																											
A. mckannai	1	1	.	1	1	2	1	1	1	1	1	.	2	.	.	.	1	.	1	1	.	1	1	1	.	.	
A. nitida	5	4	2	5	4	4	1	3	4	3	4	4	2	3	3	4	3	3	5	2	4	3	2	2	3	.	
A. strabocella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	1	.	
A. subsphaerica	.	.	.	.	2	.	1	1	1	1	1	2	2	1	.	.	1	2	.	1	.	.	.	1	.	.	
Acarinina (rounded)																											
A. acarinata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. esnaensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. gravelli	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. praepentacamerata	2	1	2	2	2	1	2	4	3	2	1	1	2	3	1	3	2	1	2	.	.	.	.	.	.	.	
A. pseudotopilensis	4	4	2	1	4	2	3	5	4	3	3	3	2	2	3	4	2	4	3	3	2	2	3	3	3	3	
A. soldadoensis	1	2	2	.	2	.	2	2	1	3	1	5	2	1	.	2	1	1	2	1	1	1	1	1	4	5	
A. triplex	2	2	2	1	2	.	1	4	3	2	.	1	1	2	2	1	2	2	1	1	2	1	1	1	1	.	
A. wilcoxensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Acarinina (angulate)																											
A. densa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. nicoli	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Acarinina (compressed)																											
A. africana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. berggreni	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
A. sibaiyaensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Chiloguembelina																											
C. circumlabiata	1	1	.	.	.	.	.	.	.	1	1	.	.	.	.	1	.	1	1	1	.	.	.	.	.	.	
C. crinta	3	4	2	1	3	2	4	1	2	5	2	2	4	2	4	5	1	3	2	1	1	1	2	2	1	.	
C. subcylindrica	1	1	.	.	.	.	1	.	.	1	1	.	1	.	1	1	.	.	.	.	.	.	.	.	.	1	
C. wilcoxensis	2	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Z. teuria	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Igorina																											
I. cf. lodoensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
I. convexa	2	1	1	1	.	2	2	2	2	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
I. lodoensis	3	2	3	2	5	2	2	4	.	2	1	1	2	1	1	2	.	.	.	.	.	.	.	.	.	.	
I. pusilla	3	2	6	3	4	5	6	7	5	9	8	3	4	2	2	3	7	7	8	12	9	13	16	17	2	.	
Morozovella (coniccate)																											
M. apenthesma	7	8	13	12	10	7	6	8	10	12	12	11	12	15	14	12	14	13	9	7	6	7	8	3	6	.	
M. edgari	5	3	2	4	4	2	2	3	3	3	3	3	2	4	2	3	3	1	.	.	.	.	.	.	.	.	
Morozovella (discoidal)																											
M. oclusa	8	10	10	12	9	9	10	5	10	8	9	9	7	9	4	4	10	12	6	11	15	13	19	16	21	.	
M. velascoensis	14	13	16	9	13	11	12	11	11	11	11	11	16	22	17	15	18	17	18	28	28	30	28	26	28	.	
Morozovella (hispid)																											
M. aequa	3	4	2	4	3	2	3	2	4	5	5	1	8	8	2	3	7	5	6	3	3	4	.	3	10	.	
M. formosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M. gracilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
M. marginodentata	.	.	.	.	.	.	1	1	.	1	1	1	1	3	.	.	2	.	.	.	.	.	.	.	.	.	
M. quetra	.	.	1	1	1	1	1	1	1	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	
M. subbotinae	12	13	8	6	8	7	8	5	6	3	3	10	6	8	7	7	8	4	.	.	.	.	.	.	.	.	
Morozovella (muriccate)																											
M. crater	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
M. lensiformis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Planorotalites																											
P. cf. pseudomenardii	1	1	2	1	3	3	2	1	1	2	4	1	2	1	2	2	.	.	.	.	.	.	.	.	.	.	
P. pseudomenardii	.	.	.	2	.	.	2	.	2	2	2	4	1	1	.	.	3	8	8	5	12	6	4	7	4	.	
P. pseudoscutula	1	2	4	1	1	1	1	3	3	3	4	1	2	1	4	3	2	2	1	1	1	1	1	1	1	2	
"Planorotalites"																											
"P". ehrenbergi	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	1	.	1	2	.	
"P". hansbolli	2	1	2	.	2	2	4	1	1	1	4	1	3	.	3	2	2	1	.	2	2	1	3	2	.	.	
"P". pseudoimitata	2	2	2	3	2	2	5	3	4	3	3	2	4	1	2	2	2	2	2	2	1	2	1	1	1	1	
"P". sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Pseudohastigerina																											
P. pseudochapmani	.	.	1	.	.	1	1	.	.	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	
P. troelseni	.	.	1	1	.	1	1	1	1	1	1	.	1	.	3	2	1	1	4	3	2	2	0	2	.	.	
P. wilcoxensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Subbotina																											
S. cf. hornibrooki	.	1	1	4	1	5	1	1	1	1	2	0	1	3	3	3	1	.	1	7	3	.	1	.	.		
S. linaperta	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	1	1	2	1	2	2	.	
S. patagonica	5	5	2	2	2	4	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
S. velascoensis	10	14	10	20	12	23	14	17	15	9	13	24	14	9	16	13	8	9	16	10	7	7	7	6	7	.	
<b>Total Counts</b>	<b>324</b>	<b>307</b>	<b>324</b>	<b>365</b>	<b>304</b>	<b>313</b>	<b>311</b>	<b>310</b>	<b>334</b>	<b>310</b>	<b>354</b>	<b>303</b>	<b>331</b>	<b>301</b>	<b>317</b>	<b>324</b>	<b>315</b>	<b>321</b>	<b>288</b>	<b>339</b>	<b>360</b>	<b>327</b>	<b>292</b>	<b>336</b>	<b>309</b>		
<b>No. Species</b>	<b>31</b>	<b>31</b>	<b>31</b>	<b>32</b>	<b>32</b>	<b>32</b>	<b>32</b>	<b>32</b>	<b>30</b>	<b>30</b>	<b>30</b>	<b>31</b>	<b>30</b>	<b>30</b>	<b>31</b>	<b>31</b>	<b>29</b>	<b>26</b>	<b>24</b>	<b>23</b>	<b>23</b>	<b>24</b>	<b>24</b>	<b>24</b>	<b>24</b>		
<b>No. FAD</b>	<b>0</b>	<b>2</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>2</b>	<b>3</b>	<b>2</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>								
<b>No. LAD</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>0</b>								

Table B2

Relative percent abundances of planktic foraminifera across the P–E transition at Ben Gurion, Israel

Sample	BG-570	BG-569	BG-568	BG-567	BG-566	BG-565	BG-564	BG-563	BG-562	BG-561	BG-560	BG-559	BG-558	BG-557	BG-556	BG-555
Acarinina (high spired)																
A. chascanona	4	2														
Acarinina (coniccate)																
A. mckannai														3	3	3
A. nitida								8	4	5	6	18	13	14	14	16
A. subsphaerica															2	2
Acarinina (rounded)																
A. acarinata	27	41	25	29	21	17	24	25	22	18	23	10	9	14	3	8
A. gravelli	4	6	9	3	3	5	3		1	4						
A. praepentacamerata	6	11	2	13	3	6	6	1	5	6	2			4	4	2
A. pseudotopilensis	22	29	13	21	13	13	9	16	7	16	14	12	3	8	11	5
A. soldadoensis	13	21	8	13	10	16	27	9	14	22	22	17	3	19	12	9
A. triplex	9	12	18	13	7	14	19	15	21	18	22	13	7	7	11	12
A. wilcoxensis	18	26	19	11	16	14	11	14	12	9	7	5	6	4	2	4
Acarinina (angulate)																
A. densa	3	4	7													
A. nicoli	9	2	12	5	2	19	6	8	16	11	12	1	5	3		4
Chiloguembelina																
C. circumlabiata	1	1	1		2	1				2	3		4	3		6
C. crinita	1	1		2	9	6	3	2	2	5	4	2	2			2
C. subcylindrica	5	3	6	1	1	1			2	1			1	4	1	
Igorina																
I. cf. albeari																
I. convexa	11	21	24	22	22	34	18	11	36	30	13	4	8	12	12	18
I. lodoensis			17	23	60	65	46	29	38	17	28	34	42	21	10	3
I. pusilla																4
Morozovella (coniccate)																
M. cf. edgari	12	4	2	15	4	7	8	9	5							
M. apenthesma	34	31	21	17	19	12	11	24	29	20	11	8	8	10	10	9
M. edgari											2	12	11	7	4	5
Morozovella (discoidal)																
M. occlusa					9	4	9	5		3	15	29	36	30	38	44
M. velascoensis											12	33	31	37	51	25
Morozovella (hispid)																
M. aequa	13	20	16	11	9	21	15	19	19	13	8	10	13	19	8	17
M. formosa		2		1				2								
M. gracilis	6	12	24	30	18	11	11	17	5	4						1
M. marginodentata	3	17	13	23	8	4	24	24	10	27	7	10	2	1	8	2
M. quetra	1	13	2		10		1	11	8	14	6	6	2	8	10	11
M. subbotinae	18	17	12	36	17	24	17	20	26	19	11	38	17	17	17	13
Planorotalites																
P. cf. pseudomenardii	23	11	12	11	7	6	8	5	2	3	7	6	14	10	4	9
P. pseudomenardii																
"Planorotalites"																
"P". chapmani														4	3	
"P". pseudoimitata																2
"P". sp.	6	8	12	7	11	7	3	5	2		2	4	6	6	4	5
Pseudohastigerina																
P. pseudochapmani	2		2	5	3	1	1	1			3	4	2	9	2	4
P. troelseni	2	1	1				2	1	1	1				4	1	
P. wilcoxensis	3		2								5	1	5	3	3	4
Subbotina																
S. cf. hornibrooki						4	5	1	8	12	4	4	4	4	4	7
S. cf. inaequispira																
S. hornibrooki	23	16	12	6	12	19	4	7	3	4	11	6	7	4	12	12
S. linaperta																
S. patagonica	46	29	40	24	42	26	29	26	19	45	44	25	34	31	53	41
S. triangularis																
S. velascoensis		2	5	6	12	16	13	9	11	14	19	17	26	20	21	18
Total counts	325	363	337	348	350	369	332	328	321	339	331	329	321	340	338	327
No. Species	28	28	28	25	27	26	27	28	27	27	28	26	28	31	30	33
No. FAD	0	1	1	0	0	0	0	1	1	1	0	0	0	0	1	0
No. LAD	1	0	1	1	0	0	1	1	0	0	2	0	0	2	1	1

Table B2 (continued).

Sample	BG-554	BG-553	BG-552	BG-551	BG-550	BG-549	BG-548	BG-547	BG-546	BG-545	BG-542	BG-540	BG-536	BG-532
Acarinina (high spired)														
<i>A. chascanona</i>														
Acarinina (coniccate)														
<i>A. mckannai</i>	1									2	3	7	2	5
<i>A. nitida</i>	20	11	16	15	22	42	22	36	32	34	27	24	14	30
<i>A. subsphaerica</i>									2	4	4	1	1	2
Acarinina (rounded)														
<i>A. acarinata</i>	19	9												
<i>A. gravelli</i>														
<i>A. praepentacamerata</i>	5	4	1	1										
<i>A. pseudotopilensis</i>	14	12	18	15	10	28	16	35	18	9	19	3	5	8
<i>A. soldadoensis</i>	20	19	19	13	19	23	28	31	35	26	10	8	19	4
<i>A. triplex</i>	8	14	22	14	13	39	54	44	83	39	14	6	3	9
<i>A. wilcoxensis</i>	7	2												
Acarinina (angulate)														
<i>A. densa</i>														
<i>A. nicoli</i>	4	6												
Chiloguembelina														
<i>C. circumlabiata</i>	4	1										1		
<i>C. crinita</i>		2												
<i>C. subcylindrica</i>		4	1	1	2			1		1				
Igorina														
<i>I. cf. albeari</i>									1	2	29	36	13	47
<i>I. convexa</i>	13	11	1	4	4	3								
<i>I. lodoensis</i>	20	20	7	13	14	7								
<i>I. pusilla</i>	8	23	4	5	1	7	8		1	4	29	35	15	22
Morozovella (coniccate)														
<i>M. cf. edgari</i>														
<i>M. apenthesma</i>	6	3	5	7	10	3	3		6	6	3	3	15	6
<i>M. edgari</i>	8	6	11	30	23	27	4	11	2	4	23	30	7	11
Morozovella (discoidal)														
<i>M. oclusa</i>	29	15	49	47	46	16	37	16	42	84	35	56	35	25
<i>M. velascoensis</i>	38	25	29	28	21	24	33	16	33	55	26	41	41	21
Morozovella (hispid)														
<i>M. aequa</i>	9	15	8	6	8	8	14	3	12	7	13	8	13	21
<i>M. formosa</i>														
<i>M. gracilis</i>			1											
<i>M. marginodentata</i>	5		6	17	5	12	10	4	1		8	2		
<i>M. quetra</i>	9	4	2		8	3	1				4	5	7	8
<i>M. subbotinae</i>	28	13	40	32	22	38	16	11	37	36	15	9		
Planorotalites														
<i>P. cf. pseudomenardii</i>	10	21		3	1	1			1	1				
<i>P. pseudomenardii</i>												3		1
"Planorotalites"														
"P". chapmani	2	4		1										
"P". pseudoimitata	1	9	1	2	6	8	4	12	10	2	1	1	3	1
"P". sp.	3	16	4	4		2	3	8	5	2				
Pseudohastigerina														
<i>P. pseudochapmani</i>	1	2												
<i>P. troelseni</i>	1	8			1							1		
<i>P. wilcoxensis</i>	2	1												
Subbotina														
<i>S. cf. hornibrooki</i>	2	3	2	5	2		1	1	2	1				
<i>S. cf. inaequispira</i>					21					4	10		12	9
<i>S. hornibrooki</i>	13	7	11	11	6	2	2	1	2					
<i>S. linaperta</i>											13	14	46	34
<i>S. patagonica</i>	42	38	46	44	34	18	17	14	7	3				
<i>S. triangularis</i>											9	7	8	6
<i>S. velascoensis</i>	9	15	33	30	32	14	22	84	46	33	10	33	58	46
Total counts	361	343	337	348	331	325	295	328	378	359	305	334	317	316
No. Species	32	32	24	24	24	21	19	17	21	22	21	23	19	20
No. FAD	0	4	1	2	0	2	0	0	0	4	0	3	0	0
No. LAD	0	0	0	0	0	0	0	0	1	1	0	0	0	0

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