

MicroForum

Reply to comment on ‘The Cretaceous–Tertiary boundary transition in the Antarctic Ocean and its global implications’

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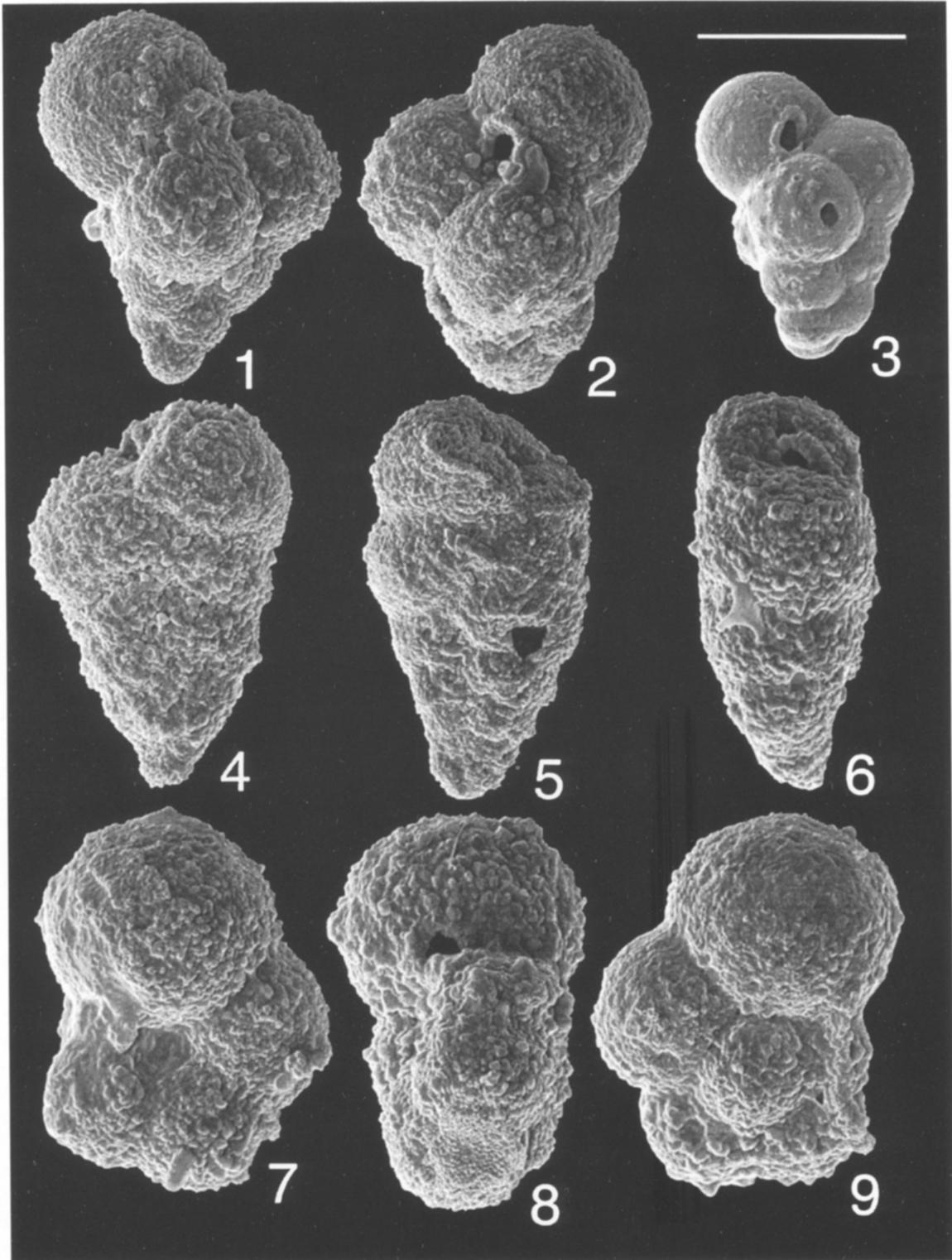
The critique of Huber et al. (1994-this volume) follows two lines of argument. The first is that Keller (1993) does not confirm Huber's (1991) earlier study. The second is devoted to criticizing Keller (1993) for not following the revised taxonomy of Olsson et al. (1992), Liu and Olsson (1992) and Olsson and Liu (1993). Huber et al. (1994-this volume) do not mention the fact that none of these studies were published at the time the paper they criticize was written (during the fall of 1991). But even if these studies had been known, they would not have influenced the arguments presented by Keller (1993) since none of these publications provides convincing arguments in favor of their proposed taxonomic revisions (for a critique see MacLeod, 1993, in press a,b). In addition, Huber et al. (1994-this volume) criticize Keller for not following the Berggren and Miller (1988) Paleogene biozonation. We respond to these issues below.

1. Faunal assemblages

Keller's (1993) planktic foraminiferal study of the K/T boundary transition at Antarctic ODP Site 738C did not confirm Huber's (1991) study of the same core and the same sample intervals. At the time, Keller suggested that this discrepancy was due to Huber's examination of only the >63 μm size fraction. Huber initially claimed to have examined the smaller (38–63 μm) size fraction (B.T. Huber, pers. commun., 1993),

but Huber et al. (1994-this volume) state that he did not use data from this size fraction because small specimens were poorly-preserved, predominantly juvenile forms and therefore difficult to identify.

Following publication of Keller (1993), Huber requested permission to examine Keller's picked and mounted faunal slides to which we agreed with the proviso that Huber bring his picked and mounted faunal slides to Princeton University where both sets of samples could be examined side by side. During that meeting Huber's faunal slides were found to be largely devoid of planktic foraminifera, even in samples where Huber (1991) noted the presence of over 100 specimens. In slides where a few specimens were present, Huber was generally unable to identify them. When asked where the many hundreds of specimens upon which he based his 1991 paper were, Huber replied that all were mounted on SEM stubs (that he failed to bring to the meeting) because he was unable to identify them using light optics. When specifically asked to produce specimens of at least his most abundant species, including *Eoglobigerina fringa* and *Chiloguembelina crinita*, he had none. It seems that Huber's inability to identify many early Danian species, along with his discarding of the small Danian species upon which the lowermost Danian biozones are based (and which are in the 38–63 μm size fraction at Site 738C), prevented him from recognizing that the Site 738C fauna could be integrated into the standard lower Danian global biostratigraphic zonal scheme. By fully illustrating the Site



738C Danian species in question herein (see Plates I–III) we demonstrate not only that the taxa identified by Keller are present (many of these same species were already illustrated in the 1993 publication based on samples from Site 690), but also that foraminiferal preservation is good and certainly sufficient for genus and species level identifications.

In support of Huber (1991), Huber et al. (1994–this volume) reported on two new samples from Site 738C, Core 20R-5. Their comment, however, only shows data from the 82.5–83.5 cm interval (see table 2 in Huber et al., 1994–this volume) from which they report 107 specimens (Note: 226 specimens were identified by Keller, 1993 from this interval.). These authors questionably identify only three Danian taxa, two of these only to genus. Cretaceous taxa are also questionably identified to genus or lumped into broad morphotypic categories (e.g., rugoglobigerinids). Huber et al. (1994–this volume) could not identify 20% of their specimens even to generic levels. The only Cretaceous species positively identified is *Chiloguembelina waiparaensis* Jenkins which they assign to the genus *Zeauvigerina* without providing any justification for this change in the generic assignment. This species accounts for 22% of their total assemblage whereas, in Keller (1993), it accounts for 77% of the so-called equivalent interval. Based on their analysis of this one sample, Huber et al. (1994–this volume) conclude that “quantitative study of such poorly preserved material is highly subjective even with the aid of an SEM.” However, they have only demonstrated their inability to identify the foraminiferal fauna in one sample.

There are many possible reasons for the discrepancy between the two groups’ faunal lists, including differences in sample processing technique, differences in

species concepts, and differences in sample size. The most likely reason for this non-reproducibility, however, is that their sample is not from the same interval as Keller’s. We believe this to be likely because Keller’s first set of samples, obtained in 1991 from ODP for Site 738C, Core 20R-5 between 83 and 96 cm, consisted largely of loose and misplaced sediment fragments from higher up in the core. The critical interval had already been depleted. Olsson, who requested his samples in 1993, would have received the same loose, and therefore likely displaced, fragments. In contrast, Keller’s published (1993) sample analysis for this interval is based on a set of consecutive 1 cm samples collected by E. Barrera in 1990 when this core interval was still intact. Additionally, the sample Huber et al. (1994–this volume) used is located just below a major lithologic break and suspected hiatus (see their fig. 1). Use of such an interval as a test case causes us further concern.

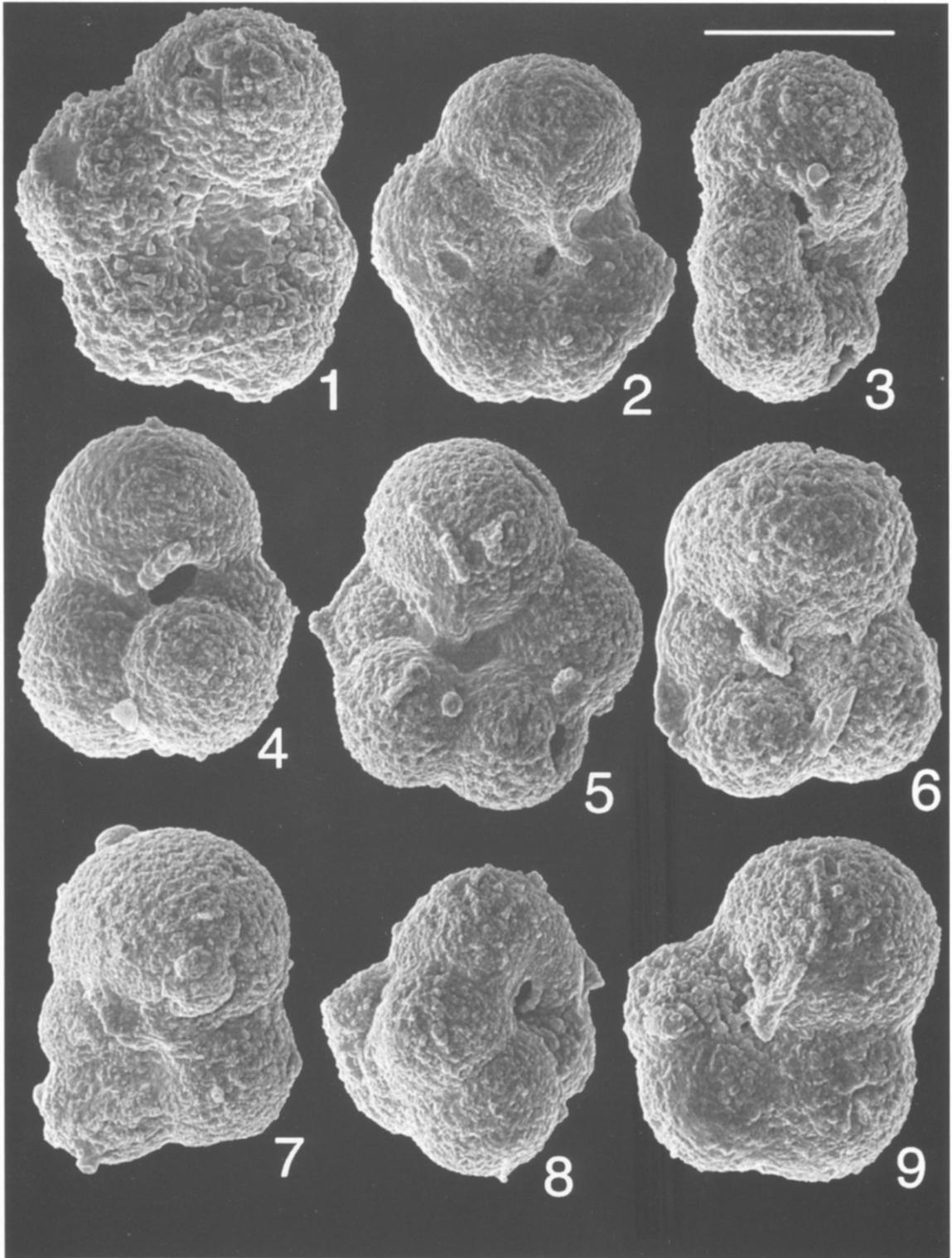
To demonstrate that foraminiferal preservation is good and that most known Danian taxa are present, we illustrate species from our sample interval 83 to 91 cm where Huber et al. (1994–this volume) claim to have examined two new samples and failed to find any unambiguously identifiable species. These authors also claimed to have found not a single whole specimen. Our SEM illustrations, shown in Plates I to III, clearly document whole specimens with reasonably good preservation. We believe that Huber’s (1991; Huber et al., 1994–this volume) failure to find whole specimens is due to differences in laboratory processing technique. Certainly, based on the specimens illustrated in Plates I to III there can no longer be any question as to either the existence or preservational state of these faunas.

Plate I

1–3. *Guembelitra cretacea* Cushman. Scale bar = 31.92 μm , 31.92 μm , and 36.06 μm , respectively. Note: triserial chamber arrangement; centrally-located, asymmetrical aperture with pronounced (2,3) but discontinuous (3) rim; and pore mounds (3); along with the fact that all specimens are whole. All samples 20R-5 (see Keller, 1993), levels 87–88 cm, 83–84 cm, and 85–86 cm, respectively.

4–6. *Chiloguembelina waiparaensis* Jenkins. Scale bar = 41.40 μm , 39.52 μm , and 39.52 μm , respectively. Note: biserial chamber arrangement and centrally-located, asymmetrical aperture with pronounced but discontinuous (4) rim; along with the fact that all specimens are whole. All samples 20R-5 (see Keller, 1993), levels 90–91 cm, 83–84 cm, and 83–84 cm, respectively (see Keller, 1993, plate I, figs. 4–9 for additional illustrations).

7–9. *Eoglobigerina danica* (Bang). Scale bar = 34.58 μm , 33.20 μm , and 31.92 μm respectively. Note: low trochospire; slowly increasing size of chambers with 4–4.5 chambers in final whorl; subglobular chambers not closely appressed or embracing; umbilicus small and open; aperture a low arch with lip, umbilical–extraumbilical. All samples 20R-5 (see Keller, 1993), levels 83–84 cm, 85–86 cm and 85–86 cm, respectively.



2. Taxonomy of planktic foraminifera of ODP Site 738c

Huber et al. (1994–this volume) claim that “there are serious flaws in the taxonomy presented by Keller (1993)”. Their criticisms are based almost entirely on Keller’s non-acceptance of their own recent taxonomic revisions (Olsson et al., 1992; Liu and Olsson, 1992; Olsson and Liu, 1993). Simple publication of a taxonomic revision cannot compel its usage. We agree with Huber et al. (1994–this volume) on “the importance of a rigorous taxonomy”, but believe that the nomenclatural and species concept-level revisions proposed by Olsson and colleagues lack both the necessary taxonomic rigor (e.g., explicit discussions of respective species concepts, along with quantitative morphometric and phylogenetic data analyses) required to justify them. Until such studies are forthcoming we believe it more prudent to retain the traditional taxonomy. Decisions such as whether or not to follow a proposed taxonomic revision are necessarily subjective and cannot be subject to enforcement over and above the standard peer-review system. Moreover, with respect to biostratigraphic analyses, so long as the morphotypes themselves are consistently identified, illustrated, and compared to either published illustrations of type material or the types themselves, the assigned names are of secondary importance.

Of the “serious flaws in the taxonomy presented in Keller (1993)”, Huber et al. (1994–this volume) list four categories of “misidentified” taxa. In their appendix 1 they assign five taxa other names without providing any discussion of the relevant type descriptions or type illustrations. In their appendix 2 they list seven species they consider “incorrectly identified” because “their stratigraphic ranges contradict all other previously established biostratigraphies”. [Note: The only previous planktic foraminiferal biostratigraphy of this region is that of Huber (1991).] Appendix 3 contains ten species considered “misidentified” because “they have never been reported from southern high latitudes”. [Note: The only previous planktic foraminiferal biostratigraphy of this region is that of Huber (1991).] And in appendix 4 they list seven species considered “misidentified” because Keller (1993) chose to use the traditional generic nomenclature, rather than follow their newly-revised (and at the time unpublished) generic taxonomy. These points are discussed below.

Of the five taxa Huber et al. (1994–this volume, appendix 1) consider misidentified *sensu stricto* by Keller (1993), two are *Globoconusa extensa* (Blow) and *G. cf. extensa* (see Keller, 1993, p. 15, plate III, figs. 4–9). Keller’s (1993) identification of this species follows Blow (1979) for the reasons given in the figs. 7–9 captions of plate III (p. 15), that states, “In this study *extensa* is placed in the genus *Globoconusa* due

Plate II

1. *Hedbergella holmdelensis* Olsson. Scale bar = 28.68 μm . Note: large test size, open umbilicus, five-chambered ultimate whorl and gradually increasing chamber size within ultimate whorl. Specimen from sample 20R-5 (see Keller, 1993), levels 90–91 cm.

2–3. *Parvularugoglobigerina eugubina* (Luterbacher and Premoli-Silva). Scale bar = 24.92 μm and 27.44 μm , respectively. Note: low trochospire, subglobular chambers, five-chambered ultimate whorl, open umbilicus, and low apertural arch, all of which are characteristic of this species’ holotypic description (see Luterbacher and Premoli-Silva, 1964). Compare with figs. 1–6 of Plate IV. Both specimens from sample 20R-5 (see Keller, 1993), level 85–86 cm.

4. *Eoglobigerina simpicissima* Blow. Scale bar = 26.21 μm . Note: small size; four-chambered last whorl; rapid increase in size of final chamber; open but slightly asymmetrical aperture with apertural rim and open umbilicus. Specimen from sample 20R-5 (see Keller, 1993), level 87–88 cm.

5. *Globanomalina pentagona* (Morozova). Scale bar = 38.00 μm . Note: high spire; open umbilicus; five chambers in final whorl; last chamber often misplaced in the normal progression of the trochospire with aperture towards central umbilical area; slit-like, low-arched aperture with lip. Specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm, (see Keller, 1993, plate IV, figs. 1–5 for additional illustration).

6–7. *Subbotina triloculinoides* (Plummer). Scale bar = 30.40 μm , 45.24 μm . Note: low trochospire; 3.5 chambers in final whorl with last chamber occupying nearly one-half of the whorl; open and deep umbilicus; aperture a low-arched opening with lip, somewhat asymmetrical with respect to the center of the umbilicus. Specimen from sample 20R-5 (see Keller, 1993), level 87–88 cm.

8. *Globoconusa conusa* Khalilov. Scale bar = 31.67 μm . Note: small size; high, tightly-coiled trochospire; appressed, subglobular chambers; and umbilical aperture. Specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm.

9. *Eoglobigerina fringa* (Subbotina). Scale bar = 23.24 μm . Note: small size; low, tightly-coiled trochospire; four-chambered ultimate whorl, and arched umbilical aperture. Specimen from sample 20R-5 (see Keller, 1993), level 87–88 cm.

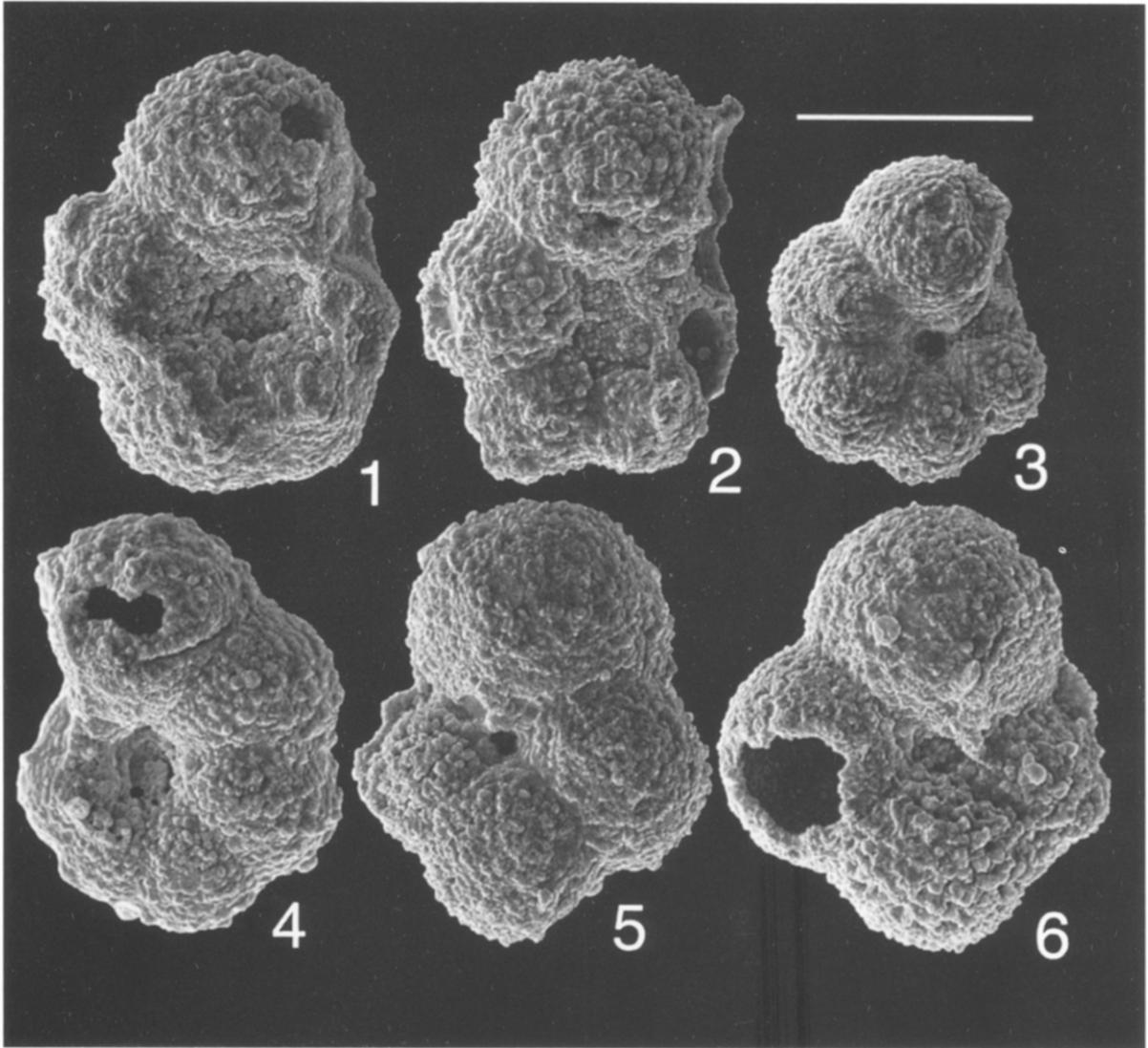


Plate III

1–2. *Subbotina pseudobulloides* (Plummer). Scale bar = 33.33 μm , respectively. Note: subglobular chambers; five-chambered ultimate whorl; open umbilicus; arched umbilical aperture with a pronounced lip (1). Specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm. (see Keller, 1993, plate II, figs. 12,13 for additional illustrations).

3. *Globanomalina taurica* (Morozova). Scale bar = 52.63 μm . Note: low trochospire; 5 chambers in final whorl; chambers subglobular; last chamber often displaced towards umbilicus; test circular in overall outline; aperture a low arch, umbilical–extraumbilical; specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm. (see Keller, 1993, plate II, figs. 14–16 for additional illustrations).

4. *Hedbergella monmouthensis* Olsson. Scale bar = 30.77 μm . Note: open deep umbilicus; slow increase in chamber size; 6 chambers in last whorl; globular appressed chambers. Specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm.

5. *Eoglobigerina fringa* (Subbotina). Scale bar = 30.77 μm . See Plate I (9) for distinguishing features. Specimen from sample 20R-5 (see Keller, 1993), level 83–84 cm.

6. *Planorotalites compressus* (Plummer). Note: compressed rapidly increasing chambers; 4.5–5 chambers in final whorl; open umbilicus; aperture low-arch with lip, umbilical–extraumbilical. Specimen from sample 20R-5 (see Keller, 1993), level 87–88 cm (see also Keller, 1993, plate II, figs. 4,8,9 for additional illustrations).

to its similar wall-structure to *G. daubjergensis* and the presence of specimens without open apertures (*G. cf. extensa*) which indicates that apertural size is not a sufficient characteristic for placement in a different genus." In their comment, Huber et al. (1994-this volume) prefer to place this species in a completely different genus and species, *Antarcticella pauciloculata* (Jenkins), based on its apertural characteristics. Given the undiscussed discrepancy between Blow's (1979) description and their own concept of this morphotype, their objection seems more a matter of opinion than fact.

The same is true of *Globanomalina pentagona* which they prefer to classify as *Eoglobigerina edita* and *Morozovella inconstans* which they prefer to call *Praemurica taurica* after Olsson et al. (1992). Neither of these specimens resembles the type illustrations of *E. edita* or *G. taurica*, and the Olsson et al. (1992) taxonomic revisions are wholly based on wall structure, an as yet unproven and likely insufficient criterion for generic or specific assignment. [Note: during the final revision of their comment Huber et al. (1994-this volume) added a paragraph that cites a long line of distinguished foraminiferal taxonomists in support of their claim that wall structure is of primary importance to generic and species identification. In fact, these taxonomists only point out the incontestable fact that wall structure has traditionally been used to organize the higher levels of foraminiferal taxonomy. The assumption that because a set of characters has historically been used to separate broad morphotypic groups, other "wall structure" characters must be of importance at lower taxonomic levels is unprecedented in previous published treatments of foraminiferal taxonomy (see their citations) as well as all general treatments of contemporary systematic practice (Mayr, 1969; Wiley, 1981; Smith, 1994). Perhaps even more importantly, though, such a proposition belies an approach to taxonomy that seeks to impose order instead of discovering it.] The fifth "misidentified" species is *Subbotina triloculinoides* (Keller, 1993, plate III, fig. 10, p. 14) which Huber et al. (1994-this volume) claim has 4 chambers rather than 3 to 3.5 in the final whorl. The illustration, in fact, has 3.5 chambers with the last chamber occupying nearly one-half of the whorl, as required by the definition of this species (Plummer, 1926). Granted, this specimen is not the best, but it is, after all, early in its evolutionary lineage. Additional

specimens of *S. triloculinoides* from Site 738C are illustrated in Plate II (6,7).

In appendix 2, Huber et al. (1994-this volume) list species they regard as "incorrectly identified" by Keller (1993) because the implied stratigraphic occurrences are anomalous with respect to the low-latitude biostratigraphy of Berggren and Miller (1988). This objection is apparently based on the assumption that the stratigraphic ranges of all planktic foraminiferal species are isochronous. Simple biostratigraphic experience and many recent empirical studies (see Hedberg, 1976; Hazel et al., 1984, Hazel, 1989; Piasis et al., 1984; Dowsett, 1988, Dowsett, 1989; Prell et al., 1986; Hills and Thierstein, 1989; Johnson et al., 1989; Keller and Benjamini, 1991; MacLeod, 1991, in press a,b,c; MacLeod and Keller, 1991a, MacLeod and Keller, 1991b, 1994; Jenkins and Gamson, 1993) as well as speciation theory (Mayr, 1982) have repeatedly shown that, at high levels of temporal resolution, species ranges are inherently diachronous, especially among different biogeographic provinces. This phenomenon is routinely encountered when comparing tropical with high-latitude species ranges. Significantly, Huber et al. (1994-this volume) do not disagree with the SEM illustrations of these species provided in plates I to IV of Keller (1993) which clearly show that these species are present. They simply deny that their ranges could be different from those previously published by Berggren and Miller (1988). Graphic correlation of over 30 K/T boundary sequences by MacLeod and Keller (1991a,b, see also Keller and Benjamini, 1991; MacLeod, in press a,b,c) has shown that many first and last appearance datums listed by Berggren and Miller (1988) are markedly diachronous across latitudes and therefore cannot be used as unambiguous chronostratigraphic markers.

In appendix 3 Huber et al. (1994-this volume) list a third group of species which they consider incorrectly identified by Keller (1993) because "they have never been reported from southern high latitudes". Very few studies of southern high-latitude sections have been published to date and even less is known of this fauna's transition across the K/T boundary. Accordingly, there is no reliable standard of comparison upon which to base such a criticism. More importantly though, there is no a priori reason why the taxa identified by Keller (1993) should not be present. Keller has identified and published (in the peer-reviewed literature) descrip-

tions of similar Maastrichtian to lower Tertiary faunas in over 35 K/T boundary sections worldwide. Keller's species concepts have also been quantitatively tested in global biogeographic studies and found to yield both consistent and ecologically-reasonable patterns of geographic expansion/contraction (MacLeod and Keller, 1994; MacLeod, in press a).

Many of the Huber et al. (1994-this volume) criticisms of Keller's (1993) taxonomy are also based on incorrect, novel, and/or completely undocumented taxonomic revisions. These are discussed below.

(1) Huber et al. (1994-this volume) claim *Heterohelix complanata* to be synonymous with *H. planata* although this has not been previously proposed in the technical literature and is not demonstrated in the context of their comment. *Heterohelix planata* (Cushman) was illustrated and described as having a compressed test, rapidly increasing chamber size, a slightly keeled periphery in the early portion of the chambers, depressed triangular areas separating chambers in the later portion, and a high arched aperture with distinct lateral flanges overlapping the preceding chamber. *Heterohelix complanata* (Marie) was described as differing from *H. planata* in the slower rate of chamber increase, more embracing and less globular chambers, smaller and less triangular sutural depressions between the chambers and the absence of a peripheral keel and sutural flanges overlapping the preceding chambers. We believe that these morphologic differences warrant the separation of these two forms into two species as originally described, at least until a thorough morphometric study of the diagnostic characters has been published.

(2) Huber et al. (1994-this volume) consider the coarsely costate species *Pseudotextularia deformis*, synonymous with the smooth-walled morphotype *P. elegans*. This is an interpretation with which we, as well as many others, disagree (e.g., Smith and Pessagno, 1973; Weiss, 1983; Masters, 1977; Caron, 1985; Keller, 1988, 1989a, 1993). They then state that, since no other high-latitude study has reported *P. elegans*, Keller must be incorrectly identifying it. However, Huber (1991, pp. 452–453) lists *P. elegans* as an important first occurrence in the *A. mayaroensis* Zone of Site 738C and Bertels (1970) identified this species from the upper Cretaceous of Patagonia (Argentina).

(3) Huber et al. (1994-this volume) state that *Pseudoguembelina palpebra*, has not been previously

reported south of 44° S paleolatitude, thereby concluding that this species must be incorrectly identified in Keller (1993) (see above).

(4) Huber et al. (1994-this volume) also consider *Parvularugoglobigerina eugubina* and *P. longiapertura* to be synonyms. Moreover, they report that they could not find any *P. eugubina* in the samples from the P1a Zone of Keller (1993). [Note: due to a typesetting error in table 1 of Keller, 1993, p. 6, a group of Danian species, including *P. eugubina*, *P. compressus*, *S. moskvini*, *S. pseudobulloides*, *S. triangularis* and *S. triloculinoides*, was offset by three samples towards the left (older) side. Because of this error, the first appearances of these species is listed in sample 20R-5, 90–91 cm, instead of sample 20R-5, 87–88 cm.] In fact, *P. eugubina* is well-represented in all samples as we illustrate in Plate II (2,3), and *P. longiapertura* is present, but rare (see plate V of Keller, 1993, p. 18). Although Huber et al. (1994-this volume) would place these specimens in *Hedbergella* or *Eoglobigerina*, this is clearly incorrect since all four of these taxa have very different morphologies, as shown in our SEM illustrations (Plate II). Huber et al. (1994-this vol., fig. 2 caption) also state that *Hedbergella monmouthensis* is easily misidentified as *S. pseudobulloides*. However, these two species are so different in overall morphology, rate of chamber increase, aperture, and spiral sides, (see Plate II, 1, Plate III, 1,2) that misidentification is difficult.

Huber et al. (1994-this volume) list Olsson and Liu (1993), Liu and Olsson (1992), and Olsson et al. (1992) in support of their contention that *P. longiapertura* is a synonym for *P. eugubina*. However, only in Liu and Olsson (1992) is the question of the proposed synonymy between *P. eugubina* and *P. longiapertura* mentioned and then only insofar as the name *G. (T.) longiapertura* is included as part of the *P. eugubina* synonymy list. The only paper known to us that explicitly deals with this topic is Smit (1982). Olsson et al. (1992) and Olsson and Liu (1993) mention the microperforate nature of their *P. eugubina* wall structure as a possible indicator of phylogenetic relationship between this species and *Guembelitria cretacea*. But these papers never mention *P. longiapertura* by name, present any morphological data pertaining to *P. longiapertura*, or formally propose the synonymy implied by Huber et al. (1994-this volume).

(5) Since *P. eugubina* is an important lower Danian biostratigraphic marker, and since several different species concepts are currently being employed under this name, it is worthwhile to briefly review the taxonomic aspects of this controversy (for a more complete discussion see MacLeod, in press b). From a systematic perspective, this controversy results from changes that have taken place in the species concept of *P. eugubina* over the last 30 years. *Globigerina eugubina* was first described and illustrated by Luterbacher and Premoli-Silva (1964; see also Toumarkine and Luterbacher, 1985) as a small form with a low trochospire, 5–6 subglobular chambers in the last whorl, an open shallow umbilicus, and an umbilical–extraumbilical aperture consisting of a low arch. Their illustrations are reproduced in figs. 1–3 of Plate IV. Blow (1979) characterized his new species *Globorotalia (Turborotalia) longiapertura* as having a most unusual primary aperture that he describes as a “widely open, elongate, opening which extends from the umbilicus, beyond the peripheral margin, to the area of the terminal anterior face of the last chamber” (p. 1086). Illustration of the *G. (T.) longiapertura* holotype is reproduced as fig. 7 of Plate IV.

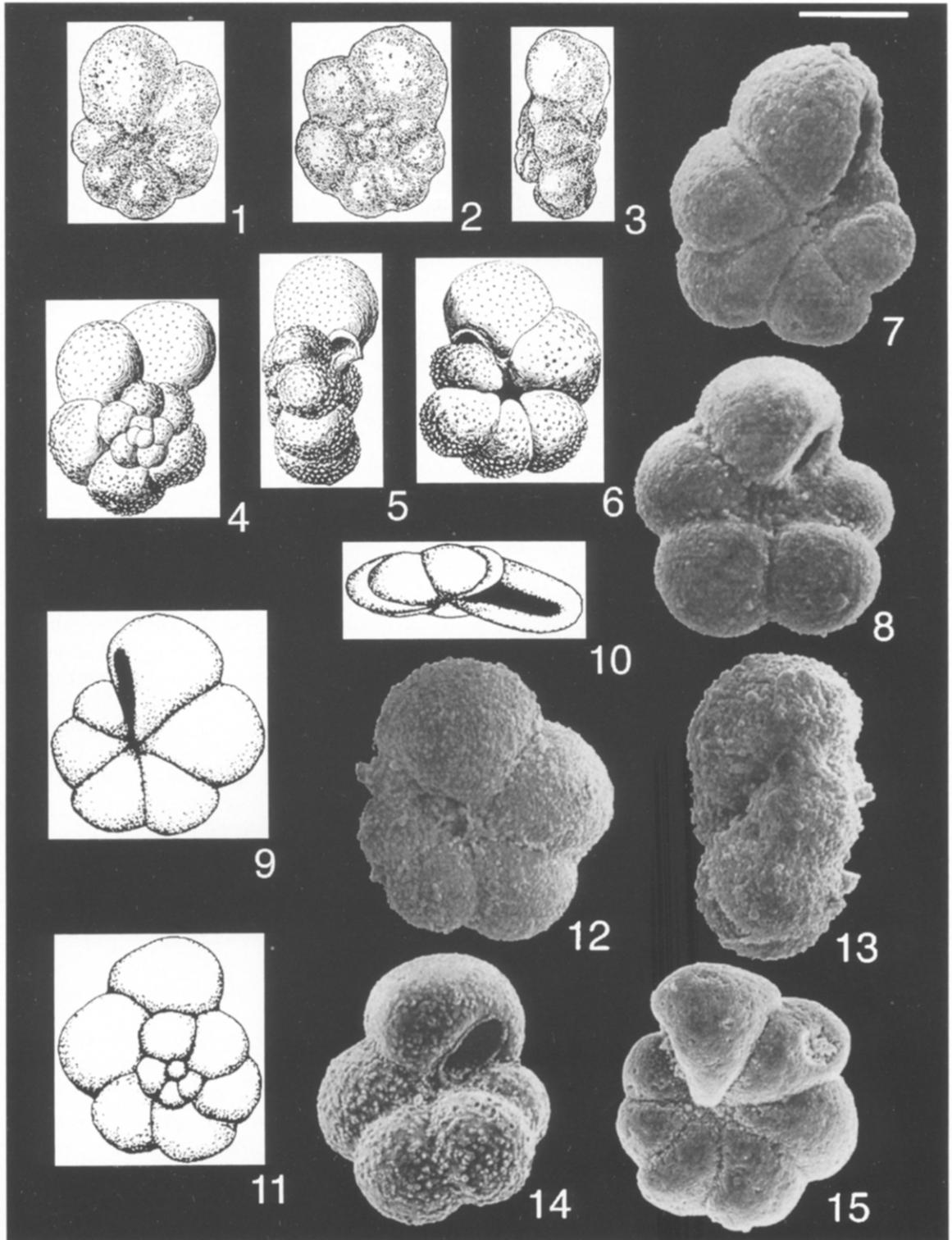
Comparing these descriptions and illustrations *G. (T.) longiapertura* is easily distinguished from *G. eugubina* by the former’s far more cuniform chamber shape, which imparts a laterally compressed aspect to individual chambers as well as to the test as a whole, its smaller and deeper umbilicus, and by its unusually elongate and parallel-sided primary aperture. Hofker (1978) published illustrations of *G. eugubina* (reproduced as figs. 4–6 of Plate IV) from DSDP Site 47.2 that clearly show the low primary aperture and subglobular aspect of this species’ chambers. Hofker (1978) also selected *G. eugubina* as the type species of his new genus *Parvularugoglobigerina* though this revision has been questioned by Premoli-Silva (1977), Bang (1980), and Toumarkine and Luterbacher (1985). The latter regard the generic affinities of the *P. eugubina* morphotype as remaining uncertain.

Blow’s (1979) selection of paratypes for *G. (T.) longiapertura* appears to be primarily responsible for the present controversy. While most of his figured paratypes resemble his holotype, others exhibit morphologies similar to *G. eugubina* with the exception of the aperture which, in Blow’s paratypes, seems to be substantially larger than the low aperture originally

described by Luterbacher and Premoli-Silva (1964) and illustrated by Hofker (1978). A representative photomicrograph of this morphotype from Blow (1979) is reproduced as fig. 8 of Plate IV. Nevertheless, Blow (1979) evidently considered the differences between his *G. (T.) longiapertura* and *G. eugubina* (which he discusses on p. 1375) to be of sufficient magnitude so as not to warrant a detailed description. In fact, Blow’s (1979) discussion of *G. eugubina* fails to even mention *G. (T.) longiapertura*.

In his study of trans-K/T faunas from the Caravaca section in southern Spain, Smit (1982) synonymized Blow’s *G. (T.) longiapertura*, along with several other minor globigerine species also described by Luterbacher and Premoli-Silva (1964), into *G. eugubina*. Smit’s illustrations reproduced as figs. 9–11 of Plate IV show all salient aspects of Blow’s (1979) *G. (T.) longiapertura* and virtually none of the distinguishing characteristics of Luterbacher and Premoli-Silva’s (1964) *G. eugubina*. It is this *G. (T.) longiapertura* species concept that Liu and Olsson (1992) use in their re-description of *P. eugubina*. Smit’s (1982) synonymy (that was accepted but not initially proposed by Liu and Olsson, 1992) changes the original concept of Luterbacher and Premoli-Silva’s (1964) *G. eugubina* into a polytypic species in which the elongate longiapertura-like morph is dominant. All of Smit’s (1982) and Liu and Olsson’s (1992, see also Olsson et al., 1992) “*eoglobigerina*-like” morphs exhibit the large, umbilical–extraumbilical apertures of Blow’s (1979) globular-chambered *G. (T.) longiapertura* paratypes instead of the smaller and more umbilically-directed aperture of Luterbacher and Premoli-Silva’s (1964) *G. eugubina*. This low-apertured morph does exist, however (see figs. 12 and 13 of Plate IV), and has been consistently identified by Keller and colleagues as their *P. eugubina* to distinguish it from the longiapertura-like morphotypes often found in the same lower Danian samples.

We concur with Blow (1979) and advocate separation of the *P. eugubina* and *P. longiapertura* morphotypes into different species based on their radically different morphologies as well as their different stratigraphic ranges (MacLeod, in press b,c). Indeed, we suspect, but have not formally presented our evidence, that these two species also belong to entirely different genera. Moreover, we believe that a complete review of a species concept’s history, such as that presented



above, is necessary prior to recommending any taxonomic revision. The taxonomic assertions that dominate the discussion in Huber et al. (1994-this volume) completely fail to provide the necessary information that would allow independent investigators to objectively judge their validity. Such an approach constitutes little more than an ascientific appeal to taxonomic "authority" instead of a reasoned discussion from morphological evidence.

(6) Huber et al. (1994-this volume) contend that both *Guembelitra danica* and *Guembelitra trifolia* are junior synonyms of *Guembelitra cretacea*, citing Liu and Olsson (1992) and unspecified "others" in defense (see their appendix 3, paragraphs f and g) of their case. As before (see above), Liu and Olsson (1992) is used to support particular positions when, in fact, this paper contains no discussion of the relevant issues whatsoever. Liu and Olsson (1992) do present a case for derivation of Paleocene microporiferate taxa from *G. cretacea*, but this paper makes no reference to either *G. danica* or *G. trifolia*, much less to any proposed synonymy between these species and *G. cretacea*.

In addition, Huber et al. (1994-this volume) refer to unspecified "others", the identity of which we are unable to determine. No reference is made to either *G.*

danica or *G. trifolia* in Olsson et al. (1992). Similarly, Olsson and Liu (1993) contains no proposal of synonymy between *G. danica*, *G. trifolia*, and *G. cretacea*. Inexplicably, Huber et al. (1994-this volume) fail to mention the two most recent analyses of trans-K/T guembelitrid phylogeny. D'Hondt (1991) recognized the taxonomic distinction between *G. cretacea* and *G. danica* (the latter of which he referred to the genus *Chiloguembelitra* following Hofker, 1978) while MacLeod (1993) recognized the separation between all three species and devoted considerable effort to clarifying the relevant morphological distinctions. Of course, many prior references supporting recognition of all three morphotypes as distinct species are also present throughout the planktic foraminiferal literature (e.g. Hofker, 1978 for *G. danica*; Smit, 1982 for *G. trifolia*). So far as we are aware, prior to Huber et al. (1994-this volume) no one has ever formally proposed a synonymy between *G. cretacea*, *G. trifolia*, and *G. danica*.

(7) Huber et al. (1994-this volume) mistakenly claim that Keller assigned the genus and species *Eoglobigerina danica* to a biserial taxon. Their claim is based on a misprint on page 40 of Keller (1993) that erroneously lists *E. danica* among biserial instead of trochospiral taxa. In the remaining discussion of her

Plate IV

1–15. Morphotypes variously attributed to *Parvularugoglobigerina eugubina* (Luterbacher and Premoli-Silva). Scale bar = 68.35 μm (1–3), 68.04 μm (4), 91.39 μm (5–7), 55.88 μm (8), 47.15 μm (9–11), 50.55 μm (12), 49.08 μm (13), 69.86 μm (14), 31.02 μm (15).

1–3. Holotypic illustrations of *G. eugubina* from Luterbacher and Premoli-Silva (1964). Note: subglobular chambers, shallow umbilicus (1), and no hint of a long umbilical–extraumbilical aperture (1–3).

4–6. *P. eugubina* morphotype illustrated by Hofker (1978). Note overall similarity with Luterbacher and Premoli-Silva's type illustration (1–3) along with the low aperture alluded to in the type description but not shown in the type illustration.

7. Holotype of *G. (T.) longiapertura* from Blow (1979). Note the distinct lateral compression of the markedly cunifiform chambers, deep umbilicus, and highly characteristic long, slit-like umbilical–extraumbilical aperture extending more than halfway up the face of the ultimate chamber.

8. Round-chambered paratype of *G. (T.) longiapertura* from Blow (1979). Note pronounced differences between this morphology and that of the *G. (T.) longiapertura* holotype (7), as well as both similarities (e.g., subglobular chambers, straight sutures) and differences (e.g., much larger and more extraumbilically-directed aperture) with respect to typical *P. eugubina* s.s. (compare to 1–6).

9–11. Dominant *G. eugubina* morphotype of Smit (1982). Note similarity in virtually all respects to the *G. (T.) longiapertura* holotype (7) as well as differences with respect to typical *P. eugubina* s.s. (1–6). Smit (1982) also figured some round-chambered morphotypes as *P. eugubina* but these exhibit morphologies much closer to Blow's (1979) round-chambered paratypes of *G. (T.) longiapertura* (8) than *P. eugubina* s.s.

12–13. Round-chambered morphotype referred to by Keller (1993, and in many previous publications) as either *P. eugubina* or *P. eugubina* (round). Note similarity in all salient respects with illustrations of *P. eugubina* s.s. (1–6), including the low, umbilically-directed aperture, as well as differences between this morphotype and Blow's (1979) round-chambered *G. (T.) longiapertura* paratypes (8).

14. Specimen identified by Olsson et al. (1992) as *P. eugubina*. Note similarity of this specimen with Blow's (1979) round-chambered *G. (T.) longiapertura* paratypes (8) but differences between this morphotype and *P. eugubina* s.s. (1–6).

15. Laterally compressed, cunifiform-chambered morphotype identified by Keller (1993, and in many previous publications) as *P. longiapertura*. Note striking similarity between this morphotype and Blow's (1979) *G. (T.) longiapertura* holotype (7) as well as differences between it and typical *P. eugubina* s.s.

paper, and in the illustrations, this morphotype is clearly identified as a trochospiral form. Moreover, they refer to this species as “probably a junior synonym of *G. planocompressa*” without discussing any morphological data or citing original descriptions.

(8) Keller (1988, 1993) identified a high-spined quadriserial morphotype as *Globoconusa conusa* Chalilov and not *Globigerina minutula* Luterbacher and Premoli-Silva as noted by Smit (1982). Liu and Olsson (1992) refer to this morphotype as *P. eugubina* and call it the most primitive stage of this species. They base this interpretation on similar surface structures between these two species. However, while both species show pore volcanoes, this is also the case for all *Guembelirria* species as well as *Woodringina hornerstownensis* (see Keller, 1989a, plate 3, p. 318). By the criteria specified in Huber et al. (1994-this volume) it would seem that these species should also be lumped into *P. eugubina*! The morphotype of *G. conusa* is so different from *P. eugubina* or *P. longiapertura* in the number of chambers, chamber arrangement, high trochospire, aperture, and wall structure that lumping it with this group makes little sense (see illustrations in Plate II, fig. 8, Plate IV as well as Keller, 1993, plate V).

(9) Huber et al. (1994-this volume) cite Liu and Olsson (1992) in support of their contention that *Subbotina moskvini* Shutskaya is a synonym of *E. simplicissima* Blow. However, (once again) these species are never mentioned in the cited paper. To date there has been no morphometric and phylogenetic analysis of these two species and their obviously different morphologies do not support the proposed synonymy.

(10) In appendix 4, Huber et al. (1994-this volume) further criticize Keller’s taxonomic assignments, this time based on the generic level. Since generic assignments are much less well-established than species concepts, and since neither they, nor any other publications have produced a detailed phylogenetic study of the genera in question, we believe it is more prudent to use established names rather than introduce further taxonomic confusion. We will only briefly remark on “*Globigerinoides*” (sic *Globigerinelloides*) *monmouthensis* which Huber et al. (1994-this volume) erroneously claim Keller (1993) combines with *Hedbergella monmouthensis*. This morphotype, which Keller usually identifies as “*G.*” *monmouthensis*” to distinguish it from *Hedbergella monmouthensis*, has an

uncertain generic affinity, and refers to the morphotype illustrated by Smith and Pessagno (1973, plate 27, figs. 7–9, pp. 60–61) as *Globotruncanella monmouthensis* (Olsson). It includes 4 to 4.5 chambered forms with relatively high trochospiral tests, inflated spherical chambers and a wide-open, highly-arched umbilical to extraumbilical aperture. Although Smith and Pessagno (1973) included this morphotype in Olsson’s *Hedbergella monmouthensis* (but placed it in the genus *Globotruncanella*), there are substantial differences that we believe warrant separation of these two forms. For instance, the initial spire in “*G.*” *monmouthensis* always protrudes significantly above the last whorl, whereas in *H. monmouthensis* coiling is in one plane; the aperture is always a wide gaping hole, more umbilical than extraumbilical, whereas in *H. monmouthensis* the aperture is a low extraumbilical to umbilical arch. We agree that the phylogenetic affinity of this morphotype still needs to be investigated before a definite generic assignment can be made, but also hasten to point out that this is similarly true for many of the species questioned by Huber et al. (1994-this volume) and re-classified by Olsson and Liu (1993), Liu and Olsson (1992) and Olsson et al. (1992).

3. Stratigraphy

Huber et al. (1994-this volume) question Keller’s statement that “a nearly continuous sedimentation record” is present citing poor core recovery. Poor core recovery is true for core 20R and 21R as a whole but not for the K/T boundary transition which is continuous in a laminated clay sequence as they illustrate in their fig. 1. The full quote of Keller is as follows: “Thus, a nearly continuous sedimentation record is present immediately below the K/T boundary. Chronologically, the age of this interval cannot be determined because of poor core recovery below this interval. The sediments present, however, are reported to be of C29R age which spans the last 350,000 years of the Cretaceous and the first 230,000 to 280,000 years of the Tertiary” (Keller, 1993, p. 15). This passage clearly states that the uppermost Maastrichtian is present and that Keller (1993) could not precisely determine its absolute age. However, since this interval is in the Maastrichtian part of C29R, it cannot be older than the last 350,000 years of the Cretaceous. Huber et al.

(1994-this volume) also question Keller's samples at 110–111 cm and 114–115 cm as possibly not in place since their core illustration shows chert nodules surrounded by calcareous sediments. We agree that these samples may have been displaced in the core, just as we believe their 82.5 to 83.5 cm interval test sample was probably displaced from its original position (see above). Possible displacement of our samples at 110 and 114 cm, however, does not change the Maastrichtian age and stratigraphy of this interval.

Huber et al. (1994-this volume) quote Keller's abstract and page 18 as claiming "a resolution of both a few thousand years and 200,000–300,000 years can be obtained from below the K/T boundary at Site 738". In fact, Keller (1993 p. 1) states "The cosmopolitan nature of the dominant fauna began during the last 200,000 to 300,000 years of the Cretaceous and continued at least 300,000 years into the Tertiary" and on page 18, "This indicates global dominance of a generalist fauna able to tolerate a wide range of conditions during at least the last 200,000 to 300,000 years of the Cretaceous." Both statements are correct given available biostratigraphic and magnetostratigraphic data. The C29R/C30N boundary at Site 738C was never at issue. But if it were, where does the sediment accumulation rate of 2.88 cm/1000 years quoted by Huber et al. (1994-this volume) come from if not from the assumption of continuous sediment accumulation? Keller's Zone P1b which is above the last appearance of *P. eugubina*, does indeed correspond to the lower part of C29N, according to the Berggren et al. (1985) time scale. Since a hiatus and major lithologic break is present at this interval at Site 738C (see fig. 1 of Huber et al., 1994-this volume) the magnetostratigraphy in the limestone above this interval is not definitive. Thus, we find no discrepancy in the biostratigraphy of Keller (1993).

4. Hiatuses

Huber et al. (1994-this volume) claim that the two Danian hiatuses identified by Keller (1993) at the P0/P1a and P1a/P1b zonal boundaries "are entirely the result of inconsistent and erroneous species identification." They support this statement by citing two nanofossil studies (Wei and Thierstein, 1991; Wei and Pospichal, 1991) plus Huber's (1991) study that failed

to identify any hiatuses. However, the Lower Danian nanofossil biozonation is well-known to have much lower stratigraphic resolution than the coeval planktic foraminiferal zonation (see Harland et al., 1990). Also, since Huber did not identify most Danian species, he was unable to employ a biozonation that would have revealed them.

The P0/P1a and P1a/P1b zonal boundary hiatuses identified by Keller (1993) are not unique to Site 738C, they have been recognized based on planktic foraminiferal biostratigraphy in many K/T boundary sections (see Keller, 1989a, b; Keller et al., 1993, 1994; Canudo et al., 1991; Keller and Benjamini, 1991). These same hiatuses have also been recognized in graphic correlations of over 35 sections globally including ODP Site 738C (MacLeod and Keller, 1991a,b; MacLeod, in press, a,b,c). Moreover, there is also physical evidence of a lithological break in the core (see fig. 1 of Huber et al., 1994-this volume at core interval 80–82 cm) that correlates with the P1a/P1b hiatus identified by Keller (1993).

5. Keller's biozonation

Huber et al. (1994-this volume) state that Keller's P-zones are "confusing and misleading for four primary reasons." (1) They bear little resemblance to those of Berggren and Miller (1988), (2) Keller's zonal definitions "have changed through a series of papers without a change in zonal terminology (Table 1)", (3) discrepancies between Keller's (1993) text and tables, and (4) incorrect taxonomy. These points are addressed individually below:

(1) Given the fact that a large number of K/T planktic foraminiferal zonations exist, the exclusive reference by Huber et al. (1994-this volume) to the Berggren and Miller (1988) zonation is striking. The Berggren and Miller (1988) zonation is demonstrably inaccurate for the lowermost Danian because it fails to recognize the basal Danian equivalent to Zone P0 of Smit (1982) and Keller (1993). Zone P0 is clearly present in the El Kef K/T stratotype section as well as all other complete K/T boundary sections known to date (e.g., Agost, Caravaca, Brazos River, Miller's Ferry, Mimbral, Nye Kløv, Site 738C). Berggren and Miller's (1988) first Danian Zone (Pa) is defined by the FAD of *P. eugubina* at its base and the FAD of *S.*

PLANKTIC FORAMINIFERAL ZONATIONS								
	Datum events	Keller, 1988a, 1993 Pardo et al., in press	Keller & Benjamini, 1991	Canudo, 1991	Keller, 1989	Keller, 1988	Berggren & Miller, 1988	
Lower Paleocene (Danian)	± M. trinidadensis	P1d	P1d	P1d	no data	P1d	P1c	
	± M. inconstans	P1c	P1c	P1c		no data	P1c	P1a & P1b
	± G. conusa ± S. varianta	P1c(1)			P1c(2)			
	± P. eugubina ± P. longiapertura	P1a	P1a(2)	P1a	P1a	P1b(1)		
	± P. compressus ± E. trivialis ± G. pentagona ± S. pseudobulloides ± S. nicolaioides ± G. daubergensis ± S. moskvini ± P. planocompressus ± G. taunca ± C. midwayensis						P1a(1)	P1a
	± P. eugubina, ± P. longiapertura ± E. subuloides ± E. edita, W. hornorst ± E. fringa, E. simplicis ± G. conusa ± P. hantkeninoides,	P0	P0	P0b	P0	P0b	unzoned	
	U. Maastr.	± P. hantkeninoides	P. hantkeninoides	K/T boundary A. mayaroensis	P0a	P. deformis	P0a	A. mayaroensis
		± A. mayaroensis	A. mayaroensis				P. deformis	

Fig. 1. Planktic foraminiferal biozonation of Keller (1993) and datum level sequence based on a composite data set of 15 of the most complete K/T boundary sequences (MacLeod and Keller, 1991a) compared with earlier published zonations of Keller's group and that of Berggren and Miller (1988). Keller's (1988) original zonal scheme was based on El Kef and incorporated Smit's (1982) zonation. Subsequent studies of over 30 K/T boundary sequences required three modifications: (1) The subdivision of Zone P0 at El Kef was based on the FAD of *G. conusa* but recent re-analysis revealed that the FAD of *G. conusa* coincides with K/T boundary, thus P0 is no longer subdivided. (2) The top of Zone P1a was originally defined by the proliferation of *Eoglobigerina* spp. at El Kef which was later found to be a local occurrence. Zone P1a was then defined as total range Zone of *P. eugubina* and/or *P. longiapertura* (see Canudo et al., 1991). (3) The Zone P1b/P1c boundary was originally defined by the last occurrence of *G. taunca* at El Kef. This datum event was later found to be diachronous and the FAD of *S. varianta* was substituted.

pseudobulloides at its top. The former species is not present at the K/T boundary in the stratotype section but first appears 50 cm above that horizon (Keller, 1988; Ben Abdalkader, 1991) while the latter is generally diachronous (see Keller and Benjamini, 1991; MacLeod and Keller, 1991a,b; MacLeod, in press b, c). Keller (1993) used *S. pseudobulloides* to subdivide her Zone P1a in order to provide a correlation point to Berggren and Miller's (1988) zonation. Above their Zone Pa there is no subdivision equivalent to Keller's zones P1a, P1b and P1c in the Berggren and Miller (1988) zonal scheme, thus the latter ignores critical biostratigraphic information (see Fig. 1). For these reasons, Keller's (1993) biozonation is preferable for high-resolution studies.

(2) The second claim, that Keller's biozonation changed over time, is both true and false. Keller's biozonation has been modified over time. This is a natural outcome of many years of K/T boundary studies. Keller's (1988) zonation was originally based on the K/T boundary section at El Kef and incorporated Smit's (1982) proposed zonation. Subsequently, over 35 K/T sections have been analyzed necessitating refinement of the original 1988 zonation (see Fig. 1). Huber et al. (1994-this volume) mistakenly claim their table 1 represents Keller's zonation (see Fig. 1 for the correct biozonation). In none of Keller's papers is Zone P0 above the K/T boundary. Nor does the last occurrence of Cretaceous taxa define the K/T boundary as Huber et al. (1994-this volume) erroneously suggest. The K/

T boundary is defined by multiple biostratigraphic and geochemical criteria based on the El Kef K/T stratotype and found to be practically applicable to K/T boundary correlations worldwide. In terms of planktic foraminifera, however, the K/T boundary is defined by the first appearance of Tertiary species (*G. conusa*) which at El Kef appears within the sample representing the first centimeter above the base of the boundary clay layer (Ben Abdalkader et al., 1992), the Ir anomaly, the Ni-rich spinels, and the drop in $\delta^{13}\text{C}$ values that also mark the K/T boundary. In no complete K/T boundary sequence is a mass extinction of all observed Cretaceous taxa coincident with the K/T boundary.

(3) Huber et al. (1994-this volume) claim that discrepancies exist between Keller's zonation (see Keller, 1993, fig. 2, p. 17 and fig. 3, p. 19) and data discussion in text and tables. This is not so. As stated in the fig. 2 caption (p. 17), the refined zonation is "based on a composite data set of 15 of the most complete K/T boundary sequences (MacLeod and Keller, 1991)". In contrast, fig. 3 (p. 19) shows the actual datum events and biozonation of Site 738C. Huber et al. (1994-this volume) are correct in noting that Keller subdivides Zone P1a(1) and P1a(2) based on the first occurrence of *S. pseudobulloides*. However, they fail to note that, at Site 738C, the first appearance of *S. pseudobulloides*, which, in all complete K/T boundary successions takes place in the middle of Zone P1a (see fig. 2 of Keller, 1993) coincides with the first appearance of *P. eugubina* and six other Danian species all of which generally first appear in the lower half of Zone P1a (see fig. 3 of Keller, 1993). It is the co-occurrence of all these species, all of which constitute a set of very different morphologies (whatever names they might be assigned), in the same sample that provides evidence for recognition of a hiatus in which the lower part of Zone P1a is inferred to be missing (see Keller, 1993, fig. 5, p. 21).

(4) Huber et al. (1994-this volume) once again fault Keller for not using their revised taxonomy. [Note: the reader is referred to the discussion of taxonomic issues above.] Specifically, they wish to label *M. inconstans* as *Praemurica taurica* (*G. taurica* of Keller) and then state that this taxon first occurs in their Zone Pa or Zone P1a of Keller. Fig. 1 of Keller (1993) shows that this is indeed correct for *G. taurica*, but certainly not for *M. inconstans*.

6. High-latitude center of origin

Keller (1993, p. 41) states that certain species, including *Eoglobigerina danica*, *Chiloguembelina waiparaensis*, *Woodringina claytonensis*, *Igorina spiralis*, *Murciglobigerina aquiensis* and *M. chascanona*, are endemic to northern and southern high-latitudes during the Danian. Huber et al. (1994-this volume) claim that, with the exception of *C. waiparaensis*, all other species are either incorrectly identified or also recognized in Danian sediments of low latitudes. In the earlier discussion they listed as incorrectly identified any species whose biostratigraphic range does not agree with that published by Berggren and Miller (1988, see discussion above), disregarding the possibility of diachronous occurrences across latitudes. Here, Huber et al. (1994-this volume) take issue with the use of the term "endemic" as pertaining to both southern and northern high-latitudes, since they believe "endemic" should be restricted to one region only. However, *The Oxford Dictionary of Natural History* (Allaby, 1985) defines endemic as the "Situation in which a species or other taxonomic group is restricted to a particular geographic region, due to factors such as isolation or response to soil or climatic conditions" (p. 224). These early Danian foraminiferal taxa are restricted to high-latitude regions, both north and south. Bipolar distributions such as these are found in many marine groups (see MacLeod and Keller, 1994 for a summary of the relevant literature).

A high-latitude center of origin for taxa is not peculiar to planktic foraminifera or to the K/T boundary (see Jenkins, 1992), although until recently this group was believed to have radiated from low latitudes. In 1988 a conference was devoted to this topic (Crame, 1989) and evidence for high-latitude centers of origin was presented for many faunas and floras, including reptiles (DeFauw, 1989; Molnar, 1989), terrestrial mammals (Case, 1989), marine mammals (Fordyce, 1989; Walting and Thurston, 1989), crustaceans (Feldmann and Tschudy, 1989), non-crustaceans (Zinsmeister and Feldmann, 1984) and plants (Dettmann, 1989; Askin, 1989). With so much evidence for high-latitude endemism and subsequent dispersal in terrestrial and marine organisms and plants, the observation of this pattern among planktic foraminifera is to be expected.

7. Extinction mode

Huber et al. (1994-this volume) question Keller's observations that Cretaceous generalist taxa survived the K/T boundary event. As evidence they cite bioturbation in Site 690. Keller (1993) was the first to demonstrate that Site 690 contains a major hiatus that removed the early Danian (see also MacLeod, in press b,c). Hence, this sequence is not a good choice for studying survivorship. These authors also cite poor preservation and poor core recovery in Site 738C as their reason for dismissing Keller's extinction data. Our SEM illustrations of Site 738C (see Plates I–III) show that preservation is relatively good and core recovery of the early Danian is continuous (Huber et al., this volume-1994, fig. 1). Moreover, laminated sediments of zones P0 and P1a in Site 738C show that there was no bioturbation. Thus, in the absence of bioturbation, and in accordance with their interpretation, all Cretaceous specimens present (over 90% of the fauna) would have to be washed-in by reworking of older sediments from some unspecified locality. Since these Cretaceous species in Danian sediments are dwarfed relative to their ancestors below the K/T boundary, and since not all, but only certain Cretaceous species are present above the K/T boundary, the implied process of bioturbation must have been very selective indeed! [Note: since there is no evidence for size sorting or graded bedding in the sediments constituting the boundary clay there is no evidence for the winnowing hypothesis Huber et al. (1994-this volume) offer to account for the test size change across the Site 738C K/T boundary.] This argument invokes special circumstances to justify an interpretation of mass extinction at the K/T boundary in spite of abundant evidence to the contrary. Since the same extinction/survivorship patterns are also found in the northern high-latitudes (Keller et al., 1993) as well as in low-latitude sections globally, the pattern observed at Site 738C is neither an accident nor particularly anomalous. A global biogeographic study by MacLeod and Keller (1994) and MacLeod (in press a) documents these trends across latitudes, biozone by biozone. These studies demonstrate the reality of Cretaceous survivor taxa as well as the trend towards high-latitude endemism in the early Danian.

8. Conclusion

We conclude that because Huber (1991) did not analyze the smaller (38–63 μm) size fraction, where most Danian species in the laminated clay sequence of ODP Site 738C reside, he did not recognize most of the Danian fauna. Consequently, Huber (1991) could not apply the appropriate Danian zonal scheme, identify the two hiatuses, and correctly evaluate the stratigraphic position or completeness of the K/T boundary interval at ODP Site 738C.

Huber et al. (1994-this volume) try to account for the differences between Huber's (1991) and Keller's (1993) studies by appealing to Keller's (1993) so-called erroneous taxonomy; specifically her decision not to follow the recently taxonomic revisions proposed by Olsson et al. (1992), Olsson and Liu (1993), and Liu and Olsson (1992) as well as many other apparent revisions not discussed in these papers or, indeed, anywhere else in the taxonomic literature of planktic foraminifera. Keller's studies have generally followed traditional taxonomic concepts. We believe that the taxonomic revisions proposed or cited by Huber et al. (1994-this volume), which form the basis of their criticism, are not appropriate because they do not appear to be based on objectively-presented evidence. Rather they constitute either simple assertions or citations to their own previous publications which in many instances do not mention the systematic questions implied by the citation.

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References

- Allaby, M., 1985. *The Oxford Dictionary of Natural History*. Oxford Univ. Press, Oxford, 688 pp.

- Askin, R.A., 1989. Endemism and heterochroneity in the Late Cretaceous (Campanian) to Paleocene Palynofloras of Seymour Island, Antarctica: implications for origins, dispersal and paleoclimates of southern floras. In: J.A. Crame (Editor), *Origins and Evolution of Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47: 107–120.
- Bang, I., 1980. Foraminifera from the type section of *eugubina* Zone compared with those from Cretaceous/Tertiary Boundary localities in Jylland, Denmark. In: T. Birkelund and R.G. Bromley (Editors), *Cretaceous–Tertiary Boundary Events I. The Maastrichtian and Danian of Denmark*. Univ. Copenhagen, Copenhagen, pp. 127–130.
- Ben Abdelkader, O., Haj Ali, N.B., Ben Salem, H. and Razgallah, S., 1992. International Workshop on Cretaceous–Tertiary Transitions (El Kef Section). Part II, Field Trip Guidebook: IGUS/GSGP/ATEIG/Tunisian Geol. Surv., Tunisia, 25 pp.
- Berggren, W.A. and Miller, K.G., 1988. Paleogene tropical planktonic foraminiferal biostratigraphy and magnetobiochronology. *Micropaleontology*, 34: 362–380.
- Berggren, W.A., Kent, D.V. and Flynn, J.J., 1985. Jurassic to Paleogene: Part 2, Paleogene geochronology and chronostratigraphy. In: N.J. Snelling (Editor), *The Chronology of the Geologic Record*. Geol. Soc. London, Spec. Publ., 10: 141–195.
- Bertels, A., 1970. Los Foraminíferos planctónicos de las ceunas Cretácico–Terciaria en Patagonia septentrional (Argentina), con consideraciones sobre la estratigrafía de Fortín General Roca (Provincia de Río Negro). *Rev. Asoc. Paleontol. Argentina*, VII: 1–56.
- Blow, W.H., 1979. *The Cainozoic Globigerinida*. Brill, Leiden, 1413 pp.
- Canudo, J.J., Keller, G. and Molina, E., 1991. Cretaceous/Tertiary boundary extinction pattern and faunal turnover at Agost and Caravaca, S.E. Spain. *Mar. Micropaleontol.*, 17: 319–341.
- Caron, M., 1985. Cretaceous planktic Foraminifera. In: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen (Editors), *Plankton Stratigraphy*. Cambridge Univ. Press, Cambridge, pp. 17–86.
- Case, J.A., 1989. Antarctica: the effect of high latitude heterochroneity on the origin of the Australian marsupials. In: J.A. Crame (Editor), *Origins and Evolutions of the Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47: 217–226.
- Crame, J.A. (Editor), 1989. *Origins and Evolution of the Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47, 297 pp.
- DeFauw, S.L., 1989. Patterns of evolution in the Diaynodontia with special reference to austral taxa. In: J.A. Crame (Editor), *Origins and Evolution of the Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47: 63–84.
- Dettmann, E.M., 1989. Antarctica: Cretaceous cradle of austral temperate rainforests? In: J.A. Crame (Editor), *Origins and Evolution of the Antarctic Biota*. Geol. Soc. London, Special Publ., 47: 89–106.
- D'Hondt, S.L., 1991. Phylogenetic and stratigraphic analysis of earliest Paleocene biserial and triserial planktonic foraminifera. *J. Foraminiferal Res.*, 21: 168–181.
- Dowsett, H.J., 1988. Diachrony of Late Neogene microfossils in the southwest Pacific Ocean: Application of the graphic correlation method. *Paleoceanography*, 3: 209–222.
- Dowsett, H.J., 1989. Application of graphic correlation to Pliocene marine sequences. *Mar. Micropaleontol.*, 14: 3–32.
- Fordeyce, R.E., 1989. Origins and Evolution of Antarctic marine mammals. In: J.A. Crame (Editor), *Origins and Evolution of the Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47: 253–268.
- Feldmann, R.M. and Tschudy, D.M., 1989. Evolutionary patterns in macrurous decapod crustaceans from Cretaceous to early Cenozoic rocks of the James Ross Island region, Antarctica. In: J.A. Crame (Editor), *Origins and Evolution of the Antarctic Biota*. Geol. Soc. London, Spec. Publ., 47: 183–196.
- Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G. and Smith, D.G., 1990. *A Geologic Time Scale 1989*. Cambridge Univ. Press, Cambridge, 263 pp.
- Hazel, J.E., 1989. Chronostratigraphy of upper Eocene microspherules. *Palaaios*, 4: 318–329.
- Hazel, J.E., Edwards, L.E. and Bybell, L.M., 1984. Significant unconformities and the hiatuses represented by them in the Paleogene of the Atlantic and Gulf Coastal province. *AAPG Mem.*, 36: 59–66.
- Hedberg, H., 1976. *International Stratigraphic Guide: A Guide to Stratigraphic Classification, Terminology, and Procedure*. Wiley, New York, 200 pp.
- Hills, S.J. and Thierstein, H.R., 1989. Plio-Pleistocene calcareous plankton biochronology. *Mar. Micropaleontol.*, 14: 67–96.
- Hofker, J., 1978. Analysis of a large succession of samples through the Upper Maastrichtian and the Lower Tertiary of drill hole 47.2, Shatsky Rise, Pacific, Deep Sea Drilling Project. *J. Foraminiferal Res.*, 8: 46–75.
- Huber, B.T., 1991. Maastrichtian planktonic foraminifer biostratigraphy and the Cretaceous/Tertiary boundary at ODP Hole 738C (Kerguelen Plateau, southern Indian Ocean). *Proc. ODP, Sci. Results*, 119: 451–465.
- Huber, B.T., Liu, C., Olsson, R.K. and Berggren, W.A., 1994. Comment on 'The Cretaceous–Tertiary boundary transition in the Antarctic Ocean and its global implications' by G. Keller. *Mar. Micropaleontol.*, 24: 000–000.
- Jenkins, D.G., 1992. Predicting extinctions of some extant planktic foraminifera. *Mar. Micropaleontol.*, 19: 239–243.
- Jenkins, D.G. and Gamson, P., 1993. The late Cenozoic *Globorotalia truncatulinoides* datum plane in the Atlantic, Pacific, and Indian oceans. In: E.A. Hailwood and R.B. Kidd (Editors), *High Resolution Stratigraphy*. Geol. Soc. London, Spec. Publ., 70: 127–130.
- Johnson, D.A., Schneider, D.A., Nigrini, C.A., Caulet, J.-P. and Kent, D.V., 1989. Radiolarian events and magnetostratigraphic calibrations for the tropical Indian Ocean. *Mar. Micropaleontol.*, 14: 33–66.
- Keller, G., 1988. Extinction, survivorship and evolution of planktic foraminifera across the Cretaceous/Tertiary boundary at El Kef Tunisia. *Mar. Micropaleontol.*, 13: 239–263.
- Keller, G., 1989a. Extended Cretaceous/Tertiary boundary extinctions and delayed population change in planktonic foraminiferal faunas from Brazos River, Texas. *Paleoceanography*, 4: 287–332.
- Keller, G., 1989b. Extended period of extinctions across the Cretaceous/Tertiary boundary in planktonic foraminifera of continen-

- tal shelf sections: Implications for impact and volcanism theories. *Geol. Soc. Am. Bull.*, 101: 1408–1419.
- Keller, G., 1993. The Cretaceous–Tertiary boundary transition in the Antarctic Ocean and its global implications. *Mar. Micropaleontol.*, 21: 1–45.
- Keller, G. and Benjamini, C., 1991. Paleoenvironment of the eastern Tethys in the Early Paleocene. *Palaios*, 6: 439–464.
- Keller, G., Barrera, E., Schmitz, B. and Mattson, E., 1993. Gradual mass extinction, species survivorship, and long-term environmental changes across the Cretaceous–Tertiary boundary in high latitudes. *Geol. Soc. Am. Bull.*, 105: 979–997.
- Keller, G., Stinnesbeck, W. and Lopez-Oliva, J.G., 1994. Age, deposition, and biotic effects of the Cretaceous/Tertiary boundary event at Mimbral, NE Mexico. *Palaios*, 9: 144–157.
- Liu, C. and Olsson, R.K., 1992. Evolutionary radiation of microperforate planktonic foraminifera following the K/T mass extinction. *J. Foraminiferal Res.*, 22: 328–346.
- Luterbacher, H. and Premoli-Silva, I., 1964. Biostratigrafia del limite Cretaceo–Terziario nell' Appennino Centrale. *Riv. Ital. Paleontol. Stratigr.*, 70: 67–128.
- MacLeod, N., 1993. The Maastrichtian–Danian radiation of triserial and biserial planktic foraminifera: Testing phylogenetic and adaptational hypotheses in the (micro)fossil record. *Mar. Micropaleontol.*, 21: 47–100.
- MacLeod, N., in press a. Cretaceous/Tertiary (K/T) biogeography of planktic foraminifera. *Hist. Biol.*, 1994.
- MacLeod, N., in press b. Graphic correlation of high latitude Cretaceous–Tertiary boundary sequences at Nye Kløv (Denmark), ODP Site 690 (Weddell Sea), and ODP Site 738 (Kerguelen Plateau): Comparison with the El Kef (Tunisia) boundary stratotype. *Modern Geol.*, 19.
- MacLeod, N., in press c. Graphic correlation of new Cretaceous/Tertiary (K/T) boundary sections. In: K.O. Mann, H.R. Lane et al. (Editors), *Graphic Correlation. SEPM Spec. Publ.*, Tulsa.
- MacLeod, N. and Keller, G., 1991a. Hiatus distributions and mass extinctions at the Cretaceous/Tertiary boundary. *Geology*, 19: 497–501.
- MacLeod, N. and Keller, G., 1991b. How complete are Cretaceous/Tertiary boundary sections? A chronostratigraphic estimate based on graphic correlation. *Geol. Soc. Am. Bull.*, 103: 1439–1457.
- MacLeod, N. and Keller, G., 1994. Comparative biogeographic analysis of planktic foraminiferal survivorship across the Cretaceous/Tertiary (K/T) boundary. *Paleobiology*, 20: 143–177.
- Masters, B.A., 1977. Mesozoic planktonic Foraminifera, a worldwide review and analysis. In: A.T.S. Ramsay (Editor), *Oceanic Micropaleontology*. Academic Press, London, pp. 301–732.
- Mayr, E., 1969. *Principles of Systematic Zoology*. McGraw-Hill, New York, 234 pp.
- Mayr, E., 1982. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Harvard Univ. Press, Cambridge, 974 pp.
- Molnar, R.E., 1989. Terrestrial tetrapods in Cretaceous Antarctica. In: J.A. Crame (Editor) *Origins and Evolution of the Antarctic Biota*. *Geol. Soc. London, Special Publ.* 47: 131–140.
- Olsson, R.K. and Liu, C., 1993. Controversies on the placement of the Cretaceous–Paleogene boundary and the K/P mass extinction of planktonic foraminifera. *Palaios*, 8: 127–139.
- Olsson, R.K., Hemleben, C.A., Berggren, W.A. and Liu, C., 1992. Wall texture classification of planktonic foraminifera genera in the Lower Danian. *J. Foraminiferal Res.*, 22: 195–213.
- Pisias, N.G., Martinson, D.G., Moore, T.C., Jr., Shackleton, N.J., Prell, W., Hays, J. and Boden, G., 1984. High-resolution stratigraphic correlations of benthic isotope records spanning the last 300,000 years. *Mar. Geol.*, 56: 119–136.
- Plummer, H.J., 1926. Foraminifera of the Midway Fm. in Texas. *Texas Univ. Bull.*, 2644: 134.
- Prell, W.L., Imbrie, J., Martinson, D.G., Morely, J.J., Pisias, N.G., Shackleton, N.J. and Streeter, H.F., 1986. Graphic correlation of oxygen isotope stratigraphy: Application to the Late Quaternary. *Paleoceanography*, 1: 137–162.
- Premoli-Silva, I., 1977. The earliest Tertiary *Globigerina eugubina* Zone: paleontological significance and geographical distribution. *Mem. 2nd Cong. Latinoam. Geol.*, 3, Spec. Publ., 7: 1541–1555.
- Smit, J., 1982. Extinction and evolution of planktonic foraminifera after a major impact at the Cretaceous/Tertiary boundary. In: L.T. Silver and P.H. Schultz (Editors), *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*. *Geol. Soc. Am. Spec. Pap.*, 190: 329–352.
- Smith, A.B., 1994. *Systematics and the Fossil Record: Documenting Evolutionary Patterns*. Blackwell, London, 223 pp.
- Smith, C.C. and Pessagno, E.A., 1973. Planktonic Foraminifera and stratigraphy of the Corsicana Formation (Maastrichtian) North-Central Texas. *Spec. Publ., Cushman Found. Foraminiferal Res.*, 12: 5–68.
- Toumarkine, M. and Luterbacher, H., 1985. Paleocene and Eocene foraminifera. In: H.M. Bolli, J.B. Saunders and K. Perch-Nielsen (Editors), *Plankton Stratigraphy*. Cambridge Univ. Press, Cambridge, pp. 87–154.
- Walting, L. and Thurston, H.M., 1989. Antarctica as an evolutionary incubator: evidence from the cladistic biogeography of the Amphipod Family Iphimediidae. In: J.A. Crame (Editor), *Origins and Evolution of the Antarctic Biota*. *Geol. Soc. London, Spec. Publ.*, 47: 297–313.
- Wei, W. and Pospichal, J., 1991. Danian calcareous nanofossil succession at ODP Site 738 in the southern Indian Ocean. *Proc. ODP, Sci. Results*, 119: 495–512.
- Wei, W. and Thierstein, H.R., 1991. Upper Cretaceous and Cenozoic calcareous nanofossils of the Kerguelen Plateau (Southern Indian Ocean) and Prydz Bay (East Antarctica). *Proc. ODP, Sci. Results*, 119: 467–493.
- Wiley, E.O., 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Wiley, New York, 439 pp.
- Zinsmeister, W.J. and Feldmann, R.M., 1984. Cenozoic high latitude heterochroneity of southern hemisphere marine faunas. *Science*, 224: 281–283.
- Weiss, W., 1983. Heterohelicidae (seriale planktonische Foraminiferen) der tethyalen Oberkreide (Santon bis Maastricht). *Geol. Jahrb.*, 72: 3–93.