The biostratigraphy and paleobiogeography of Maastrichtian inoceramids

Kenneth G. MacLeod and Brian T. Huber
Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, MRC: NHB 121, Washington, DC 20560
Peter D. Ward
Department of Geological Sciences, AJ-20, University of Washington, Seattle, Washington 98195

ABSTRACT

During the mid-Maastrichtian there was a pulse of extinction that affected inoceramids living in all of the world's oceans. We have documented this event at localities from tropical to austral paleolatitudes and from shelfal to abyssal paleodepths. Locally, the decline in inoceramid abundance occurred over a resolvable interval of geologic time, and globally, the extinction occurred at different times in different areas. This event is distinct from the Cretaceous/Tertiary boundary event; however, it is an important part of the transition from the Cretaceous Period to the Tertiary Period. Cooling and enhanced production of deep waters at high latitudes during the Maastrichtian could have caused increased ventilation of the bottom waters in the regions in which many inoceramids were living. As a causal mechanism for the extinction, this change is consistent with constraints provided by the observed distribution of inoceramid remains.

INTRODUCTION

Discussions concerning the Maastrichtian have been dominated by the Cretaceous/Tertiary (K/T) boundary debate, but significant events that occurred during the Maastrichtian Age are increasingly well documented. Among the biological changes documented in the marine realm are extinction among inoceramid bivalves (e.g., Dhondt, 1983a; Kauffman, 1988; MacLeod and Orr, 1993; MacLeod, 1994a), extinction among rudist reef faunas (Kauffman, 1988; Johnson and Kauffman, 1990), and shifts in the latitudinal distribution of planktonic foraminifera and calcareous nannoplankton (Huber, 1992; Huber and Watkins, 1992). The latter, in combination with oxygen isotopic analyses, indicate that surface and deep water temperatures decreased during most of the Maastrichtian (e.g., Douglas and Savin, 1975; Boersma and Shackleton, 1981; Boersma, 1984; Barrera et al., 1987; Barrera and Huber, 1990). Further, pole-to-equator temperature gradients were greater during the Maastrichtian than during earlier ages of the Cretaceous (Spicer and

Corfield, 1992; Huber et al., 1995). Other proposed changes in the Maastrichtian oceans include positive carbon isotopic shifts of greater than 1‰ in benthic foraminiferal tests (Barrera and Huber, 1990; Seto et al., 1991), change in the oceanic strontium budget (Nelson et al., 1991), regression (e.g., Haq et al., 1987), and an increase in the intensity of bioturbation in bathyal sediments (MacLeod, 1994b). In the terrestrial realm, both floral (Wolfe and Upchurch, 1987; Johnson and Hickey, 1990; 1992; Spicer and Parrish, 1990; Spicer and Corfield, 1992) and faunal (Clemens, 1986; Lehman, 1987; Clemens and Nelms, 1993) biogeographic shifts have been recognized. Predating the K/T boundary by up to millions of years, these changes could not have been caused by the K/T bolide, but they are an important part of the larger K/T interval.

It has been suggested that there was a global bio-event during the Maastrichtian (e.g., Kauffman, 1988; MacLeod and Ward, 1990; MacLeod, 1994b), but rigorous documentation has been lacking. Although the studies cited in the previous paragraph demonstrate that changes occurred across the globe dur-

ing the Maastrichtian, they do not necessarily demonstrate that there was a coordinated episode of global change in the mid-Maastrichtian. The terrestrial data are limited to North America and are mostly derived from the Great Plains region; samples for stable isotopic analyses were largely collected from either high southern paleolatitudes or from a few paleotropical sites in the central Pacific; detailed study of inoceramids has been concentrated in the Basque region of France and Spain; and rudists and associated faunas are best documented in the Caribbean. In addition to geographic limitations, temporal resolution across these studies varies considerably. Correlation, both regionally and globally, is often crude, and paleoecological conclusions are not always in agreement. For example, climatic changes inferred for the late Maastrichtian based on leaf physiognomy of fossils from the Great Plains (Wolfe and Upchurch, 1987; Johnson and Hickey, 1990) are opposite to those inferred from similar data collected in contemporaneous deposits in Alaska (Spicer and Parrish, 1990), and the stratigraphic distribution of dinosaur fossils collected in Montana has been used to support proposals of both declining (Clemens, 1986) and constant (Sheehan et al., 1991) diversity through the Maastrichtian. Despite the geographic and topical spread of evidence concerning Maastrichtian paleoecology, relationships among various events are speculative and potential cause(s) are not well constrained.

To test whether there was an episode of global change during the mid-Maastrichtian, we have examined the stratigraphic distribution of the remains of inoceramids from 31 localities that collectively provide wide geographic coverage (Fig. 1). The Inoceramidae is an excellent group to focus on in an examination of Maastrichtian events because (1) inoceramids were common and globally distributed during the early Maastrichtian, (2) they did not survive the age (i.e., they undergo change during the interval), and (3) they have left a rich, accessible record in the form of characteristic microfossils. Some inoceramids grew to be very large; however, even the largest often passively disaggregated and are preserved as hundreds of millions of columnar, polygonal prisms of calcite ~100 μm across. This taphonomic process has greatly increased the inoceramid fossil record and provides a means of objectively estimating changes in their standing population (MacLeod and Orr, 1993). In addition, because these prisms commonly occur in Deep Sea Drilling Project (DSDP) and Ocean Drilling Program (ODP) cores, it is relatively easy to generate a truly global data base (MacLeod and Ward, 1990).

MATERIALS AND METHODS

In this chapter the observed abundance of inoceramid prisms is used as a proxy for the local abundance of inoceramid bivalves (MacLeod and Ward, 1990; MacLeod and Orr, 1993). Samples discussed are from upper Campanian, Maastrichtian,
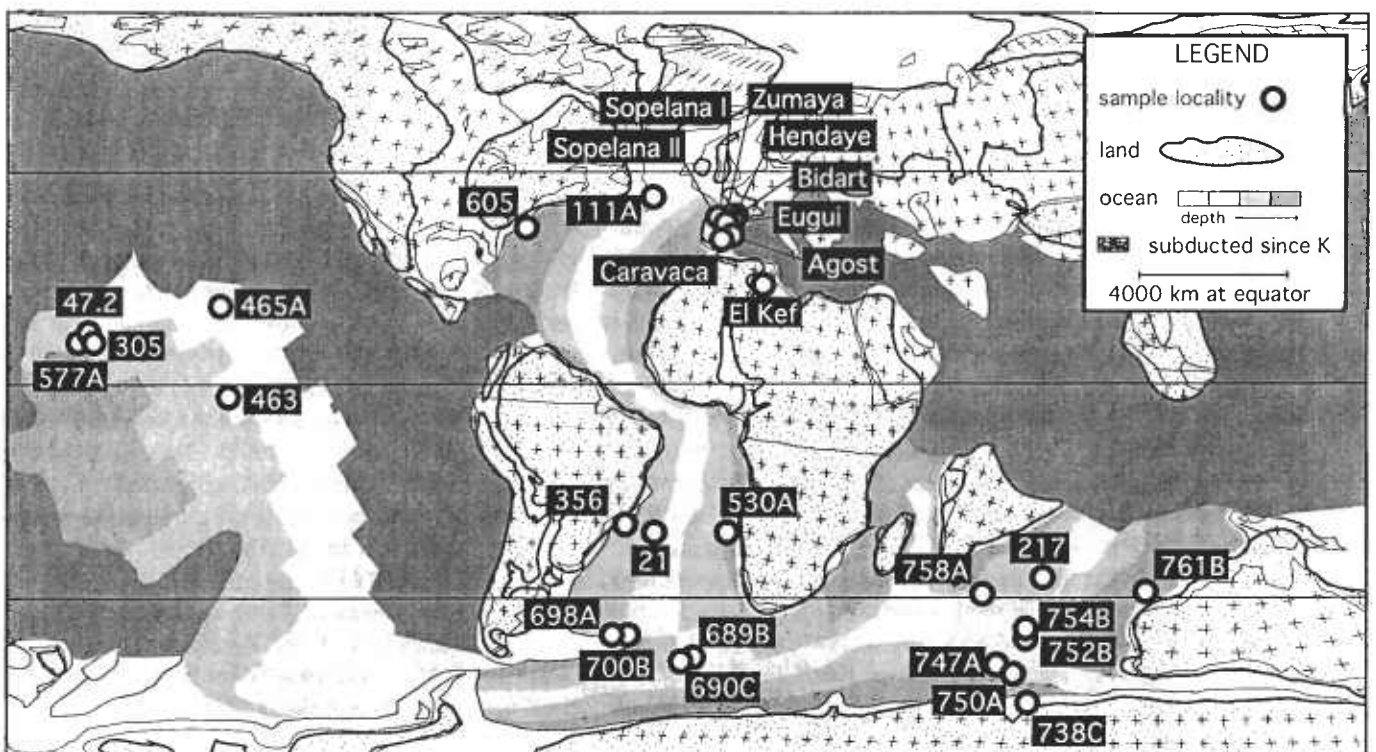

Figure 1. Approximate early Maastrichtian (70-Ma) paleogeographic position of the localities studied. Reconstruction was generated using the PGIS/Mac™ software package. Land/sea distributions modified from Barron (1987) and Huber (1992). Paleobathymetry modified from Barron (1987).

and lower Danian strata. The various sections are correlated using the base of the Maastrichtian, the base of the *Abathomphalus mayaroensis* planktonic foraminiferal zone, and the K/T boundary. In samples from DSDP/ODP cores, the position of these datums was taken from published reports. In other sections, they are based on our observations. Samples were disaggregated using standard micropaleontological techniques and washed on a 90-µm or a 63-µm screen. The abundance of the prisms in these washed samples was scored on a qualitative scale relative to co-occurring microfossils from absent to abundant or as a quantitative estimate of the number of prisms in 50 g of bulk sample (MacLeod and Orr, 1993). Qualitative estimates are based on washed residues of either a >63-µm or a >90-µm fraction; quantitative results are all based on the >90-µm fraction. For the purpose of discussing methodology, the samples for which we report results can be divided into three categories.

One category represents samples for which one or more of us has independently examined the distribution of inoceramid prisms. Samples that fall into this category include all the samples from DSDP holes 21, 111A, and 530A (MacLeod and Ward, 1990) and ODP Hole 689B (Huber, 1990); most of the samples from ODP holes 698A and 700B (Huber, 1991a); about half of the samples from ODP Hole 690C (Huber, 1990); and all of the samples from the Bidart, Hendaye, Zumaya, Sopelana I, and Sopelana II sections (MacLeod and Orr, 1993). Qualitative estimates of the abundance of prisms were recorded for all the DSDP/ODP material, but two different scales were used. MacLeod and Ward (1990) estimated abundance on a relative scale from 0 (prisms absent) to 10 (prisms abundant), whereas Huber (1991a) scored abundance as absent, rare, few, common, or abundant. We integrated these two schemes by equating absent with 0, rare with 2.5, few with 5, common with 7.5, and abundant with 10. Huber (1990) found no prisms, so we report a score of 0/absent for the samples examined in that study. MacLeod and Orr (1993) reported quantitative estimates.

A second category is composed of DSDP/ODP Micropaleontological Reference Center samples, processed samples from other studies not previously examined for prism abundance, or samples reexamined for the purpose of this chapter. This category includes all the material from DSDP holes 217 and 747A, a small number of samples from ODP holes 698A and 700B, and the upper nine samples from ODP Hole 738C. For these samples we used the qualitative scale of MacLeod and Ward (1990).

The final category is composed of samples from sections chosen to expand the available data such that they provide global constraints on the stratigraphic distribution of Maastrichtian inoceramids. Samples in this category include all samples from Eugui, Agost, Caravaca, and El Kef; all samples from DSDP holes 47.2, 305, 356, 463, 465A, 577A, and 605A; all samples from ODP holes 750A, 752B, 754B, 758A, and 761B; about half of the samples from ODP Hole 690C; and the lower 15 samples from ODP Hole 738C. Site selection was based on each section's paleogeographic position rel-

ative to other available Maastrichtian sections, on the presence of relatively undisturbed Maastrichtian sediments that could be disaggregated, on the reported occurrence of calcareous microfossils, on the amount of lithologic variability (i.e., we chose sections that seemed to represent a relatively constant depositional setting over those with evidence of high frequency variation; e.g., compare ODP Hole 761B [selected] with 762C [passed over]), and on the absence of evidence for large-scale reworking. Previous reports of the occurrence of inoceramid remains in a section were not considered in the selection process. Samples were collected with the goal of achieving complete coverage with highest sampling density in the region of the first appearance of *A. mayaroensis*. For core samples, we collected at relatively even intervals (at any given sampling density). If the "evenest" level fell in an interval of apparent reworking (e.g., turbidity current deposits, drilling disturbance), where there was a largely void or previously sampled interval, or where lithology was inappropriate (e.g., chert); we sampled at the nearest horizon that was not disqualified based on these criteria. Proximity to visible inoceramid remains on the cut surface of the cores was not considered in sample selection. Sample preparation and counting procedures follow MacLeod and Orr (1993).

RESULTS

Land-based sections, southwestern Europe and northern Africa

These sections preserve Tethyan to Tethyan/warm temperate faunas. Deposited in a shelfal setting (Keller, 1989), the section at El Kef, Tunisia, represents the shallowest environment sampled. Based on paleogeographic reconstructions (Mathey, 1988) and the higher proportion of terrigenous material, the section at Eugui (near Pamplona, Spain) represents a more shoreward, shallower position in the Basque–Cantabrian Basin than the Bidart, Hendaye, Zumaya, and two Sopelana sections. The latter five sections represent bathyal, basin floor to slope settings (Mount and Ward, 1986; Mathey, 1988; Ward and Kennedy, 1993; MacLeod, 1994a). The Agost and Caravaca sections (southern Spain) were deposited in a similar setting; Coccioni and Galeotti (1994) estimated paleodepths for the Caravaca section at 600 to 1000 m. Figure 2 shows the abundance of prisms through these nine sections. Inoceramid prisms are most abundant below the *A. mayaroensis* Zone, they decline in abundance near the base of this zone, and there is an extended stratigraphic interval between last appearance datum (LAD) of prisms and the K/T boundary. At Eugui prisms are less common, and their LAD is lower than in other sections from the region. The base of the *A. mayaroensis* Zone is defined by the first appearance datum (FAD) of the nominative taxon at all sections except El Kef, where *A. mayaroensis* is extremely rare and therefore an unreliable index fossil. For the
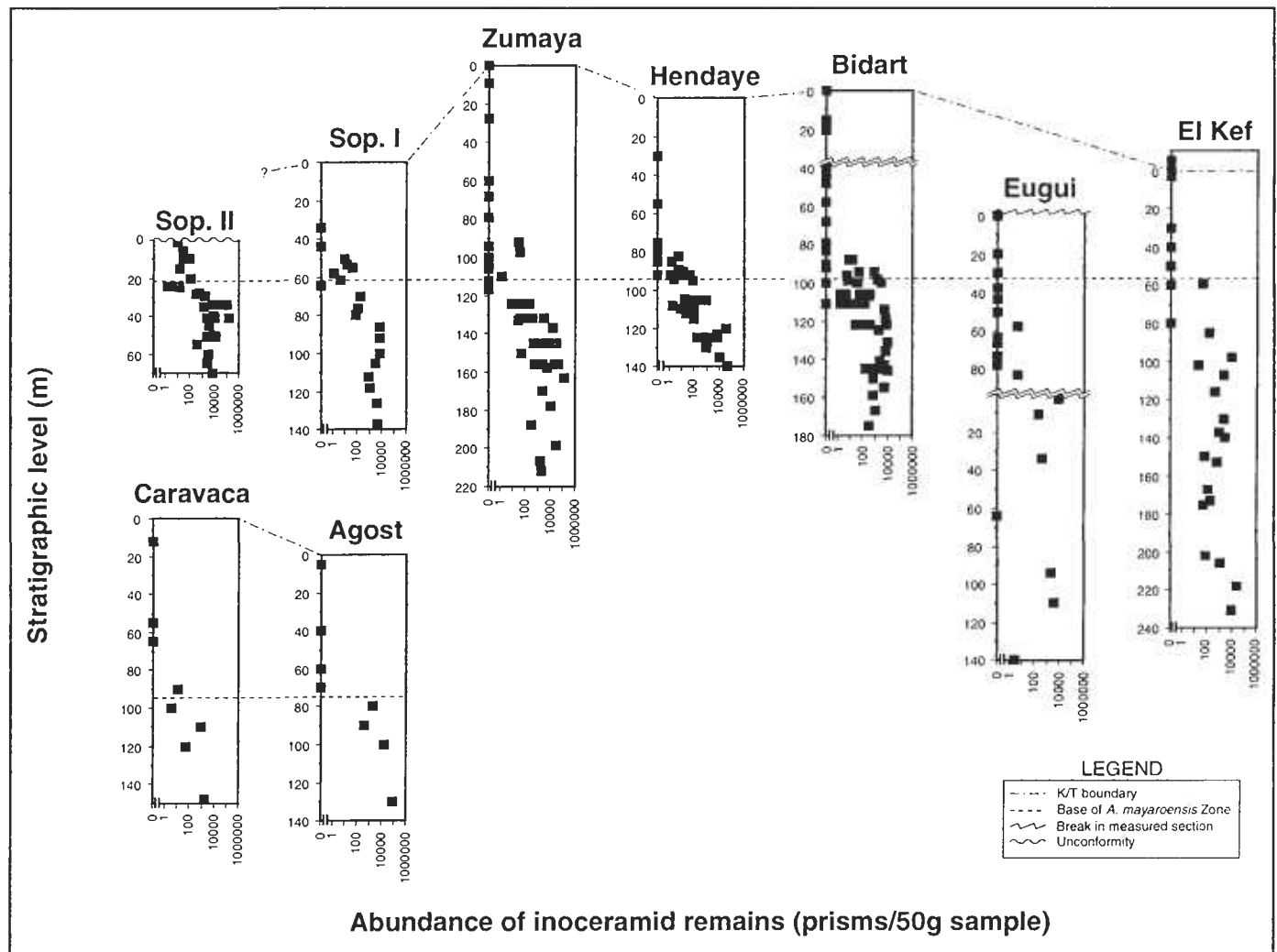
Figure 2. The abundance of prisms plotted on a log scale against stratigraphic level in meters for the nine land-based sections from southwestern Europe and Tunisia. Data for the Sopelana II, Sopelana I, Zumaya, Hendaye, and Bidart sections from MacLeod and Orr (1993).

El Kef section the *A. mayaroensis* Zone is recognized based on associated taxa and is placed slightly above the FAD of *Rugoglobigerina scotti* (W. N. Orr, unpublished data).

Atlantic Ocean deep-sea cores

Sections from the Atlantic represent mid-latitudes from both sides of the equator. Paleobathymetric estimates range from 200 to 400 m for Hole 111A (Ruffman, 1972) to 3,500 to 4,500 m for Hole 530A (Saltzman and Barron, 1982; Barron et al., 1984). Hole 530A is the deepest site in the data set, and washed residues from this hole are small and show considerable evidence of dissolution. Estimated paleodepths for the other three sections are approximately 500 m for Site 21 (Saltzman and Barron, 1982), 2,000 to 2,500 m for Site 356 (Sliter, 1977), and about 2,400 m for Site 605 (Jansen and Kroon, 1987). As with the land-based sections, the LAD of inoceramid prisms occurs near or below the base of the *A. mayaroensis* Zone

(Fig. 3). Samples from sites 356 and 605 have relatively low abundances of prisms and a relatively early LAD of prisms (i.e., in the Campanian and before the FAD of *A. mayaroensis*, respectively). In addition, prismatic shell fragments and individual small prisms were common to abundant in samples from the upper Maastrichtian of Site 605 (Fig. 4). These prisms (both individually and in the shell fragments) are smaller than the prisms recorded lower in the section and at other sites in this study; however, they are similar to presumed *Tenuipteria argentea* shell fragments found in the upper Maastrichtian strata of the coastal sections from the Basque region of France and Spain (MacLeod and Orr, 1993).

Indian Ocean deep-sea cores

Site 217 was migrating northward with the Indian Plate during the Late Cretaceous, and by the late Maastrichtian it had entered the Tethyan Realm. Holes 752B, 754B, 758A, and

761B contain subtropical to mid-latitude foraminiferal assemblages, and holes 738C, 747A, and 750A (discussed below) contain austral assemblages. Thus, our Indian Ocean samples form part of a latitudinal transect of a Maastrichtian ocean. Specific paleodepth estimates have not been published for the Indian Ocean sites examined, but benthic foraminifera in the *Initial Reports* volumes (e.g., *Nuttalides truempyi* and *Stensioina beccariiformis*) indicate generally bathyal depositional settings. Figure 5 shows the distribution of prisms through the sections. At all five sites prisms are found in the *A. mayaroensis* Zone. Holes 754B and 758A are truncated by unconformities above the FAD of *A. mayaroensis* but below the LAD of inoceramid prisms. The other three sites show a gradual decline in the abundance of prisms in the mid-Maastrichtian. The LAD of prisms is relatively low in Hole 761B, and sporadic occurrences of prisms occur quite high at Site 217.

Pacific Ocean deep-sea cores

All five sections examined from the Pacific represent low paleolatitudes and contain tropical to subtropical planktonic foraminiferal assemblages. Lower bathyal (about 1,500 m) paleodepths have been estimated for Hole 465A (Boersma, 1981). Paleodepth estimates are not available for the other sites, and we have not attempted to supply such constraints. Prism abundances through the Pacific sections are shown in Figure 6. These data are unusual in the relative scarcity of inoceramid remains. In our samples prisms were found only in material from Hole 465A. Although inoceramid remains are known from holes 47.2 and 48.2 (Heezen et al., 1971a, b; Boersma, 1981; Saltzman and Barron, 1982), we found no prisms in our samples from Hole 47.2 and saw no inoceramid remains on the cut surface of the archive half of the Cretaceous cores from Hole 48.2. Where we did observe prisms in Pacific sediments (Hole 465A), they occurred below the *A. mayaroensis* Zone.

Southern Ocean deep-sea cores

Samples from seven sites representing high southern paleolatitudes (>55°S) were examined. Estimated paleodepths for the Maastrichtian intervals are 1,000 to 1,500 m for Hole 689B (Thomas, 1990), 1,500 to 2,000 m for Hole 690C (Thomas, 1990), approximately 1,000 m for Hole 747A (Quilty, 1992), and 650 to 850 m for Hole 750A (Quilty, 1992). Barrera and Huber (1991) estimated a 1,000-m paleodepth for Hole 738C at K/T boundary time. Estimated paleodepths for the Paleocene of Holes 698A and 700B are 800 to 1,500 m and 2,000 to 2,500 m, respectively (Katz and Miller, 1991); we assume that Maastrichtian depths were slightly shallower but generally comparable. Figure 7 shows the distribution of prisms in these high-latitude sections. A single

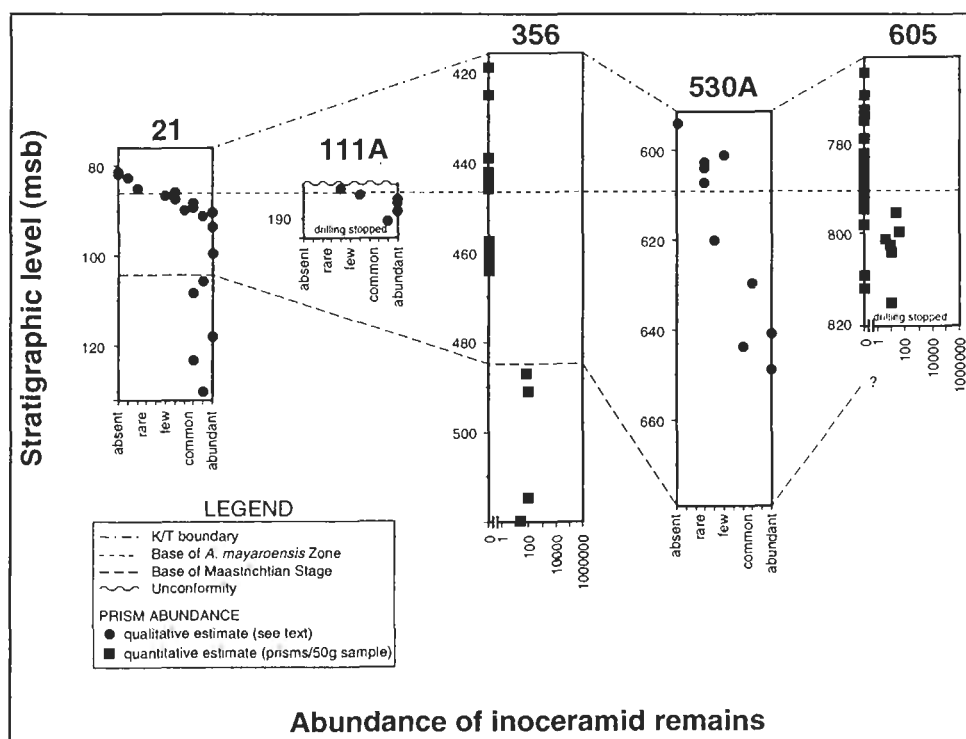**Abundance of inoceramid remains**

Figure 3. The abundance of prisms plotted against stratigraphic level (meters subbottom [msb]) for the five Atlantic mid-latitude localities. Qualitative estimates are from MacLeod and Ward (1990); their scale is equated with the scale of Huber (1991a) as described in methodology section.
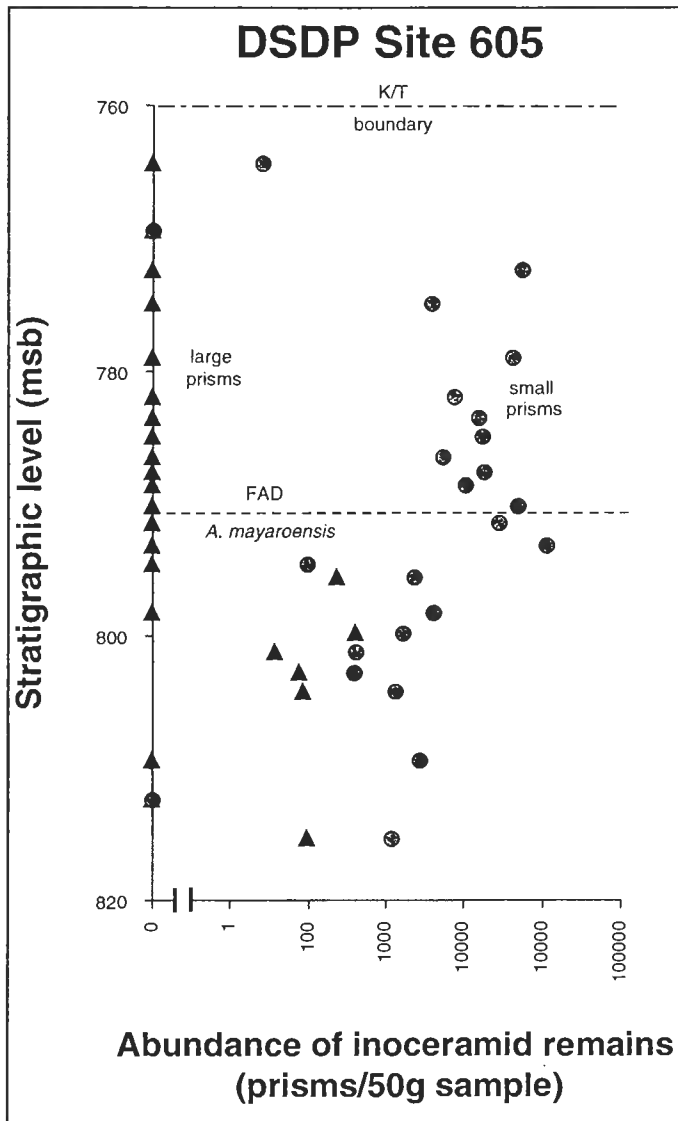
Figure 4. The abundance of two morphologic categories of prisms and prismatic shell fragments (number of pieces per 50-g bulk sample) plotted against stratigraphic level for DSDP Site 605. The category of small prisms and prismatic shell fragments (circles) matches material previously identified as *Tenuipteria* remains, whereas the large prisms (triangles) match *Inoceramus* remains (MacLeod and Orr, 1993). These results thus support a stratigraphic overlap between the two inoceramid taxa (MacLeod, 1994a).

prism was observed in a single sample from Hole 690C, but prisms are absent from all the rest of our samples from holes 689B and 690C. In Hole 738C prisms occur at high, relatively constant abundances throughout the Maastrichtian and into the Danian; prisms at this site occur in sediments as young as the Eocene (Huber, 1991b). At Hole 747A prisms are also common to abundant in every sample analyzed, but all samples come from below the *A. mayaroensis* Zone. With the exception of a single prism in a single sample in Hole 750A,

the LAD of prisms occurs below the *A. mayaroensis* Zone in the remaining three sites.

DISCUSSION

First-order patterns

The global distribution of Maastrichtian inoceramids demonstrates that these bivalves were ubiquitous during the early Maastrichtian. Inoceramids are known from all continents, and we found prisms in 25 out of our 30 localities containing strata below the FAD of *A. mayaroensis*. These 25 inoceramid-bearing localities span shelfal (El Kef) to abyssal (DSDP Hole 530A) paleodepths, represent a wide range of paleolatitudes, and include localities in the Atlantic, Tethys, Pacific, Indian, and Southern oceans. In most sections containing inoceramids, prisms are found in every sample collected across tens to hundreds of meters of section. Prism abundances of 10,000 to 100,000 prisms/50 g of bulk sample are typical.

Despite their wide paleogeographic and paleobathymetric distribution, inoceramids largely disappeared in a pulse of extinction that occurred during the mid-Maastrichtian. Inoceramids decline gradually but over a relatively short stratigraphic interval near the base of the *A. mayaroensis* planktonic foraminiferal Zone. The rate at which the extinction progressed falls between the catastrophic (e.g., Kauffman, 1988) and gradual (Dhondt, 1983a) scenarios previously proposed for this event. One unusual inoceramid taxon, *Tenuipteria*, survived after the mid-Maastrichtian event and disappeared at the K/T boundary (e.g., Speden, 1970; Dhondt, 1983b; MacLeod, 1994a). We think it likely that the shell fragments and small prisms that we found in DSDP Site 605 are remains of *Tenuipteria*. If this identification is correct, it represents the first time *Tenuipteria* shell fragments have been reported in DSDP/ODP core material and supports a stratigraphic overlap between *Tenuipteria* and other inoceramids (MacLeod, 1994a).

The distribution of prisms in Hole 738C seems to contradict a proposed mid-Maastrichtian extinction event, but we think the record at that locality is influenced by large-scale reworking. Age diagnostic foraminiferal and nannofossil taxa have been recognized at anomalous positions at this site, and prisms are reported to occur sporadically as high as the lower Eocene (Huber, 1991b; Wei and Thierstein, 1991). The K/T boundary occurs in a laminated interval, a circumstance that initially raised hopes that this stratigraphic interval did not contain reworked fossils (Barron, Larsen, et al., 1989); Huber (this volume) addresses reworking in the immediate region of the boundary in more detail. The amount of mixing necessary to account for uniformly high abundance of prisms into the Danian, though, exceeds all previous estimates. In support of a reworking explanation for the anomalous prisms (i.e., prisms isolated from above the expected LAD in mid-Maastrichtian strata), MacLeod and Huber (1996) reported that these prisms

have strontium isotopic ratios expected for Campanian fossils, whereas co-occurring planktonic foraminifera near their FAD have strontium isotopic ratios appropriate for their stratigraphic position.

At a much smaller scale, six other samples from four separate sites may be compromised by reworking or contamination. The uppermost inoceramid-bearing sample for holes 690C, 750A, and 752B and one sample from Site 217 contained a single prism each (Figs. 5 and 7). We think the simplest and most conservative explanation for these isolated occurrences is contamination during collection or processing. The two highest inoceramid-bearing samples from Site 217, on the other hand, contain enough prisms to make this explanation untenable. Pessango and Michael (1974) suggested common reworking in the late Maastrichtian portion of this section, which would explain the anomalous occurrences of prisms, but we cannot cite any independent corroboration of reworking in our samples. Regardless, holes 217, 750A, and 752B all show the dramatic mid-Maastrichtian decline in inoceramid abundance, and Hole 690C is otherwise devoid of prisms.

Second-order patterns

Although the data presented above suggest a single global pulse of extinction among inoceramids during the mid-Maas-

trichtian, the LAD of prisms occurs earlier in high southern latitudes than elsewhere. In Antarctic localities (ODP holes 698A, 700B, and 750A), prisms disappear at or below the FAD of *A. mayaroensis*. At many low to mid-latitude sites (e.g., Bidart, Sopelana II, ODP Hole 758A), inoceramid remains are found above that datum. The first appearance of *A. mayaroensis* is itself time transgressive, but in such a fashion that it strengthens the evidence for a diachronous LAD of inoceramids. *A. mayaroensis* appears earliest in high southern latitudes (Huber, 1992; Huber and Watkins, 1992; Fig. 8) where inoceramids disappear first. Therefore, there seems to be a general Antarctic-to-equator progression in the timing of the pulse of extinction among inoceramids.

Inoceramids also seem to disappear earlier in onshore sites than they do in offshore sites. In the Basque country of France and Spain, the decline and disappearance of inoceramid macrofossils and microfossils occurs at a lower level (based on lithostratigraphic as well as biostratigraphic correlation) in the shoreward Eugui section than it does in nearby sections (Bidart, Hendaye, Zumaya, Sopelana I, and Sopelana II) representing more offshore environments. ODP Hole 761B, located off the northwest coast of Australia, records the lowest (relative to the FAD of *A. mayaroensis*) LAD of prisms among localities in the Indian Ocean. Along the São Paulo Plateau–Rio Grande Rise in
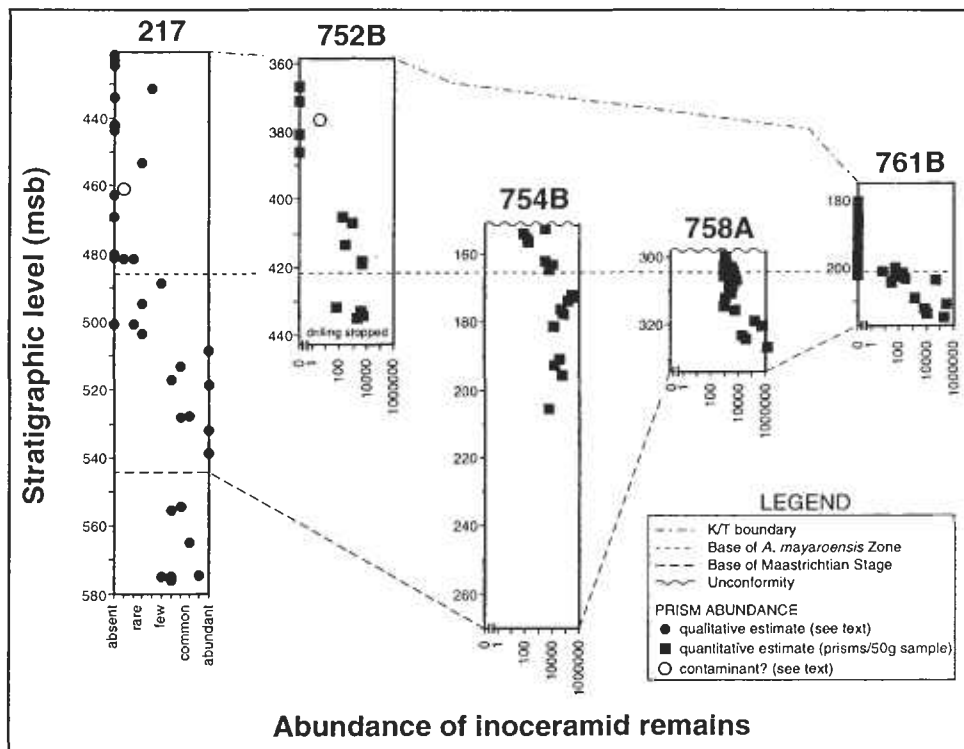

Abundance of inoceramid remains

Figure 5. The abundance of prisms plotted against stratigraphic level (meters subbottom [msb]) for the five Indian Ocean localities. Qualitative estimates follow the scale of MacLeod and Ward (1990) and are equated with the scale of Huber (1991a) as described in methodology section. Larger, open circles for holes 217 and 752B represent samples containing a single prism whose occurrence is attributed to contamination.
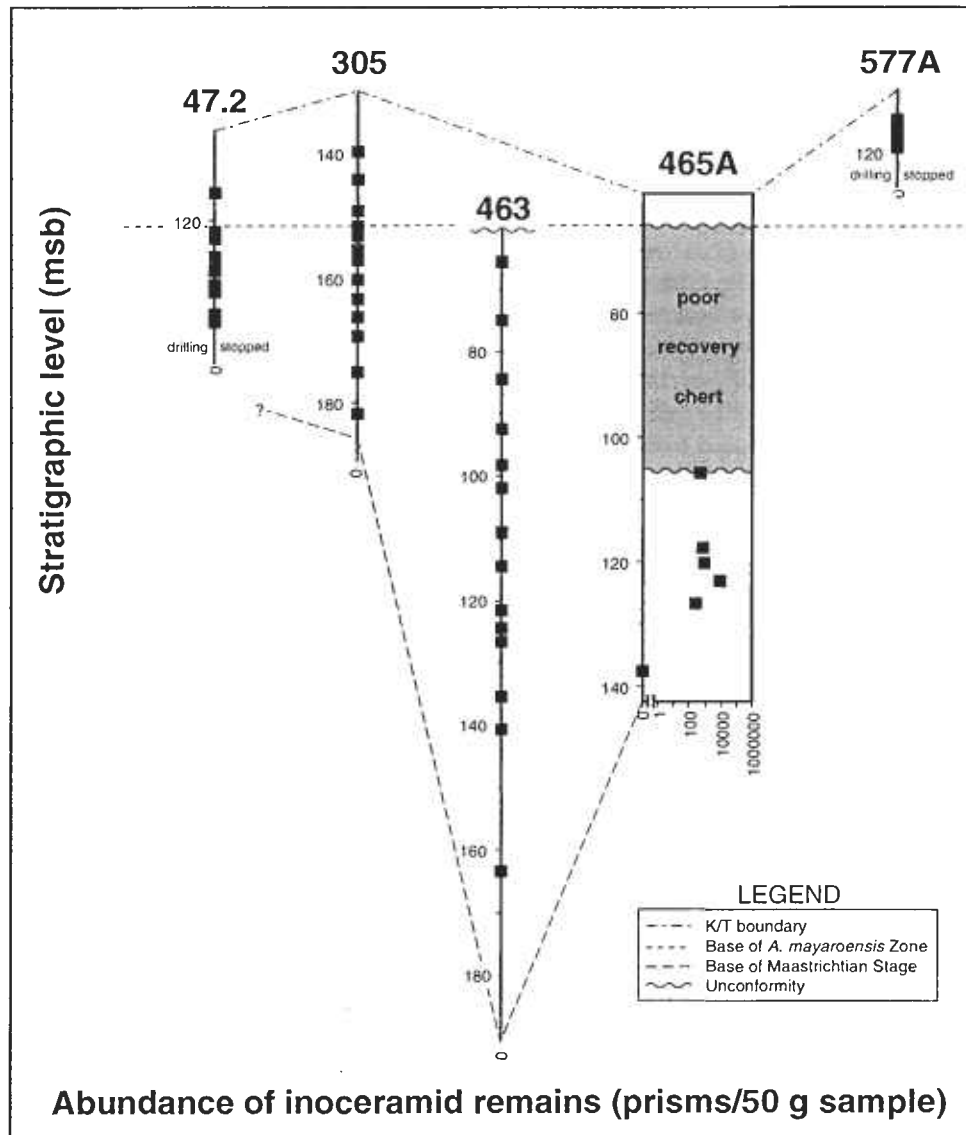
Figure 6. The abundance of prisms plotted against stratigraphic level (meters subbottom [msb]) for the five Pacific Ocean localities. Prisms were absent from most of the samples examined, but where they occur, they are found below the first appearance datum (FAD) of *A. mayaroensis*.

the South Atlantic, inoceramid prisms last occur in Campanian strata in a shoreward site (DSDP Site 356) but continue to be found above the FAD of *A. mayaroensis* in a more offshore site (DSDP Site 21). Finally, inoceramids last occur in shelfal Campanian strata on James Ross Island—neither body-fossils nor prisms have ever been reported from Maastrichtian strata on Seymour Island (Zinsmeister and Macellari, 1988; Huber, 1988; Zinsmeister and Feldmann, 1994)—whereas in offshore ODP sites from high southern latitudes inoceramid prisms range into mid-Maastrichtian strata. Interestingly, the shoreward site in the South Atlantic (DSDP Site 356) is interpreted to have been deposited in deeper water than the corresponding offshore site (DSDP Site 21). Thus, if the observed offshore

trend is meaningful, it may not be the result of a simple depth progression of the extinction pulse.

Inoceramid remains are ubiquitous below the FAD of *A. mayaroensis*, but they are absent from five (including Hole 690C) of the 30 sections that include lower Maastrichtian strata. Based on our samples, inoceramids were less common in the central Pacific than they were elsewhere. Perhaps inoceramid occurrences are reflecting oceanographic differences between the relatively old, wide Maastrichtian Pacific Ocean, and the relatively young, narrow Maastrichtian Atlantic and Indian oceans. Conversely, the scarcity of inoceramids in Pacific sites may be an artifact of sampling or dilution. The recovery of Cretaceous calcareous sediments is relatively sparse in
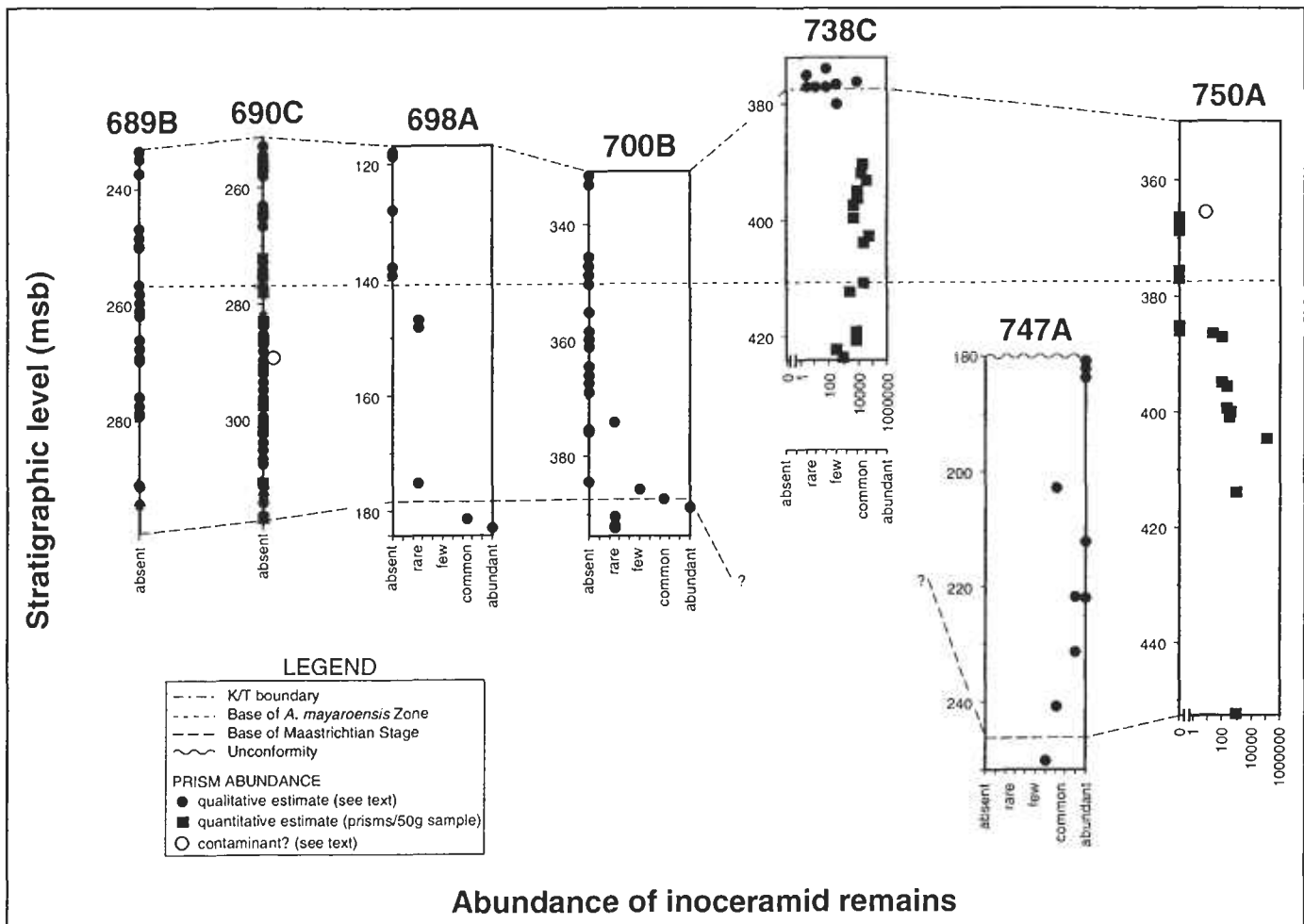
Figure 7. The abundance of prisms plotted against stratigraphic level (meters subbottom [msb]) for the seven Southern Ocean localities. Qualitative estimates follow the scale of MacLeod and Ward (1990) and are equated with the scale of Huber (1991a) as described in methodology section. Both qualitative and quantitative estimates of prism abundance were made on material from Hole 738C, so two axes are shown. Larger, open circles for holes 690C and 750A represent samples containing a single prism whose occurrence is attributed to contamination. Most of the prisms from Hole 738C are also interpreted as reworked. Data for holes 698A and 700B from Huber (1991a), except that LAD of prisms was moved up one sample in Hole 698A based on reexamination of that sample for this study.

the Pacific Ocean and the sites sampled represent areas of high surface productivity. More problematic is the absence of inoceramid remains in two ODP holes from Maud Rise (689B and 690C). Compared to nearby, inoceramid-bearing holes (698A and 700B), the Maud Rise sites were deposited a little farther south. However, planktonic foraminiferal assemblages indicate no environmental differences among the sites (Huber, 1991a), and within the resolution of available estimates, benthic foraminifera indicate broadly similar paleodepths (Thomas, 1990; Katz and Miller, 1991). We do not yet have an explanation for the absence of inoceramids on Maud Rise.

Associated patterns

Data regarding the noninoceramid benthos, although scarce, confirm widespread changes in the deep oceans during the Maas-

trichtian. Typically inoceramid-bearing strata contain few other benthic macrofossils, but trace-fossils indicate that a significant community of burrowing organisms lived with the inoceramids. Changes in the distribution of inoceramid prisms through the Basque sections suggest that the population of these burrowers increased at the same time that inoceramids declined (MacLeod, 1994b). Among benthic foraminifera in ODP holes 689B and 690C there is a slight increase in diversity during the mid-Maastrichtian (Thomas, 1990) and a nearly correlative 1‰ positive excursion in benthic foraminiferal $\delta^{13}C$ values (Barrera and Huber, 1990). In ODP Hole 752B there is an increase in abundance of benthic foraminifera and a greater than 1‰ positive shift in benthic foraminiferal ^{13}C values across the inoceramid extinction interval (Nomura, 1991; Seto et al., 1991, Fig. 9). Finally, relative abundance of benthic foraminiferal morphotypes
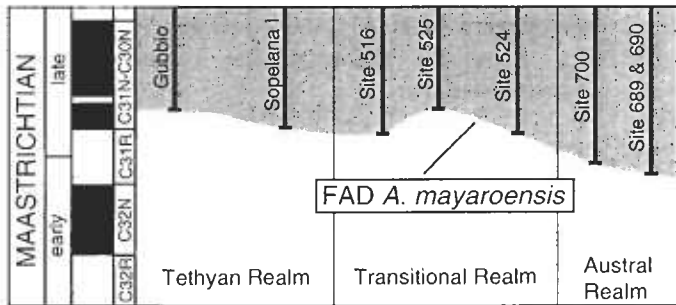
Figure 8. Stratigraphic position of the FAD of *A. mayaroensis* along a latitudinal transect (modified from Huber and Watkins, 1992). This taxon first appears earlier in high southern latitudes than it does in lower-latitude sites. Because the last appearance datum (LAD) of prisms occurs at or below the first appearance datum (FAD) of *A. mayaroensis* in the high-latitude sites but after that datum in mid- to low latitudes, the extinction pulse among inoceramids seems to progress from the Antarctic toward the equator.

changes across the inoceramid extinction interval in the Basque sections (M. Ducharme, unpublished data).

Except for evidence of cooling, examination of planktonic and nektonic organisms shows that surface waters were not greatly affected by the mid-Maastrichtian changes. Cooling is demonstrated by a ~1‰ increase in planktonic foraminiferal calcite $\delta^{18}O$ values (e.g., Barrera et al., 1987; Barrera and Huber, 1990), an equatorward expansion of the biogeographic range of austral planktonic foraminifera and nannofossils species (Huber, 1992; Huber and Watkins, 1992), and an equatorward contraction of the range of Tethyan species (Huber, 1992). On the other hand, ammonites preserved in the well-studied coastal sections of the Basque region (e.g., Wiedmann, 1988; Ward and Kennedy, 1993) show no apparent changes in abundance or diversity at the time that the inoceramid fauna collapsed. In these sections the planktonic foraminiferal assemblage also does not change significantly through the Maastrichtian (M. Ducharme, unpublished data; W. N. Orr, unpublished data). Similarly, we found no significant difference in the planktonic foraminiferal assemblages before and after the inoceramid extinction in ODP holes 750A and 761B.

Paleoceanographic implications

In addition to demonstrating an interval of global change during the Maastrichtian, inoceramid biostratigraphy and paleobiogeography also place constraints on the nature of that change. Whereas the global stratigraphic distribution of inoceramid remains requires an event that affected all the world's oceans, the effects are time transgressive and highly selective. As discussed above, change is concentrated in the benthos, and among benthic taxa only inoceramids seem to have been adversely affected.

MacLeod (1994b) proposed a model in which a change in ocean circulation during the mid-Maastrichtian led to enhanced
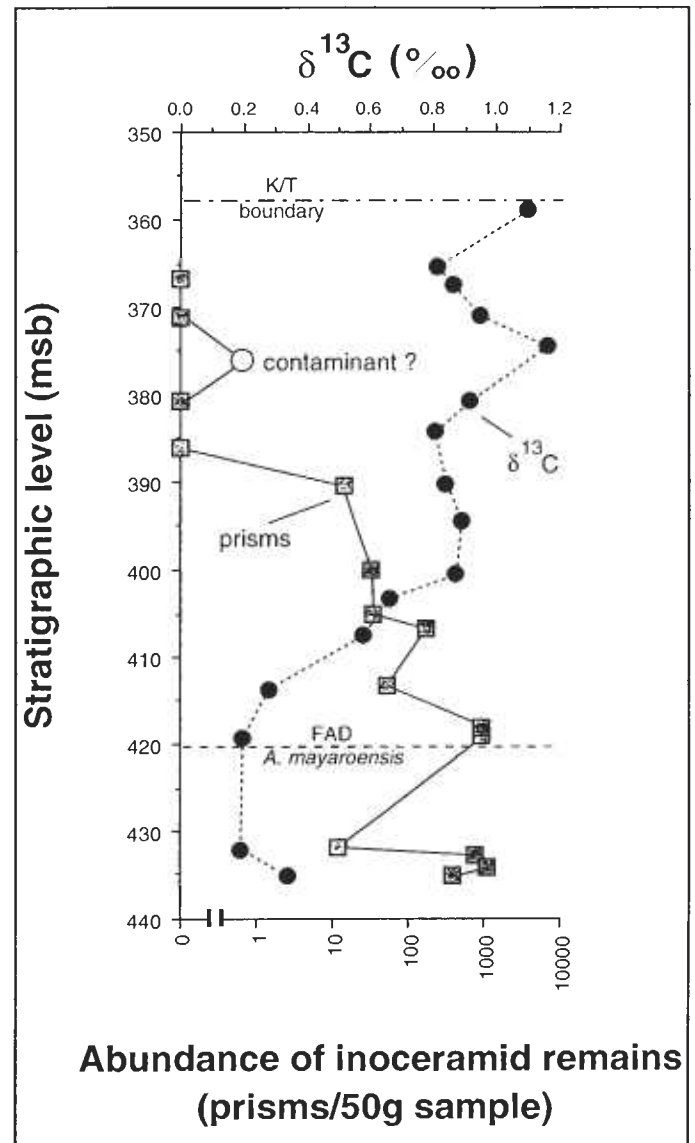

Figure 9. The carbon isotopic value measured for groups of 10 individuals of *Stensioina beccariiformis* (Seto et al., 1991) and the abundance of inoceramid prisms (number of prisms per 50-g bulk sample) plotted against stratigraphic position (meters subbottom) in Hole 752B.

ventilation of the deep oceans and to extinction among inoceramids. The temporal progression of the inoceramid extinction is consistent with cool, deep waters sourced in austral latitudes displacing warm, saline deep waters sourced in tropical latitudes (Saltzman and Barron, 1982). The $\delta^{13}C$ shift associated with the decline of inoceramid prisms in Hole 752B (Seto et al., 1991; Fig. 9) could be the signature of a change from one bottom water mass to another. However, the absence of inoceramids at some sites suggests complexity and regional variability in details of the vertical structure of the Maastrichtian oceans not addressed by the model. The circulation model does allow the possibility of refugia (presumably in low latitudes) where

locally the seafloor continued to be bathed in warm, saline waters long after these conditions had been eliminated from the rest of the globe. Prisms from the upper Maastrichtian of Site 217 could be evidence of a surviving population of inoceramids. Until the anomalous prisms at this site can be shown to be in place, though, we think it is more conservative to interpret them as reworked.

The circulation model also explains associated changes among the benthic and planktonic organisms. Both increases in the intensity of bioturbation (MacLeod, 1994b) and changes among benthic foraminifera (M. Ducharme, unpublished data) suggest increasing oxygen levels at or near the sediment-water interface in sections in France and Spain. Ultimate causes of a reorganization of ocean circulation (e.g., global cooling) might cause shifts in geographic distributions of planktonic organisms (Huber, 1992; Huber and Watkins, 1992) but might not eliminate any planktonic habitats.

One significant assumption of this paleoceanographic model is that most Maastrichtian inoceramids must have required environmental conditions associated with low concentrations of dissolved oxygen in bottom waters. Many inoceramids are known to have lived under low-oxygen conditions (e.g., Kauffman, 1981; Elder, 1985). MacLeod (1994b) hypothesized that such individuals would have benefited from warm temperatures, substrate stability (due to low populations of burrowing organisms), exclusion of molluscovores, and/or conditions favorable to chemosynthetic symbionts (MacLeod and Hoppe, 1992, 1993; Grossman, 1993). Determining which, if any, of these variables was most important to any given population of inoceramids may be an intractable problem; however, a consistent stratigraphic association between the inoceramid extinction and evidence for increasing oxygen concentrations (e.g., MacLeod, 1994b) would support the low-oxygen assumption. It should be noted that although inoceramids occur in well-aerated nearshore facies during the Late Cretaceous, we know of no such occurrences in the mid- to late Maastrichtian. Ecological restriction of inoceramids toward the end of their range is an intriguing evolutionary prediction implicit in the model, but it falls outside the scope of this chapter.

Even assuming that Maastrichtian inoceramids occupied a narrow ecological niche, the geographic and bathymetric range of Maastrichtian inoceramids poses difficulties for any model proposing to explain their disappearance. Regression during the Maastrichtian (Haq et al., 1987) may ameliorate these difficulties. Falling sea levels could have forced the shoreward margin of a low-oxygen benthic environment over the edge of the continental shelf. At the same time, draining of epicontinental seas in low latitudes would have reduced the surface area of effective evaporative basins and thereby have reduced the production of warm, saline deep water and promoted the expansion of cool deep water sourced in high latitudes. Thus, the habitat of inoceramids may have been encroached upon from above and below. Unfortunately, stratigraphic resolution on a global scale precludes testing this hypothesis. On the other hand, examination of

independent signals (e.g., stable isotopic ratios) in conjunction with paleontological changes has considerable potential in future investigations.

CONCLUSIONS

The pattern of disappearance among Maastrichtian inoceramids demonstrates that there was a major ecological event during the mid-Maastrichtian that affected all the world's oceans across a wide range of depths and latitudes. Although there were changes in the temperature of surface waters, planktonic foraminifera and ammonites were not greatly affected by the event. The duration and the diachronous nature of the inoceramid extinctions suggest that the forcing mechanism was gradual change and not a sudden, catastrophic perturbation. If most Maastrichtian inoceramids were adapted to low-oxygen environments, a reorganization of ocean circulation leading to increasing influence of oxygenated, Antarctic bottom waters fits the constraints imposed by inoceramid biostratigraphy and paleobiogeography and also explains associated data (MacLeod, 1994b). In this scenario typical inoceramids would be expected to survive longest in somewhat isolated basins in low latitudes. Documenting such trends is at the limit of stratigraphic resolution, and accurate predictions are compromised by uncertainties regarding details of Maastrichtian paleobathymetry. However, parallel study of other paleoecological indicators can provide independent constraints on the nature of mid-Maastrichtian changes and, thus, on the interplay of ecological variables on a global scale across a geologically resolvable interval of time.

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REFERENCES CITED

Barrera, E., and Huber, B. T., 1990, Evolution of Antarctic waters during the Maastrichtian: Foraminifer oxygen and carbon isotope ratios, ODP Leg 113, *in* Barker, P. F., Kennett, J. P., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 113: College Station, Texas, Ocean Drilling Program, p. 813–823.

Barrera, E., and Huber, B. T., 1991, Paleogene and early Neogene oceanography of the southern Indian Ocean: Leg 119 foraminiferal stable isotope results, *in* Barron, J. A., Larsen, B. L., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 119: College Station, Texas, Ocean Drilling Program, p. 693–717.

Barrera, E., Huber, B. T., Savin, S. M., and Webb, P. N., 1987, Antarctic marine temperatures: Late Campanian through early Paleocene: Paleoceanography, v. 2, p. 21–47.

Barron, E. J., 1987, Global Cretaceous paleogeography—International Geologic Correlation Program Project, Volume 191: Palaeogeography,

Palaeoclimatology, Palaeoecology, v. 59, p. 207–216.

Barron, E. J., Saltzman, E., and Price, D. A., 1984, Occurrence of Inoceramus in the South Atlantic and oxygen isotopic paleotemperatures in Hole 530A, *in* Hay, W. W., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 75: Washington, D.C., U.S. Government Printing Office, p. 893–904.

Barron, J. A., Larsen, B. L., and others, 1989, Proceedings, Ocean Drilling Program, Initial reports, Volume 119: College Station, Texas, Ocean Drilling Program, 942 p.

Boersma, A., 1981, Cretaceous-Tertiary foraminifers from Deep Sea Drilling Project Leg 62 sites in the Central Pacific, *in* Thiede, J., Vallier, T. L., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 62: Washington, DC, U.S. Government Printing Office, p. 377–396.

Boersma, A., 1984, Campanian through Paleocene paleotemperature and carbon isotope sequence and the Cretaceous-Tertiary boundary, *in* Berggren, W. A., and Van Couvering, J. A., eds., Catastrophes and Earth history: Princeton, New Jersey, Princeton University Press, p. 247–277.

Boersma, A., and Shackleton, N. J., 1981, Oxygen and carbon isotope variations and planktonic foraminiferal depth habitats: Late Cretaceous to Paleocene, Central Pacific, DSDP Sites 463 and 465, Leg 65, *in* Thiede, J., Vallier, T. L., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 65: Washington, D.C., U.S. Government Printing Office, p. 513–526.

Clemens, W. A., 1986, Evolution of the terrestrial vertebrate fauna during the Cretaceous-Tertiary transition, *in* Elliot, D. K., ed., Dynamics of extinction: New York, John Wiley and Sons, p. 63–85.

Clemens, W. A., and Nelms, L. G., 1993, Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes: Geology, v. 21, p. 503–506.

Coccioni, R., and Galeotti, S., 1994, K-T boundary extinction: Geologically instantaneous or gradual event? Evidence from deep-sea benthic foraminifera: Geology, v. 22, p. 779–782.

Dhondt, A. V., 1983a, Campanian and Maastrichtian inoceramids: A review: Zitteliana, v. 10, p. 689–701.

Dhondt, A. V., 1983b, Tegulated inoceramids and Maastrichtian biostratigraphy: Newsletters on Stratigraphy, v. 12, p. 43–53.

Douglas, R. G., and Savin, S. M., 1975, Oxygen and carbon isotope analyses of Tertiary and Cretaceous microfossils from the Shatsky Rise and other sites in the North Pacific Ocean, *in* Larson, R. L., Moberly, R., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 32: Washington, D.C., U.S. Government Printing Office, p. 509–520.

Elder, W. P., 1985, Biotic patterns across the Cenomanian- Turonian extinction boundary near Pueblo, Colorado, *in* Pratt, L. M., Kauffman, E. G., and Zelt, F. B., eds., Fine-grained deposits and biofacies of the Cretaceous Western Interior Seaway: Evidence of cylic sedimentary processes: SEPM Field Trip Guidebook No. 4, p. 157–169.

Grossman, E. L., 1993, Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts: Comment: Geology, p. 94–95.

Haq, B. V., Hardenbol, J., and Vail, P. R., 1987, Chronology of fluctuating sea levels since the Triassic: Science, v. 235, p. 1156–1167.

Heezen, B. C., et al., 1971a, Site 47, *in* Fischer, A. G., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 6: Washington, D.C., U.S. Government Printing Office, p. 67–143.

Heezen, B. C., et al., 1971b, Site 48, *in* Fischer, A. G., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 6: Washington, D.C., U.S. Government Printing Office, p. 145–169.

Huber, B. T., 1988, Upper Campanian–Paleocene foraminifera from the James Ross Island region (Antarctic Peninsula), *in* Feldmann, R. M., and Woodburne, M. O., eds., Geology and paleontology of Seymour Island, Antarctica: Geological Society of America Memoir 169, p. 163–252.

Huber, B. T., 1990, Maestrichtian planktonic foraminifer biostratigraphy of the Maud Rise (Weddell Sea, Antarctica): ODP Leg 113 Holes 689B and 690C, *in* Barker, P. F., Kennett, J. P., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 113: College Station, Texas, Ocean Drilling Program, p. 489–513.

Huber, B. T., 1991a, Planktonic foraminifer biostratigraphy of Campanian-Maestrichtian sediments from ODP Leg 114, Sites 698 and 700, southern South Atlantic, *in* Ciesielski, P. F., Kristoffersen, Y., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 114: College Station, Texas, Ocean Drilling Program, p. 281–297.

Huber, B. T., 1991b, Maastrichtian planktonic foraminifer biostratigraphy and the Cretaceous/Tertiary boundary at ODP Hole 738C (Kerguelen Plateau, southern Indian Ocean), *in* Barron, J. A., Larsen, B. L., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 119: College Station, Texas, Ocean Drilling Program, p. 451–465.

Huber, B. T., 1992, Paleobiogeography of Campanian-Maastrichtian foraminifers in the southern high latitudes: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 92, p. 325–360.

Huber, B. T., Hodell, D. A., and Hamilton, C. P., 1995, Middle–Late Cretaceous climate of the southern high latitudes: Stable isotopic evidence for minimal equator-to-pole thermal gradients: Geological Society of America Bulletin, v. 107, p. 1164–1191.

Huber, B. T., and Watkins, D. K., 1992, Biogeography of Campanian-Maastrichtian calcareous plankton in the region of the Southern Ocean: Paleogeographic and paleoclimatic implications, *in* Kennett, J. P., and Warnke, D. A., eds., The Antarctic paleoenvironment: A perspective on global change: Washington, D.C., American Geophysical Union, Antarctic Research Series, v. 56, p. 31–60.

Jansen, H., and Kroon, D., 1987, Maestrichtian foraminifers from site 605, Deep Sea Drilling Project Leg 93, northwest Atlantic, *in* van Hinte, J. E., Wise, S. W., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 93: Washington, D.C., U.S. Government Printing Office, p. 555–575.

Johnson, C. C., and Kauffman, E. G., 1990, Originations, radiations and extinctions of Cretaceous rudistid bivalve species in the Caribbean, *in* Kauffman, E. G., and Walliser, O. H., eds., Extinction events in Earth history: Berlin and Heidelberg, Springer-Verlag, p. 305–324.

Johnson, K. R., and Hickey, L. J., 1990, Megafloral change across the Cretaceous/Tertiary boundary in the northern Great Plains and Rocky Mountains, U.S.A., *in* Sharpton, V. L., and Ward, P. D., eds., Global catastrophes in earth history: An interdisciplinary conference on impacts, volcanism, and mass mortality: Geological Society of America Special Paper 247, p. 433–444.

Johnson, K. R., and Hickey, L. J., 1992, Foliar physiognomy of Maastrichtian leaf floras from the northern Great Plains: Implications for paleoclimate: Mesozoic of the western interior: SEPM 1992 Theme Meeting, Mesozoic of the Western Interior, Ft. Collins, Colorado, Abstracts, p. 36.

Katz, M. E., and Miller, K. G., 1991, Early Paleogene benthic foraminiferal assemblages and stable isotopes in the Southern Ocean, *in* Ciesielski, P. F., Kristoffersen, Y., and others, eds., Proceedings, Ocean Drilling Program Scientific Results, Volume 114: College Station, Texas, Ocean Drilling Program, p. 481–512.

Kauffman, E. G., 1981, Ecological reappraisal of the German Posidonienschiefer (Toarcian) and the stagnant basin model, *in* Gray, J., Boucot, A. J., and Berry, W. B. N., eds., Communities of the past: Stroudsburg, Pennsylvania, Hutchinson Ross, p. 311–382.

Kauffman, E. G., 1988, The dynamics of marine stepwise extinction: Revista Española de Paleontología, v. Extraordinario, p. 57–71.

Keller, G., 1989, Extended period of extinctions across the Cretaceous/Tertiary boundary in planktonic foraminifera of continental-shelf sections: Implications for impact and volcanism theories: Geological Society of America Bulletin, v. 101, p. 1408–1419.

Lehman, T. M., 1987, Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 60, p. 189–217.

MacLeod, K. G., 1994a, The extinction of inoceramid bivalves in Maastrichtian strata of the Bay of Biscay region of France and Spain: Journal of Paleontology, v. 68, p. 1048–1066.

MacLeod, K. G., 1994b, Bioturbation, inoceramid extinction, and mid-

Maastrichtian ecological change: Geology, v. 22, p. 139–142.

MacLeod, K. G., and Hoppe, K. A., 1992, Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts: Geology, v. 20, p. 117–120.

MacLeod, K. G., and Hoppe, K. A., 1993, Evidence that inoceramid bivalves were benthic and harbored chemosynthetic symbionts: Reply: Geology, p. 95–96.

MacLeod, K. G., and Huber, B. T., 1996, Strontium isotopic evidence for extensive reworking in sediments spanning the Cretaceous-Tertiary boundary at ODP Site 738: Geology (in press).

MacLeod, K. G., and Orr, W. N., 1993, The taphonomy of Maastrichtian inoceramids in the Basque region of France and Spain and the pattern of their decline and disappearance: Paleobiology, v. 19, p. 235–250.

MacLeod, K. G., and Ward, P. D., 1990, Extinction pattern of *Inoceramus* (Bivalvia) based on shell fragment biostratigraphy, *in* Sharpton, V. L., and Ward, P. D., eds., Global catastrophes in Earth history: An interdisciplinary conference on impacts, volcanism, and mass mortality: Geological Society of America Special Paper 247, p. 509–518.

Mathey, B., 1988, Paleogeographical evolution of the Basco-Cantabrian domain during the Upper Cretaceous: Revista EspaRevista Española de Paleontología, v. Extraordinario, p. 142–147.

Mount, J. F., and Ward, P. D., 1986, Origin of limestone/marl alternations in the upper Maastrichtian of Zumaya, Spain: Journal of Sedimentary Petrology, v. 56, p. 228–236.

Nelson, B. K., MacLeod, K. G., and Ward, P. D., 1991, Rapid change in strontium isotopic composition of sea water before the Cretaceous/Tertiary boundary: Nature, v. 351, p. 644–647.

Nomura, R., 1991, Paleoceanography of upper Maastrichtian to Eocene benthic foraminiferal assemblages at sites 752, 753, and 754, eastern Indian Ocean, *in* Weissel, J., Peirce, J., Taylor, E., Alt, J., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 121: College Station, Texas, Ocean Drilling Program, p. 3–29.

Pessagno, E. A., and Michael, F. Y., 1974, Mesozoic foraminifera, leg 22, site 217, *in* von der Borch, C. C., Sclater, J. G., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 22: Washington, D.C., U.S. Government Printing Office, p. 629–634.

Quilty, P. G., 1992, Upper Cretaceous benthic foraminifers and paleoenvironments, southern Kerguelen Plateau, Indian Ocean, *in* Wise, S. W., Schlich, R., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 120: College Station, Texas, Ocean Drilling Program, p. 393–443.

Ruffman, A. S., 1972, Discussion of site 111, *in* Laughton, A. S., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 12: Washington, D.C., U.S. Government Printing Office, p. 77–78.

Saltzman, E. S., and Barron, E. J., 1982, Deep circulation in the Late Cretaceous: Oxygen isotope paleotemperatures from *Inoceramus* remains in DSDP cores: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 40, p. 167–181.

Seto, K., Nomura, R., and Niitsuma, N., 1991, Data report: Oxygen and carbon isotope records of the upper Maastrichtian to Lower Eocene benthic foraminifers at site 752 in the eastern Indian Ocean, *in* Weissel, J., Peirce, J., Taylor, E., Alt, J., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 121: College Station, Texas, Ocean Drilling Program, p. 885–889.

Sheehan, P. M., Fastovsky, D. E., Hoffman, R. G., Berghaus, C. B., and Gabriel, D. L., 1991, Sudden extinction of the dinosaurs: Latest Cretaceous, upper Great Plains, U.S.A.: Science, v. 254, p. 835–839.

Sliter, W. V., 1977, Cretaceous foraminifers from the southwestern Atlantic Ocean, Leg 36, Deep Sea Drilling Project, *in* Barker, P. F., Dalziel, I. W. D., and others, eds., Initial reports of the Deep Sea Drilling Project, Volume 36: Washington, D.C., U.S. Government Printing Office, p. 519–573.

Speden, I. G., 1970, Generic status of the *Inoceramus*? *tegulatus* species group (Bivalvia) of the latest Cretaceous of North America and Europe: Postilla, v. 145, p. 1–45.

Spicer, R. A., and Corfield, R. M., 1992, A review of terrestrial and marine climates in the Cretaceous with implications for modelling the "Greenhouse Earth": Geological Magazine, v. 129, p. 169–180.

Spicer, R. A., and Parrish, J. T., 1990, Latest Cretaceous woods of the central North Slope, Alaska: Palaeontology, v. 33, p. 225–242.

Thomas, E., 1990, Late Cretaceous through Neogene deep-sea benthic foraminifers (Maud Rise, Weddell Sea, Antarctica). *in* Barker, P. F., Kennett, J. P., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 113: College Station, Texas, Ocean Drilling Program, p. 571–594.

Ward, P. D., and Kennedy, W. J., 1993, Maastrichtian ammonites from the Biscay region (France, Spain): Journal of Paleontology, Memoir v. 34, p. 1–58.

Wei, W., and Thierstein, H. R., 1991, Upper Cretaceous and Cenozoic calcareous nannofossils of the Kerguelen Plateau (southern Indian Ocean) and Prydz Bay (East Antarctica), *in* Barron, J. A., Larsen, B., and others, eds., Proceedings, Ocean Drilling Program, Scientific Results, Volume 119: College Station, Texas, Ocean Drilling Program, p. 467–494.

Wiedmann, J., 1988, The Basque coastal sections of the K/T boundary—A key to understanding "Mass Extinction" in the fossil record: Revista Española de Paleontología, v. Extraordinario, p. 127–140.

Wolfe, J. A., and Upchurch, G. R., Jr., 1987, North American nonmarine climates and vegetation during the Late Cretaceous: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 61, p. 33–77.

Zinsmeister, W. J., and Feldmann, R. M., 1994, Antarctica, the forgotten stepchild: A view of KT extinction from the high southern latitudes [abs.]: New developments regarding the KT event and other catastrophes in Earth history: Houston, Texas, Lunar and Planetary Institute Contribution 825, p. 134–135.

Zinsmeister, W. J., and Macellari, C. E., 1988, Bivalvia (Mollusca) from Seymour Island, Antarctic Peninsula, *in* Feldmann, R. M., and Woodburne, M. O., eds., Geology and paleontology of Seymour Island, Antarctica: Geological Society of America Memoir 169, p. 253–284.