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THE BIOSTRATIGRAPHY AND PALEOGEOGRAPHY OF MAASTRICHTIAN INOCERAMIDS. K. G. MacLeod¹, B. T. Huber¹, and P. D. Ward², ¹Department of Paleobiology, Smithsonian Institution, MRC: NHB 121, Washington DC 20560, USA, ²Department of Geological Sciences, AJ-20, University of Washington, Seattle WA 98195, USA.

The global distribution of Maastrichtian inoceramids is now known in enough detail that the patterns of disappearance can be used to place first-order constraints on paleoceanographic changes that may have occurred during that age. The Inoceramidae is an excellent group to focus on in a study of Maastrichtian events because (1) they were globally distributed in 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 microfossil and macrofossil record. Some inoceramids grew to be very large; however, even the largest often passively disaggregated and are preserved as hundreds of millions of characteristic, 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 [1]. 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 database. The existing macrofossil record of inoceramids has less temporal and spacial resolution but greater taxonomic resolution than the microfossil record. In concert the microfossil and macrofossil records of inoceramids demonstrate that important changes occurred during the Maastrichtian. These changes are distinct from the KT boundary catastrophe but are part of the larger KT transition.

One striking aspect of the inoceramid record is how ubiquitous these bivalves were during the early Maastrichtian. Inoceramids are known from all continents and we have documented prism occurrences in early Maastrichtian strata from deep-sea cores collected in the North Atlantic, the South Atlantic, and the Pacific, Indian, and Southern Oceans. In sections containing inoceramids, prisms are found in every sample collected across tens of meters of section. In land-based sections we have studied, inoceramids form virtual shell pavements on some bedding planes, and prism densities >100,000 prisms/50 g samples are typical in high-abundance intervals.

During the mid Maastrichtian, though, there was a concentrated, worldwide pulse of extinction among inoceramids. At the more than 25 sites where we have recorded this event, inoceramids decline gradually but over a relatively short stratigraphic interval. The rate at which the extinction progressed falls between catastrophic [e.g., 2] and gradual [3] scenarios that have previously been proposed for the event. One unusual inoceramid taxon, *Tenuipteria*, survives after the mid Maastrichtian event and disappears at the KT boundary. We think we have recently found the first known occurrence of *Tenuipteria* shell fragments in core material (DSDP hole 605 off Delaware).

Although the major pulse of extinction falls in the mid Maastrichtian, this extinction horizon is demonstrably diachronous on a global scale. In high southern latitudes (e.g., ODP holes 698A and 700B [4], and 750A) the last occurrence of inoceramid remains is stratigraphically below the first appearance of *Abathomphalus mayaroensis*. At lower-latitude sites in southwestern Europe [1] and in Indian Ocean ODP holes 754B and 758A, inoceramid remains are found above that datum. The first appearance of *A.*

mayaroensis is itself diachronous, but in a direction that accentuates the diachroneity of the inoceramid extinction. *A. mayaroensis* appears earliest in high southern latitudes [5,6] 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.

A second trend is that the disappearance of inoceramids seems to occur earlier in onshore areas than in nearby offshore areas. This pattern is not yet well constrained, but it has been observed in four regions:

1. In the Basque region of northern Spain, the decline in the abundance of inoceramid macrofossils occurs at a lower level (based on lithostratigraphic correlation) in sections that represent more shoreward areas than it does in more offshore areas.

2. ODP Hole 761B, located off the northwest coast of Australia, records an early extinction level compared to the other Indian Ocean sites.

3. In the South Atlantic, inoceramid prisms disappear earlier in a shoreward site (DSDP Hole 356) than they do in a more offshore site at the same latitude (DSDP Hole 21).

4. Finally, inoceramids disappeared in Campanian strata on Seymour Island [7], while in offshore ODP sites from high southern latitudes inoceramid prisms clearly range into Maastrichtian strata.

Although inoceramid remains are ubiquitous in early Maastrichtian strata, they are not omnipresent. We have found inoceramids to be less common in Pacific Ocean sites than in Atlantic or Indian Ocean sites. Perhaps inoceramid occurrences reflect 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 as the recovery of Cretaceous, calcareous sediments is relatively sparse in the Pacific Ocean. More problematic is the absence of inoceramid remains in two ODP sites from Maud Rise (689 and 690). Compared to nearby, inoceramid-bearing ODP localities (698, 700, and 750), the Maud Rise sites may represent slightly cooler environments as they were deposited a little further south; however, foraminiferal assemblages indicate no significant environmental differences among the sites. At present we do not have an explanation for the absence of inoceramids on Maud Rise.

In addition to these global patterns, where the stratigraphic distribution of whole inoceramids is well documented, there is an ordered pattern of species extinction [8,9]. As already noted, only *Tenuipteria* ranges through the late Maastrichtian, but there is also structure in the pattern of disappearance of species of *Inoceramus* within the mid Maastrichtian pulse of extinction. In the Basque region large platyceramids and endocostids disappear first; the youngest *Inoceramus* taxon found is *I. (Trochoceramus) morgani*, which is a relatively small form [9]. Anecdotal evidence suggest that this morphologic pattern of disappearance is repeated outside the Basque region, and ongoing research is attempting to confirm these reports. If the pattern holds up, it suggests that the more typical, large, flat inoceramids were least tolerant of the changes occurring during the Maastrichtian.

The pattern of disappearance of inoceramids indicates that there was a major event during the mid Maastrichtian, which affected the benthic environment in all the world's oceans. The duration and the diachroneity of the inoceramid extinctions suggests that the forcing mechanism was a gradual change, not a sudden, catastrophic pertur-

bation. If most Maastrichtian inoceramids were adapted to low-O environments, a reorganization of ocean circulation leading to increasing influence of oxygenated, Antarctic bottom waters fits the constraints imposed by inoceramid biostratigraphy and paleogeography. In this scenario typical inoceramids would be expected to survive longest in somewhat isolated basins in low latitudes. Regardless of the ultimate fate of this hypothesis, though, changes occurring during the mid Maastrichtian provide the opportunity to examine the interplay of ecological variables on a global scale across a geologically resolvable interval of time.

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AN EVALUATION OF CRITERIA THAT MAY BE USED TO IDENTIFY SPECIES SURVIVING A MASS EXTINCTION. N. MacLeod^{1,2}, ¹Department of Geological and Geophysical Sciences, Princeton University, Princeton NJ 08544, USA, ²Present address: Department of Palaeontology, The Natural History Museum, Cromwell Road, London, SW7 5BD, UK.

One of the most difficult obstacles to establishing a causal connection between mass extinctions and large body impacts is the existence of what appear to be many more KT survivor species than previously suspected. Though interpretations of "Cretaceous" faunal elements in lowermost Danian sediments differ, this enigmatic fauna has now been recovered from every biozone-complete boundary section, including the El Kef stratotype. In terms of their potential for providing constraints on scenarios seeking to account for the KT extinction event, the significance of such observations cannot be overstated.

Owing to the consistency with which these observations have been made over the last several years, the possibility of widespread trans-KT biotic survivorship can no longer be dismissed. Rather, the survivorship hypothesis must be tested alongside its alternative (the reworking hypothesis) to determine which explains the available data in the most complete yet parsimonious manner. Moreover, valid tests for survivorship cannot be based on negative evidence or on the assumption that only a small cohort of species could have survived the KT boundary event. Several authors have recently proposed various criteria that might be used to test alternative interpretations for this aspect lowermost Danian biotic record (Table 1). These are evaluated below.

Preservational State: The most commonly applied test for survivor identification is based on the principle that physically reworked specimens should exhibit abrasions, breaks, recrystallized surface texture, or other signs of degraded preservation. Although it is possible to collect and quantify evidence bearing on preservational state, all reports of degraded physical condition of Cretaceous species in lowermost Danian sediments offered thus far

have been qualitative and anecdotal. Nevertheless, several authors have noted that when specimens of "Cretaceous" species collected from Danian sediments are compared side by side with conspecific uppermost Cretaceous specimens, predicted differences in preservational state often fail to be observed. In addition, recent statistical analyses [1] indicate that the planktic foraminiferal survivor fauna is dominantly composed of species that are susceptible, rather than resistant, to abrasion and diagenesis.

Relative Abundance/Population Ratio: Olsson and Liu [2] explain this test as follows: "If one species survived (the KT boundary) its population size in the lower Paleocene would be composed of both the reworked and indigenous surviving fractions while that of the extinct species consists only of the reworked fraction. As a result, the relative abundance of the survivor taxon to that of the extinct species would significantly increase after the extinction of the other species" (p. 136). Applying the relative abundance/population ratio test to depositional rate-normalized KT planktic foraminiferal data of [2] and [3] shows that patterns of abrupt relative abundance decline in Danian occurrences of "Cretaceous" planktic foraminiferal species are not consistently observed for either established or putative KT survivor species. Nevertheless, patterns of post-boundary relative abundance variation exhibited by many "Cretaceous" species are indistinguishable from patterns present in widely-accepted survivor species. Overall, these data support recognition of an expanded survivor fauna and a progressive faunal turnover.

Stable Isotope Geochemistry: This test involves determining whether the stable isotopic signature of postboundary populations differs from that of preboundary populations. Recovery of different isotopic signatures from these populations constitutes a direct species-level test of survivorship. However, adequate controls must be maintained to insure that the observed difference cannot be accounted for through diagenetic or species-specific metabolic factors. Comparative analyses of planktic and benthic foraminiferal species from Brazos River (Texas), Nye Kløv (Denmark), and ODP Site 738 (South Indian Ocean) suggest that several survivor species are present in these faunas. Changes in the isotopic signatures of these survivor populations also begin in the upper Cretaceous; well below the appearance of any putative impact debris.

Quantitative Morphology: Like the stable isotope test, consistent changes in test size and shape parameters provide another means of identifying survivor species. MacLeod and Keller [4] demonstrated that lowermost Danian samples of *Heterohelix globulosa* and *H. navarroensis* from Brazos Core undergo statistically significant test size reductions, while at the same time preserving the ontogenetic trajectories of comparably sized uppermost Maastrichtian populations. Once again, this size reduction does not coincide with the KT boundary but rather takes place well below this horizon, within the uppermost Maastrichtian. Since this initial study, similar size/shape patterns have been documented for several other "Cretaceous" survivor species in other boundary sections/cores.

Comparative Biogeography: Occurrence of Danian populations of "Cretaceous" species in areas in which they were not observed during the upper Cretaceous is consistent with trans-KT survivorship. Also, comparison of changes in the biogeographic structures of survivor and indigenous Danian faunas can be used to determine whether the spatial organization of these faunas are