

Ammonite extinction and nautilid survival at the end of the Cretaceous

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ABSTRACT

One of the puzzles about the end-Cretaceous extinctions is why some organisms disappeared and others survived. A notable example is the differential extinction of ammonites and survival of nautilids, the two groups of co-occurring, externally shelled cephalopods at the end of the Cretaceous. To investigate the role of geographic distribution in explaining this outcome, we compiled a database of all the occurrences of ammonites and the nautilid genus *Eutrephoceras* in the last 0.5 m.y. of the Maastrichtian. We also included recently published data on ammonite genera that appear to have briefly survived into the Paleocene. Using two metrics to evaluate the geographic range of each genus (first, a convex hull encompassing all of the occurrences of each genus, and second, the maximum distance between occurrences for each genus), we documented that most ammonite genera at the end of the Maastrichtian were restricted in their geographic distribution, possibly making them more vulnerable to extinction. The geographic distribution of those genera that may have briefly survived into the Paleocene is significantly greater than that of non-surviving genera, implying that more broadly distributed genera were more resistant to extinction. This pattern is further emphasized by the broad distribution of *Eutrephoceras*, which matches that of the most widely distributed ammonites at the end of the Maastrichtian. However, even the most widely distributed ammonites eventually succumbed to extinction, whereas *Eutrephoceras* survived. Evidently, a broad geographic distribution may have initially protected some ammonites against extinction, but it did not guarantee their survival.

INTRODUCTION

The selective nature of the end-Cretaceous mass extinctions has prompted debates on the factors responsible for these divergent patterns (D'Hondt, 2005). Among the best known examples are the contrasting fates of ammonites and nautilids, the two groups of externally shelled cephalopods that lived at the end of the Maastrichtian. This case is particularly puzzling because, from most points of view, the ammonites were in the stronger position at the time: they were more abundant, with apparently larger population sizes (e.g., 800 ammonite fossils versus 1 nautilid fossil in the upper Maastrichtian section at Kalaat Senan, Tunisia; Goolaerts, 2010), more diverse (~30 genera of ammonites versus 6 genera of nautilids; for ammonites, see following; for nautilids, see Dzik, 1984), and more morphologically complex (e.g., elaborate sutures of ammonites versus simple sutures of nautilids). Yet the ammonites disappeared and the nautilids survived.

This outcome has traditionally been attributed to a difference in early life history (Landman, 1984; Sheehan et al., 1996). Ammonites of all types hatched at a small size (<1 mm in diameter) and may have spent some time in the planktonic realm, perhaps as passive vertical migrators (Landman et al., 1996). In contrast, nautilids hatched at a much larger size (>10 mm in diameter) and may have followed a nektonic mode of life

immediately after hatching (Landman, 1988). This difference in early ontogeny may have had a neutral effect during background time but proved to be an Achilles heel for ammonites during stressful times (Arkhipkin and Laptikhivsky, 2012). According to this hypothesis, the ammonites perished along with many species of planktic foraminifera in an ephemeral episode of surface-water acidification following the Chicxulub asteroid impact (Alegret et al., 2012). The nautilids, which hatched and lived near the sea bottom, would have escaped this fate.

In an effort to explore the patterns of extinction more fully, we examine a second factor, the geographic distribution of genera. Geographic range is not a simple correlative of early life history (reflecting dispersal ability), but can vary even within groups with similar ontogenies (Jablonksi and Hunt, 2006). It is therefore important to consider geographic range as an independent factor related to extinction probability. We compiled a database of the occurrences of all ammonites that lived at the end of the Maastrichtian, incorporating new data from recently published studies suggesting that some ammonites may have briefly survived into the Paleocene. In addition, we compile occurrences of *Eutrephoceras*, one of the best-documented nautilid genera that lived at the end of the Maastrichtian and survived into the Paleocene. To evaluate the effect of geographic distribution on the patterns of extinction, we compare the geographic distribution of non-surviving ammonites to that of surviving ammonites and *Eutrephoceras*.

METHODOLOGY

Because we are only targeting ammonites and nautilids that lived at the end of the Cretaceous and were likely to have been affected by the events at the Cretaceous-Paleogene (K/Pg) boundary, we restrict our study to sites that record the last 0.5 m.y. of the Maastrichtian. This is the shortest interval of time that we could safely identify using standard biostratigraphic indices (e.g., calcareous nannofossils, planktic foraminifera, and dinoflagellates), magnetostratigraphy, cyclostratigraphy, and fossil occurrences in relation to the K/Pg boundary in apparently continuous sections. Our investigation yielded a total of 29 sites encompassing 14 regions around the world (Fig. 1; Table DR1 in the GSA Data Repository¹). These sites represent different environmental settings with different preservation potentials; e.g., the shallow-water (<100 m) Gulf coastal plain and Atlantic coastal plain of North America versus the deeper-water Bay of Biscay and Bulgaria. In addition, some sites have been more extensively studied than others, e.g., Denmark versus Turkmenistan, leading to unavoidable discrepancies in sampling.

We restrict our analysis to genera rather than species because many species from this interval are in open nomenclature due to poor preservation,

¹GSA Data Repository item 2014264, methodology, locality information, Table DR1 (geographic occurrence of ammonite genera), and Table DR2 (computed data for geographic distribution of ammonite genera), is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

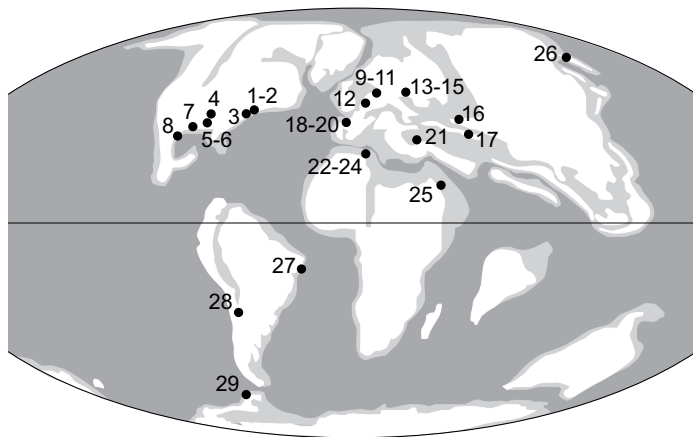


Figure 1. Map of localities of latest Maastrichtian ammonites and nautilid *Eutrephoceras* plotted on paleogeographic reconstruction of Earth at 70 Ma (after Blakey, 2011). 1—central Monmouth County, New Jersey (USA); 2—northeastern Monmouth County, New Jersey; 3—Anne Arundel County, Maryland; 4—Stoddard and Scott Counties, Missouri; 5—Tippah County, Mississippi; 6—Chick-saw County, Mississippi; 7—Falls County, Texas; 8—northeastern Mexico; 9—Stevns Klint, Denmark; 10—Kjølby Gård, Denmark; 11—Dania Quarry, Denmark; 12—Maastricht, Netherlands; 13—Nasiłów, Poland; 14—Mełgiew, Poland; 15—Lechówka, Poland; 16—Kyzylsay, Kazakhstan; 17—Sumbar River, Turkmenistan; 18—Zumaya, Spain; 19—Hendaye, France; 20—Bidart, France; 21—Bjala, Bulgaria; 22—Kalaat Senan, Tunisia; 23—El Kef, Tunisia; 24—Garn Halfaya, Tunisia; 25—Dababiya quarry core, Egypt; 26—Sakhalin Island, Russia; 27—Poty Quarry, Brazil; 28—Bajada de Jagüel, Argentina; 29—Seymour Island, Antarctica. For a description of localities, see the Data Repository (see footnote 1).

making species-level comparisons difficult. In addition, because nautilid fossils are much rarer than ammonite fossils, and are not as useful in biostratigraphy, information on their occurrence is scarce. We focus here on the nautilid *Eutrephoceras*, which originated in the Jurassic and persisted into the Miocene. Still, because of the rarity of these fossils, it is possible that the absence of *Eutrephoceras* at some sites is due to collection failure.

To compare the geographic distributions of genera, we rotated modern latitudes and longitudes for each site to their paleopositions at 70 Ma using the program PointTracker (Scotese, 2001b) and then imported locality data into ArcGIS (Esri, 2011). The accuracy of point rotations was confirmed by overlaying the site data on a 70 Ma paleogeographic reconstruction (Scotese, 2001a). Sites were then projected onto a global Mollweide equal-area projection. Two measures of the extent of occurrence were used to assess the geographic ranges of each genus (Gaston and Fuller, 2009). First, we created a convex hull encompassing all of the occurrences of a genus and calculated its geographic area (in km²). Second, we determined the distance (km) between the two most distant sites for each genus. For genera known from only a single site, geographic area and maximum distance were arbitrarily set to 10 km² and 1 km, respectively. For genera known from only 2 sites, geographic area was defined as 1 km × distance between the sites. Areas and distances were log₁₀ transformed (see Table DR2). A Mann-Whitney U-test was used to assess whether the median geographic ranges of non-surviving ammonites and surviving ammonites and *Eutrephoceras* are significantly different.

AMMONITE SURVIVORS

Recent work based on field studies and statistical analyses has demonstrated that some ammonites may have survived briefly into the Paleocene. In the Maastricht region in southeast Netherlands, *Hoploscaphites*, *Baculites*, and *Eubaculites* occur in Unit IVf-7 of the Meerssen Member above the Berg en Terblijt Horizon in the section exposed at the former Curfs quarry in southern Limburg (Jagt, 1996; Jagt et al., 2003; Machalski, 2005).

The clay beds at the base of this unit are assigned to Planktonic Foraminiferal Zone P0, implying that the ammonites above the clay beds are earliest Danian in age (Smit and Brinkhuis, 1996; Jagt and Jagt-Yazykova, 2012). The species of *Baculites* are different from those below this horizon and many of them are preserved with their apertures intact. The presence of this feature indicates that the ammonites were buried without significant reworking or transport, which would have otherwise destroyed their delicate apertures. In addition, many of the specimens contain incompletely filled phragmocones with voids left after dissolution of the aragonite, implying that they were buried rapidly enough to prevent complete infilling of the phragmocone. All of this evidence suggests that these ammonites are early Danian survivors and not reworked Maastrichtian material (Jagt et al., 2003; Machalski et al., 2009; Jagt and Jagt-Yazykova, 2012).

Survivors have also been reported from Denmark, where the section exhibits nearly continuous deposition across the K/Pg boundary (Birke-lund, 1993; Surlyk et al., 2006). Specimens of *Baculites* and *Hoploscaphites* have been reported from the basal Danian Cerithium Limestone Member (Machalski and Heinberg, 2005). A comparison of the microfossils in these specimens with those in the surrounding matrix suggests that these specimens were fossilized at the same time as the deposition of the surrounding sediment. In addition, the most common fossils in the underlying Maastrichtian chalk are virtually absent in the Cerithium Limestone; this is inconsistent with a hypothesis of reworking, but points instead to the likelihood that these species persisted into the Paleocene.

Surviving ammonites have also been reported from the Atlantic coastal plain in New Jersey (USA). The upper part of the Tinton Formation in this area consists of a fossiliferous unit (the Pinna layer) that yields numerous specimens of *Discoscaphites* and *Eubaculites*. The Pinna layer is overlain by the Burrowed unit, which only bears species of *Eubaculites* associated with isolated jaws. The base of the Pinna layer is marked by an increased concentration of iridium (Landman et al., 2007). If the iridium anomaly is in place, the ammonites in the Pinna layer and Burrowed unit represent Danian survivors. However, even if the iridium anomaly has migrated downward from the top of the Pinna layer, a more conservative hypothesis favored here and described elsewhere (Miller et al., 2010; Landman et al., 2012b), the species of *Eubaculites* in the Burrowed unit are still Danian survivors. The associated jaws are relatively fragile and are absent in the underlying strata, further emphasizing that they were not reworked from below but were instead fossilized during the deposition of the surrounding sediment.

In addition to these examples of ammonite survival, statistical approaches can be used to identify genera that possibly persisted into the Paleocene. Although originally such studies were performed to determine if the ranges of ammonite species extended to the K/Pg boundary, they can also be used to comment on the likelihood that these ranges extended above the boundary. Such methods rely on the abundance and stratigraphic distribution of the fossils and are expressed as probabilities that the actual ranges extended above the recorded ranges.

In the Bay of Biscay, statistical methods have been applied to the ranges of ammonite species in the top 1.5 m of the Maastrichtian section (Marshall and Ward, 1996). Based on 50% range extensions, results suggest that two genera, *Pseudophyllites* and *Pachydiscus*, may have occurred above the K/Pg boundary, even though they are not actually recorded at this level. A similar technique has been applied to evaluate the ranges of ammonite species in Antarctica (Wang and Marshall, 2004). Based on 20% range extensions (a more conservative approach, and using a refined methodology), the results of Wang and Marshall (2004) suggest that one genus, *Diplomoceras*, may have persisted above the boundary.

Thus, based on actual observations, three ammonite genera are thought to have survived into the Paleocene (*Hoploscaphites*, *Eubaculites*, and *Baculites*), and based on statistical predictions, three additional genera are also hypothesized to have survived into the Paleocene [*Diplomoceras*, *Pachydiscus* (*Pachydiscus*), and *Pseudophyllites*].

RESULTS

We tabulated the global occurrence of ammonite genera at the end of the Maastrichtian (Fig. 2; Tables DR1 and DR2). According to both metrics of geographic range, geographic area (Fig. 2A) and maximum distance (Fig. 2B), the distribution of non-surviving ammonites is right skewed with a long tail, implying that most ammonite genera at the time were very restricted in their distribution. Of these genera, ~50% occurred at only one or two sites, implying a high level of endemism. The geographic distribution of the six surviving genera at the end of the Maastrichtian is also plotted in Figure 2. The geographic distribution of these genera is significantly greater than that of genera that became extinct at, or shortly before, the K/Pg event (Mann-Whitney U-test, $p = 0.002$ for geographic area and $p = 0.004$ for maximum distance). The geographic distribution of *Eutrephoceras* in the latest Maastrichtian is similar to that of the most widely distributed ammonites.

DISCUSSION

The ammonites at the end of the Maastrichtian comprise 31 genera and subgenera representing all four Mesozoic suborders (Table DR1). There are nine genera of phylloceratids and lytoceratids, groups characterized by relatively compressed shells without much ornament (Westermann, 1996). They usually occur in deeper water settings (>100 m deep), including the Bay of Biscay, Bulgaria, the Tunisian Trough, the Pacific margin of Russia, and Antarctica.

The Ammonitina comprise 11 genera, 10 of which are desmoceratoids (Table DR1). Desmoceratoids represent modified members of the Ammonitina that converge on the compressed, lightly ornamented morphology of the lytoceratids and phylloceratids (Westermann, 1996). These forms also favored deeper water settings such as the Bay of Biscay, the Tunisian Trough, and Antarctica, but occasionally occurred in shallower water settings such as the Netherlands. The only other genus of Ammonitina at the end of the Maastrichtian is *Sphenodiscus*. These streamlined ammonites occurred exclusively in shallow-water facies such as the Gulf and Atlantic coastal plains of North America, and northern and Central Europe (Ifrim and Stinnesbeck, 2010).

The remaining suborder of ammonites is the Ancyloceratina (heteromorphs) with 11 genera (Table DR1). The geographic distribution of baculitids and diplomoceratids is very broad, suggesting that these ammonites were independent of facies. Scaphitids preferred shallow-water settings (Landman et al., 2012a) such as the Gulf and Atlantic coastal plains of North America; they occasionally occurred in deeper water settings such as Turkmenistan (Machalski et al., 2012), but never in the deepest water settings (>300 m), such as the Pacific margin of Russia.

Most ammonite genera at the end of the Cretaceous were restricted in their geographic distribution, which may have made them more vulnerable to extinction. However, the geographic distribution of ammonites that may have briefly survived into the Paleocene is significantly greater than that of non-surviving genera (despite their similar early life histories), implying that more broadly distributed genera were more resistant to extinction. This pattern is further emphasized by the broad geographic distribution of the nautilid *Eutrephoceras* at the end of the Maastrichtian. Similar geographic patterns of survivorship have been observed in other molluscs at the K/Pg boundary (e.g., marine bivalve genera; Jablonski, 2008).

The importance of early life history on the pattern of differential survival and extinction is more difficult to evaluate. The early life history of the surviving and non-surviving ammonites is the same: both groups possessed small embryonic shells and may have spent some time in the planktonic realm after hatching (Landman et al., 1996). This similarity suggests that early life history did not contribute to the differential outcome among ammonites. Indeed, in studies of other organisms, early life history does not appear to correlate with success or failure at the end of the Cretaceous (bivalves, Valentine and Jablonski, 1986; echinoids, Smith and Jeffery, 1998). However, even the most broadly distributed

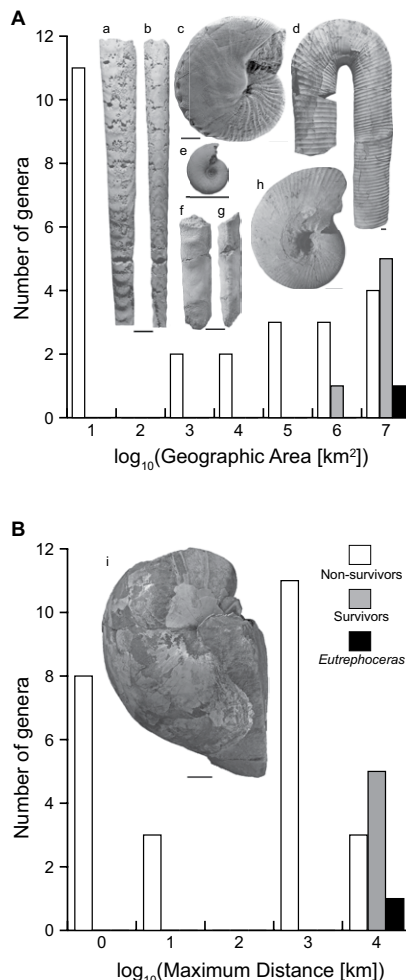


Figure 2. Geographic distribution of ammonite genera and nautilid *Eutrephoceras* at the end of the Maastrichtian (see Methodology discussion in text). A: \log_{10} (geographic area). B: \log_{10} (maximum distance). Each bin X contains values ranging from X.00 to X.99. The \log_{10} transformation was used so that each bin represents values one order of magnitude larger than the previous bin. The geographic ranges of ammonite genera that survived the Cretaceous-Paleogene event are significantly greater than those of genera that became extinct at or shortly before the event (Mann-Whitney U-test, $p = 0.002$ for geographic area and $p = 0.004$ for maximum distance). Ammonites that briefly survived into the Paleocene: a,b—*Baculites*, c—*Hoploscaphtites*, d—*Diplomoceras*, e—*Pseudophyllites*, f,g—*Eubaculites*, h—*Pachydiscus* (*Pachydiscus*); i—the nautilid *Eutrephoceras*. Scale bar = 1 cm.

ammonites eventually succumbed to extinction, whereas *Eutrephoceras*, with its smaller population sizes and larger embryonic shells, survived. Evidently, a broad geographic distribution may have initially protected some ammonites from extinction, but it did not guarantee their long-term survival.

CONCLUSIONS

The ultimate extinction of the ammonites and survival of the nautilids may have been influenced by a variety of factors; e.g., an ephemeral episode of surface-water acidification (Alegret et al., 2012) and a period of rapid cooling following the Chicxulub impact (Vellekoop et al., 2014). However, regardless of the particular killing mechanism, the geographic distribution of ammonite genera appears to have played a role in the pattern of extinction. Most ammonite genera at the end of the Cretaceous exhibited a restricted distribution, increasing their vulnerability to extinction even from stochastic processes. Those ammonites that briefly survived into the Paleocene were significantly more widely distributed than those that disappeared at the end of the Cretaceous. Furthermore, the geographic distribution of *Eutrephoceras*, which unquestionably survived into the Paleocene (and into the Miocene), was similar to that of the most widely distributed ammonites.

ACKNOWLEDGMENTS

Landman thanks J.K. Cochran (Stony Brook University) for helpful discussions. Goolaeerts thanks E. Steurbaut (Royal Belgian Institute of Natural Sciences), C. Dupuis and M. Hennebert (University of Mons, Belgium), and M. Yahia (Kalaat Senan, Tunisia) for helpful discussions and assistance in the field. This research was supported by U.S. National Science Foundation grant DEB-1353510 to Landman.

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Manuscript received 15 April 2014

Revised manuscript received 28 May 2014

Manuscript accepted 2 June 2014

Printed in USA

Geology

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Geology 2014;42;707-710
doi: 10.1130/G35776.1

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