

Evolution of habitat depth in the Jurassic–Cretaceous ammonoids

Kazuyoshi Moriya¹

Department of Earth Sciences, Faculty of Education and Integrated Arts and Sciences, Waseda University, Shinjuku-ku, Tokyo 169-8050, Japan

Ammonoids, a group of cephalopods with external chambered shells, arose in the early Devonian and went extinct at the Cretaceous/Paleogene (K/Pg) boundary. During their 340-million-y history, ammonoids suffered three major diversity crises at the end of the Devonian, Permian, and Triassic Periods, and the terminal extinction event at the K/Pg boundary. Because of their rapid morphological evolution and rich fossil record, ammonoids have been used to determine the relative age of marine strata and correlation since the dawn of stratigraphy. Although the morphological analyses of shell materials have provided some insights into ontogeny and evolution, their biological nature is poorly understood because of the lack of soft

body fossils and close modern relatives. For example, although one may usually imagine that ammonoids were planktic or nekctic organisms within a water column, like the *Nautilus*, which is the sole surviving cephalopod bearing an external chambered shell, there is very little direct evidence showing the habitat depth of ammonoids within an ancient water column.

Sessa et al. (1) shed new light on the habitat depth of the Cretaceous ammonoids using geochemical proxy records. When calcium carbonate, which composes the shell material of many marine invertebrates, is secreted within the ocean, the stable oxygen isotopic composition of the carbonate is predominantly determined by the ambient ocean temperature. Therefore,

oxygen isotopic analyses of shell materials of ammonoids reveal the temperature at which the shell was secreted. This technique, called oxygen isotopic thermometry, has been widely used in paleoclimatological and paleobiological research. It was also applied to ammonoid fossils more than 40 y ago (2, 3). Many scientists, however, assumed that ammonoids were planktic or nekctic organisms, so their discussion focused mainly on growth rates inferred by identifying sinusoidal patterns, hence seasonality, in the temperature data. Among those previous workers, Anderson et al. (4) analyzed oxygen isotopic composition of the middle Jurassic ammonoids and compared the results with those of co-occurring benthic and planktic organisms. The isotopic temperatures of *Kosmoceras* (Stephanoceratoidea) were significantly warmer than those of benthic bivalves and slightly cooler than those of surface-dwelling organisms, indicating a planktic or nekctic mode of life of *Kosmoceras* (i.e., a position high in the water column) (Fig. 1). In contrast, when Moriya et al. (5) analyzed isotopic temperatures of the late Cretaceous ammonoids and co-occurring planktic and benthic organisms, isotopic temperatures of all ammonoids analyzed, regardless of their taxonomic and morphological relationships, were essentially identical to those of benthic foraminifers and bivalves, and significantly cooler than those of planktic foraminifers, indicating a demersal (bottom dwelling) habitat of these ammonoid species (Fig. 1). Because paleontologists working on ammonoids expected that the morphological features of the external shells must, at least partly, represent their ecology, these results raised many arguments on ammonoid ecology. Since the works of Anderson et al. (4) and Moriya et al. (5), the use of isotopic thermometry on ammonoid fossils for identifying their ecology has become more widespread (6–8) (Fig. 1). However, because of technical difficulties in identifying thermal structure of the water column with analyzing apparent planktic and benthic organisms, a full set of data for planktic and benthic organisms

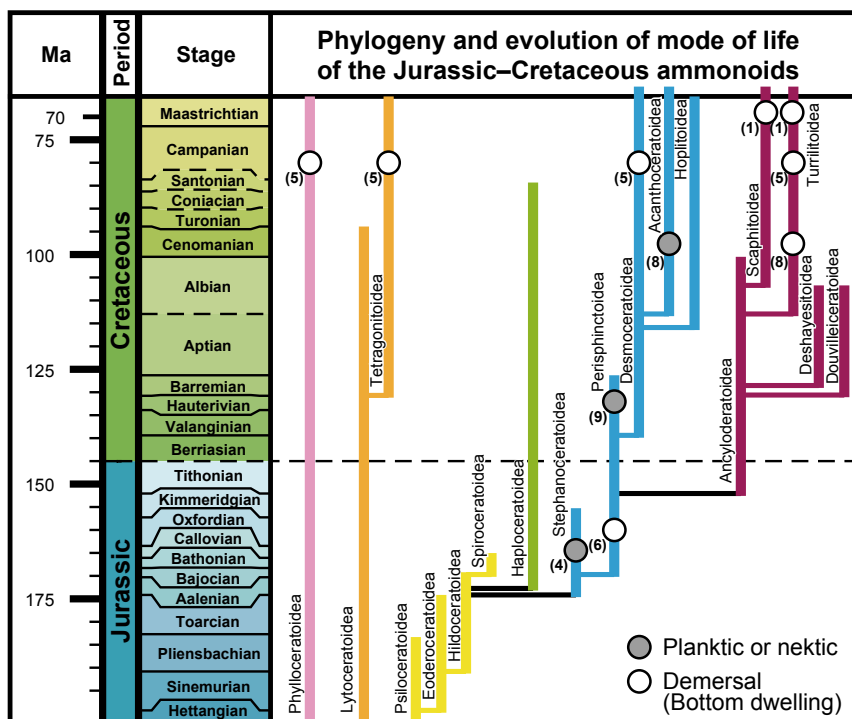


Fig. 1. Phylogeny and evolution of mode of life of the Jurassic–Cretaceous ammonoids. Age of each stage boundary is from Gradstein et al. (16). Phylogeny of ammonoids is cited from Yacobucci (17). Open white circles represent isotopic results indicating demersal (bottom dwelling) habitat at the age plotted on each lineage. Gray filled circles indicate planktic or nekctic habitat. Numbers at left bottom of each circle represent references for each data. Pink bar, Phylloceratina (5); orange bar, Lytoceratina (5); yellow bar, Ammonitina; pale green bar, Haploceratina; pale blue, Perisphinctina (4–6, 8, 9); purple bar, Ancyloceratina (1, 5, 8).

Author contributions: K.M. wrote the paper.

The author declares no conflict of interest.

See companion article on page 15562.

¹Email: kmoriya@waseda.jp.

co-occurring with ammonoids have rarely been described since Moriya et al. (5). An additional unanswered question is how habitat depth preferences evolved in ammonoids, especially in the latest Cretaceous time just before the terminal extinction event. For discussing mechanisms and dynamics of paleobiodiversity, paleoecosystem, and extinction events, a fundamental knowledge about habitat depth of ammonoids is crucial.

The report by Sessa et al. (1) is the first paper to describe the habitat of ammonoids in the latest Cretaceous Western Interior Seaway of North America with a full set of concrete evidence from oxygen isotopic thermometry. Isotopic temperatures calculated from planktic foraminifers inhabiting the mixed layer of the water column and benthic organisms on the sea floor show temperatures of $\sim 26^\circ\text{C}$ and $\sim 19^\circ\text{C}$, respectively, indicating $\sim 7^\circ\text{C}$ differences between surface and bottom waters. The mean isotopic temperatures of the latest Cretaceous ammonoids, *Eubaculites carinatus* and *Eubaculites latecarinatus* (Turrilitoidea), and *Discoscaphites iris* (Scaphitoidea) are estimated as $\sim 18^\circ\text{C}$, comparable to those of benthic organisms (1). In addition to isotopic results, careful examination of the preservation of shell materials excludes potential postmortem drift, often a concern in organisms with potentially buoyant shells. These lines of evidence clearly indicate that these ammonoid species were demersal (bottom dwelling) organisms, providing the first direct evidence of habitat depths for the latest Cretaceous lineages that became extinct at or just above the K/Pg boundary (9).

Although data are still sparse, an overview of evolutionary history of habitats of the Jurassic–Cretaceous ammonoids indicates a very interesting view (Fig. 1). Although many previous workers expected that ammonoids were predominantly planktic or nektic organisms, isotopic data suggest that bottom-dwelling habitat seems to be more frequent among the ammonoids after the Triassic/Jurassic diversity crisis. Additionally, in Perisphinctoidea, habitat depth reverted back from demersal to planktic/nektic even within a lineage. As Sessa et al. (1) show, many groups of ammonoids (Phylloceratoidea, Tetragnostoidea, Desmoceratoidea, Scaphitoidea, and Turrilitoidea), which possessed a demersal habitat, went extinct at the K/Pg boundary (Fig. 1). However, the planktic/nektic group (Acanthoceratoidea) also went extinct at the same time. These facts suggest that the habitat depth of submature and mature individuals was not the determinant of extinc-

tion, and other ecological factors must have been critical for ammonoids at the K/Pg boundary. One potential hypothesis is the food habit. Kruta et al. (10) presented that the late Cretaceous baculites preyed upon planktic microorganisms. Because it is

The report by Sessa et al. is the first paper to describe the habitat of ammonoids in the latest Cretaceous Western Interior Seaway of North America with a full set of concrete evidence from oxygen isotopic thermometry.

expected that marine planktic ecosystem of microorganisms was severely damaged at the K/Pg boundary (11), Kruta et al. (10) proposed that the collapse of the marine planktic food web was the trigger of the ammonoid extinction event. However, Tanabe (12) argued that other groups of ammonoids with a jaw apparatus similar to modern nautiloids (e.g., phylloceratids and gaudryceratids), which are assumed to prey on macroorganisms, also became extinct at the boundary, indicating that feeding habits at submature and mature growth stages were also not related to loss of ammonoids in the

K/Pg terminal extinction event. Alternatively, habitat of hatchling and juvenile ammonoids is the other candidate for the fatal ecology for the latest Cretaceous ammonoids. On the basis of their small embryonic shell size (0.5–1.8 mm in diameter) and the occurrence of massive accumulation of embryonic shells, eggs and hatchlings are thought to have been planktic, feeding during early development on planktic microorganisms (12–14). If this were the case, the abrupt demise of planktic ecosystems at the K/Pg boundary would have had a great impact on the survival of newly hatched ammonoids, but not on the direct-developing nautiloids. However, Landman et al. (15) pointed out the differences in the timing of extinction between cosmopolitan and endemic ammonoids. Although both cosmopolitans and endemics share the similar embryonic shell size, only endemics went extinct at the K/Pg boundary, and few cosmopolitans survived into the earliest Paleocene, indicating embryonic shell size; hence, embryonic ecology may not have been the key to survival. However, the termination of all ammonoids—including cosmopolitans—at the earliest Paleocene ad extremum, and the survival of the nautiloid cephalopods, indicate that the fatal ecology for ammonoids has yet to be identified. The hypotheses mentioned above can be tested further with developments of new analytical techniques and using exceptionally well-preserved materials.

1 Sessa JA, et al. (2015) Ammonite habitat revealed via isotopic composition and comparisons with co-occurring benthic and planktonic organisms. *Proc Natl Acad Sci USA* 112:15562–15567.

2 Stahl W, Jordan R (1969) General considerations on isotopic paleotemperature determinations and analyses of Jurassic ammonites. *Earth Planet Sci Lett* 6(3):173–178.

3 Jordan R, Stahl W (1970) Isotopische Paläotemperatur Bestimmungen an jurassischen Ammoniten und grundsätzliche Voraussetzungen für diese Methode. *Geol Jahrb* 89:33–62.

4 Anderson TF, Popp BN, Williams AC, Ho L-Z, Hudson JD (1994) The stable isotopic record of fossils from the Peterborough Member, Oxford Clay Formation (Jurassic), UK: Palaeoenvironmental implications. *J Geol Soc London* 151(1):125–138.

5 Moriya K, Nishi H, Kawahata H, Tanabe K, Takayanagi Y (2003) Demersal habitat of Late Cretaceous ammonoids: Evidence from oxygen isotopes for the Campanian (Late Cretaceous) northwestern Pacific thermal structure. *Geology* 31(2):167–170.

6 Lécuyer C, Bucher H (2006) Stable isotope compositions of a late Jurassic ammonite shell: A record of seasonal surface water temperatures in the southern hemisphere? *Earth* 1:1–7.

7 Henderson RA, Price GD (2012) Palaeoenvironment and paleoecology inferred from oxygen and carbon isotopes of subtropical mollusks from the Late Cretaceous (Cenomanian) of Bathurst Island, Australia. *Palaios* 27(9–10):618–627.

8 Stevens K, Mütterlose J, Wiedenroth K (2015) Stable isotope data ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) of the ammonite genus *Simbirskites*—Implications for habitat reconstructions of extinct cephalopods. *Palaeogeogr Palaeoclimatol Palaeoecol* 417:164–175.

9 Landman NH, Garb MP, Rovelli R, Ebel DS, Edwards LE (2012) Short-term survival of ammonites in New Jersey after the End-Cretaceous Boliide impact. *Acta Palaeontol Pol* 57(4):703–715.

10 Kruta I, Landman NH, Rouget I, Cecca F, Tafforeau P (2011) The role of ammonites in the Mesozoic marine food web revealed by jaw preservation. *Science* 331(6013):70–72.

11 Huber BT, MacLeod KG, Norris RD (2002) Abrupt extinction and subsequent reworking of Cretaceous planktonic foraminifera across the Cretaceous-Tertiary boundary: Evidence from the subtropical North Atlantic. *Catastrophic Events and Mass Extinction: Impacts and Beyond*, eds Koeberl C, MacLeod KG (Geological Society of America, Boulder, CO), pp 277–289.

12 Tanabe K (2011) Paleontology. The feeding habits of ammonites. *Science* 331(6013):37–38.

13 Landman NH, Tanabe K, Shigetani Y (1996) Ammonoid embryonic development. *Ammonoid Paleobiology*, eds Landman NH, Tanabe K, David RA (Plenum, New York), pp 343–405.

14 De Baets K, et al. (2015) Ammonoid embryonic development. *Ammonoid Paleobiology: From Anatomy to Ecology*, eds Klug C, Korn D, de Baets K, Kruta I, Mapes RH (Springer, The Netherlands), pp 113–205.

15 Landman NH, et al. (2014) Ammonite extinction and nautiloid survival at the end of the Cretaceous. *Geology* 42(8):707–710.

16 Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (2012) *The Geologic Time Scale 2012* (Elsevier, Boston).

17 Yacobucci MM (2015) Macroevolution and paleobiology of Jurassic–Cretaceous ammonoids. *Ammonoid Paleobiology: From Macroevolution to Paleogeography*, eds Klug C, Korn D, de Baets K, Kruta I, Mapes RH (Elsevier, The Netherlands), pp 189–228.