Belemnite extinction and the origin of modern cephalopods 35 m.y. prior to the Cretaceous–Paleogene event

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ABSTRACT

Belemnites, a very successful group of Mesozoic cephalopods, flourished in Cretaceous oceans until the Cretaceous–Paleogene event, when they became globally extinct. Following this event the modern types of cephalopods (squids, cuttlefish, octopus) radiated in the Cenozoic in all oceans. In the North Pacific, however, a turnover from belemnites to the modern types of cephalopods about 35 m.y. before the Cretaceous–Paleogene event documents a more complex evolutionary history of cephalopods than previously thought. Here we show that the modern types of cephalopods originated and prospered throughout the Late Cretaceous in the North Pacific. The mid-Cretaceous cephalopod turnover was caused by cooling and the closure of the Bering Strait, which led to a subsequent faunal isolation of this area. In the Late Cretaceous the former niches of the fast-swimming belemnites were taken over by the modern types of cephalopods, which evolved endemically. The Cretaceous–Paleogene event only allowed the modern types of cephalopods to spread globally and to take over the niches previously held by belemnites.

INTRODUCTION

The mollusk group of the belemnites includes extinct coleoid cephalopods, which were stenothermal inhabitants of shelf seas providing a significant biomass in Mesozoic ocean, as do modern squids now (Doyle, 1992; Christensen, 2002; Rexfort and Mutterlose, 2006). They had an important position in ancient ecosystems, both as predators and important prey for marine reptiles and sharks (Doyle and Macdonald, 1993; Rexfort and Mutterlose, 2006). Belemnites appeared in the earliest Jurassic, had a remarkable taxonomic and morphological diversification in the world's oceans for more than 130 m.y., and became extinct at the end of the Cretaceous (Doyle, 1992; Doyle et al., 1994; Christensen, 2002). Following the global Cretaceous–Paleogene extinction event, during the Cenozoic, there was rapid diversification of the modern types of cephalopods, which dominate modern oceans (e.g., Boyle and Rodhouse, 2005). The rich and continuous fossil record of belemnites offers the potential for understanding the evolutionary dynamics of nektonic biota. Their diversity variations through the Jurassic and Cretaceous are well correlated with Earth's environmental changes, such as diversity increasing with high sea-level periods and decreasing with oceanic anoxic events (e.g., Mutterlose, 1998). The evolutionary history of belemnites is well documented from Europe, the Arctic, the Antarctic–South Pacific, and the Western Interior Seaway (Doyle, 1992; Christensen, 1997; Mutterlose, 1998).

The evolutionary history of this group is, however, hardly known from the North Pacific. The Pacific was the largest ocean in the Cretaceous, and therefore plays a key role for the understanding of macroevolutionary dynamics on a global scale. Belemnites occur in Jurassic to Early Cretaceous marine strata in Japan, western North America, and south Alaska (e.g., Hanai, 1953; Doyle, 1987). They are, however, absent in strata of Late Cretaceous age in these areas, though fossiliferous marine deposits of this age are widespread. This pattern suggests that belemnites disappeared from the North Pacific in the mid-Cretaceous. Fossil records of the modern types of cephalopods (Decabrachia and Vampyropoda), including their earliest findings, have, however, been reported in recent studies of the Late Cretaceous of the North Pacific (e.g., Tanabe et al., 2008). Our study sheds light on this major faunal shift by relating it to geological observations; we unravel the extinction of belemnites in the North Pacific and address the environmental background.

STRATIGRAPHY OF BELEMNITES

Fossiliferous strata of Cretaceous age are widely distributed in the circum–North Pacific; the most continuous and fossiliferous sequences are known from Japan and northern California (Fig. 1A). This study focuses on the Albian successions of both regions in order to better understand the belemnite extinction. Age determination of the strata studied is based on diagnostic ammonite species. Evaluations of museum collections (Mikasa City Museum, and Kyushu University, Japan; California Academy of Science, USA) have also been done. Details of the localities, horizons, and the precise stratigraphic ages of Albian belemnites are shown in Table DR1 in the Data Repository.[1]

Northwest Pacific

While belemnites are common in Jurassic and pre-Albian Cretaceous strata, they became rare in the Albian. Our extensive field studies of Albian strata in Japan supplied rostra from five localities (Figs. 1A and 2A–2F; Table DR1). All belemnites from the early to late Albian belong to *Neohibolites*. *N.* cf. *praeultimus* (Loc. 3; Fig. 2E) and *N.* sp. (Loc. 5; Fig. 2F) from the latest Albian represent the last record of belemnites in the Northwest Pacific (Table DR1).

The Yezo Group in northern Hokkaido (Loc. 2; Fig. 1A) shows a continuous record of Cretaceous strata from the late Aptian to the late Campanian (Fig. 1B). Although megafossils are rare in the Aptian–Albian of the Yezo Group, *Neohibolites* occurs continuously from the late Aptian to the middle–late Albian of this unit (Fig. 1B). The belemnites are found in various facies, from mudstones and sandstones to conglomerates deposited by turbidity currents. These different types of facies are also common in the Late Cretaceous part of the Yezo Group, where numerous well-preserved molluscan fossils have been elucidated by many paleontological and biostratigraphical studies (e.g., Takahashi et al., 2003). Belemnites, however, have never been found in the fossiliferous successions of the post-Albian Cretaceous (Fig. 1B).

Northeast Pacific

Cretaceous marine deposits in northern California (Ono area), the Budden Canyon Formation, are represented by a thick sequence of Hauterivian–

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[1] GSA Data Repository item 2011153, Table DR1, details of *Neohibolites* from the Albian of North Pacific regions, is available online at www.geosociety.org/pubs/ft2011.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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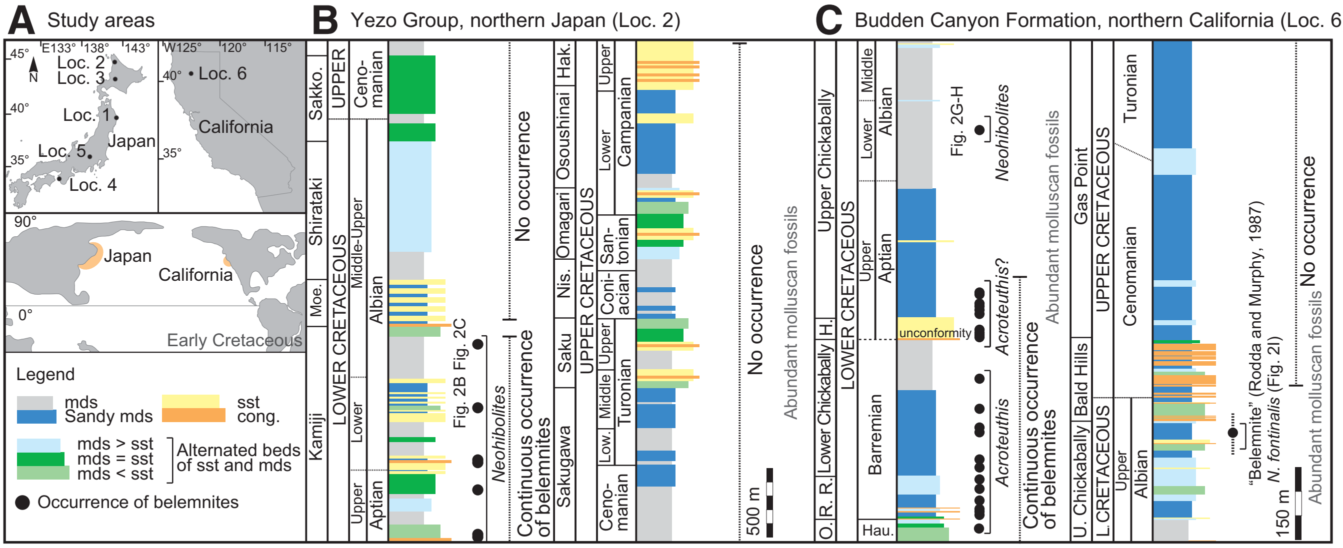

Figure 1. Stratigraphic distribution of belemnites in reference sections of North Pacific regions. A: Localities of Albian belemnites and Cretaceous paleomap. Loc.—locality. B: Stratigraphic distribution of belemnites in Yezo Group, Nakagawa area, northern Japan (Loc. 2). Generalized lithological columnar section based on Hashimoto et al. (1967), Takahashi et al. (2003), Iba (2009), and Yoshida et al. (2010), who researched exposures along the tributaries of the Teshio River. Moe.—Moehoro, Sakko.—Sakkotandake, Nis.—Nishichirashinaigawa, Hak.—Hakobuchi Formation. C: Stratigraphic distribution of belemnites in Budden Canyon Formation, Shasta County, northern California (Loc. 6). Generalized lithological columnar section based on field work along North Fork Cottonwood Creek and its tributaries. Ammonite biostratigraphy based on Murphy et al. (1969) and Amédro and Robaszynski (2005). O.—Ogo, R.R.—Roaring River, H.—Huling Sandstone Member, Hau.—Hauterivian, mds—mudstone, sst—sandstone, cong.—conglomerate. The stratigraphic sections of B and C are split into two lithostratigraphic columns each. Details of localities of Albian belemnites are shown in Table DR1 (see footnote 1).

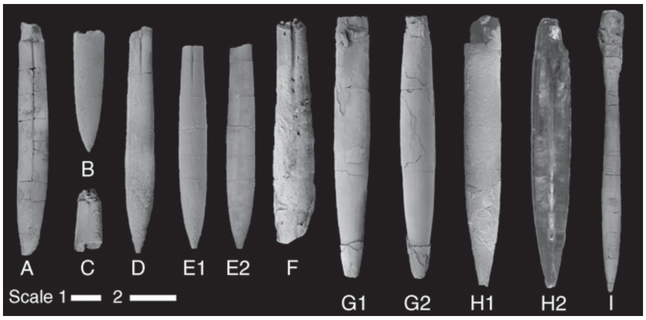

Figure 2. *Neohibolites* from Albian of North Pacific. A: *Neohibolites miyakoensis* (early Albian; Loc. 1). B, C: *N.* sp. (early Albian and middle–late Albian, Loc. 2). D: *N.* cf. *praeultimus* (middle Albian, Loc. 4). E: *N.* cf. *praeultimus* (latest Albian, Loc. 3). E1—ventral, E2—left lateral view. F: *N.* sp. (latest Albian, Loc. 5). G, H: *N.* sp. (early Albian, Loc. 6). G1, H1—ventral view, G2—left lateral, H2—cross section. I: *N. fontinalis* (latest Albian, Loc. 6). Holotype of Anderson (1938) (CASG 61687). A–F are from Japan and G–I are from northern California. Scale bars are 1 cm. Scale 1 for A and I, and scale 2 for B–H. Details of localities, horizons, precise ages of Albian belemnites, and repository numbers are shown in Table DR1 (see footnote 1).

Turonian fossiliferous clastics (Figs. 1A and 1C). Belemnites (*Acroteuthis*) are very common in various lithofacies from the late Hauterivian to early late Aptian of the Budden Canyon Formation (Fig. 1C). Belemnites are, however, rare in the latest Aptian to Albian, although numerous well-preserved megafossils occur in these strata (Fig. 1C). The Albian belemnite *Neohibolites* sp. was observed in beds of early Albian age (*Douvilleiceras mammillatum* Zone) (Figs. 1C, 2G, and 2H). Rodda and Murphy (1987) reported a belemnite without precise identification co-occurring with *Beudanticeras haydeni*, indicating the latest Albian *Mortoniceras perinflatum* Zone (Fig. 1C). Anderson (1938) described *Neohibolites fontinalis* from the same biozone (Figs. 1C and 2I). No belemnites have, however, been recorded from Late Cretaceous strata, though fossiliferous marine deposits of this age are widespread in northern California. The belemnites thus declined in abundance in the latest Aptian to Albian, and disappeared completely from northern California in the latest Albian. Apparently the latest Albian extinction of belemnites occurred both in Japan and in northern California.

DISCUSSION

Belemnite Extinction and the Origination of Modern Cephalopods

Belemnites have also been reported in high abundances from the Early Cretaceous of other areas of the North Pacific, such as south Alaska, British Columbia, and Oregon (Anderson, 1938; Jeletzky, 1964; Doyle, 1987). However, they have never been observed in the fossiliferous Late Cretaceous of these regions. The following biogeographical patterns have been compiled for the North Pacific (Fig. 3A): (1) continuous occurrence of belemnites throughout the Jurassic–Early Cretaceous; (2) extinction of belemnites in the latest Albian; and (3) a long-term absence throughout the Late Cretaceous.

Neohibolites, the last genus to occur, prospered in other parts of the world until the middle Cenomanian (Tethys, North Europe, Russian Platform, Caribbean, Antarctic–South Pacific) (Doyle, 1987, 1992; Christensen, 1997, 2002; Mitchell, 2005). In the Late Cretaceous, belemnites (Belemnitellidae) were common in the Boreal seas, the Western Interior Seaway, and the Northern Tethyan Sea (Christensen, 1997). The belemnite family Dimitobelidae occurred in the Antarctic–South Pacific until the end of the Cretaceous (Doyle, 1992). The Albian extinction of belemnites is thus an enigmatic bioevent restricted to the North Pacific.

This mid-Cretaceous extinction influenced the evolution of the modern types of cephalopods, which became common in the Late Cretaceous of the North Pacific. Modern cephalopods are abundant; biomass estimates range from 193 to 375 × 10^6 t (Boyle and Rodhouse, 2005). They expose a remarkable morphological and ecological diversity in coastal to pelagic environments

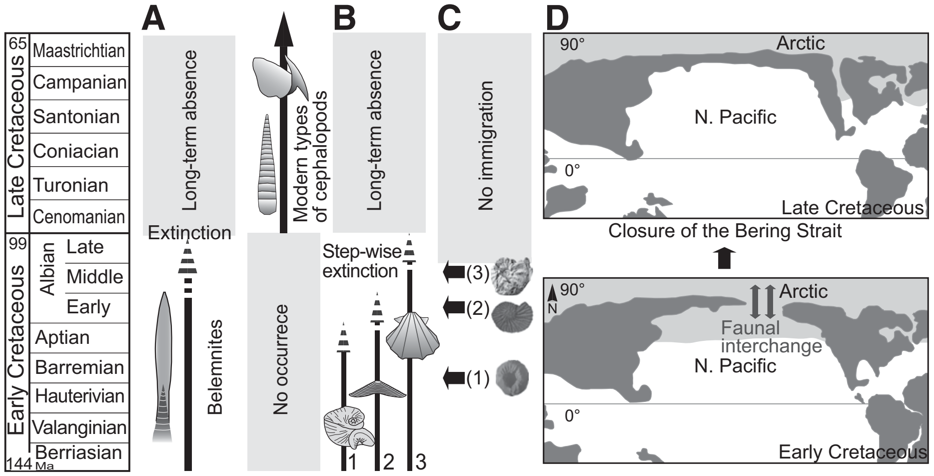

Figure 3. Mid-Cretaceous cephalopod turnover in North Pacific. A: Extinction of belemnites and subsequent origination of modern types of cephalopods. B: Step-wise demise of carbonate platform biota that indicate Albian cooling in North Pacific (Iba and Sano, 2007, 2008). 1—Mesogean key reference taxa (e.g., rudists); 2—Mesogean indicators (e.g., orbitolinids); 3—Tethyan bivalve *Neithea*. C: Occurrence of Arctic ammonites in the North Pacific. 1—*Simbirskites* in the early Barremian (Matsukawa, 1988); 2—*Arcthoplites* in the early Albian (Iba, 2009); 3—*Gastroplites* in the middle Albian (Amédro and Robaszynski, 2005). D: Tectonic history of Arctic–North Pacific connection (see text for details).

in the modern world oceans (Boyle and Rodhouse, 2005), making them one of the most important groups of marine nektonic organisms. Coleoids that live in the modern oceans consist of 10-armed Decabrachia (squids, cuttlefish, and Spirulida) and 8-armed Vampyropoda (vampire squids and octopus) (Fuchs, 2006). Among these only the vampire squid (Vampyromorpha) is a conservative form that has a long evolutionary history going back to the Triassic (Fuchs, 2006). A recent phylogenetic reconstruction of Phanerozoic coleoids assigned all "fossil Teuthida (squids)" described from Jurassic and Cretaceous sediments (e.g., Germany and Lebanon) in previous studies (e.g., Doyle et al., 1994) to the ancestral group of eight-armed vampire squids (Fuchs, 2006).

Following the Albian extinction of belemnites, the spirulid genus *Naefia* and related forms with a small internal shell evolved in the early Cenomanian of the North Pacific. *Naefia* is common in the Late Cretaceous of the North Pacific (e.g., Fuchs and Tanabe, 2010), occurring in the same lithofacies as *Neohibolites*. The recent coleoid phylogeny suggests that the early Cenomanian *Naefia* of the North Pacific is reliably the oldest record of the Decabrachia (Fuchs, 2006). *Naefia*, which was almost restricted to the North Pacific until the Campanian, is therefore here viewed as the ancestor of modern 10-armed cephalopods. There are no Lagerstätten-like deposits in the Late Cretaceous of the North Pacific. Nevertheless, 8-armed taxa (vampire squids and octopus), which have a low potential of preservation due to the lack of an internal shell, are abundant in the Late Cretaceous record of the North Pacific (Tanabe et al., 2006, 2008; Tanabe and Hikida, 2010). The octopus Cirroctopoda and Octopoda, which are included in the modern types of cephalopods, are reported from the Santonian of the North Pacific, being the earliest and second-earliest records, respectively. These findings imply that the North Pacific was the nursery ground of the modern types of cephalopods. The faunal turnover from *Neohibolites* to the modern types of cephalopods is here considered as the nucleus for the evolution of modern cephalopods (Fig. 3A). In contrast to the previously held view, i.e., that modern types of cephalopods originated in the Cenozoic (e.g., Boyle and Rodhouse, 2005), our findings suggest that this shift had already occurred in the mid-Cretaceous (Fig. 3A).

Possible Cause of Belemnite Extinction

It has been suggested that most belemnites were stenothermal organisms, their biogeographical distribution being restricted by paleotemperature and ocean currents (Mutterlose, 1987; Doyle, 1992; Christensen, 1997). *Neohibolites*, however, shows a remarkable taxonomical diversification, and invaded all the world's oceans during the mid-Cretaceous warming period (Doyle, 1992). *Neohibolites* is thought to have been dwelling in warm water conditions, while the genus is very rare or even absent in sediments deposited under cool water conditions (Mutterlose, 1987). The shrinkage of warm water habitats in the Albian of the North Pacific may have been one cause for the extinction of *Neohibolites*.

A significant global warming trend spanning the Aptian to Turonian interval has been reconstructed from oxygen isotopic records of calcareous fine fraction and bulk sediments (e.g., Clarke and Jenkyns, 1999). Consistent with this warming trend was a significant poleward expansion and diversification of carbonate platform biota (e.g., rudists) that dwelled in the tropical to subtropical environment, in the Mediterranean, the Caribbean, and the Western Interior Seaway (e.g., Johnson et al., 1996). Their geographical expansion and subsequent decline are a good proxy of changes in heat transportation (Johnson et al., 1996).

There are no oxygen isotopic records that indicate fluctuations of paleotemperatures from the Albian of the North Pacific, due to a lack of continuous strata without diagenesis. Spatiotemporal changes of carbonate platform biota in the North Pacific, however, suggest a cooling in the North Pacific. A stepwise demise of carbonate platform biota during the Albian in the Northwest Pacific has been documented (Iba and Sano, 2007, 2008) (Fig. 3B). This gradual demise of carbonate platform biota contrasts the global biotic trend of poleward expansion and diversification of carbonate platform biota, and suggests a shrinkage of warm water habitats in the North Pacific. This interpretation is supported by various independent findings: (1) ooids disappeared in the Northwest Pacific in the early–middle Albian transition (Iba and Sano, 2007), and (2) episodic immigration events of Arctic-type ammonites into Japan and California occurred in the Albian (Amédro and Robaszynski, 2005; Iba, 2009) (Fig. 3C).

Causes of the reduction of Albian warm water habitats in the North Pacific include changes in paleogeography and oceanic circulation. A numerical simulation suggests that an increase of heat flow from the western Pacific into the Atlantic and decreased heat export from the Atlantic into the eastern Pacific were caused by the opening of the South Atlantic in the Albian (Poulsen et al., 2003). Numerical simulations of oceanic circulation in the Albian of the Pacific Ocean by Poulsen and Huynh (2006) that pay special attention to the increase in atmospheric CO$_2$ and the Albian opening of the Equatorial Atlantic Gateway also indicate (1) a strongly weakened paleo-Kuroshio warm current and a current flow from the equatorial Atlantic to the East Pacific, and (2) generation of cold water mass in the Pacific, contrasting the warm conditions in the Atlantic and Indian Oceans.

Impact of the Closure of the Bering Strait

Late Cretaceous belemnites exhibit a bipolar distribution (Doyle, 1992) with occurrences in the northern high latitudes (Arctic–northern Atlantic) and the southern high latitudes (Antarctic–southern Pacific). These paleobiogeographic patterns make a belemnite migration from the Antarctic–southern Pacific via the equatorial Pacific into the North Pacific unlikely.

From the Cenomanian onward, the center of species richness of belemnites was in the Boreal seas, from where belemnites migrated into the northern Tethys (e.g., Christensen, 1997). A potential explanation of the absence of these immigration faunas in the North Pacific is here seen in the closure of the Bering Strait in the mid-Cretaceous (Fig. 3D). This strait is important for both global marine and terrestrial biogeography and has strongly controlled faunal interchange between the Arctic–North Atlantic and the Pacific during Mesozoic to Cenozoic time (Marincovich and Gladenkov, 1999).

The age of the closure of the Bering Strait can be derived from migration patterns of marine and land organisms. The immigration of arctic-type ammonites into the North Pacific was terminated in the late Albian (Amédro and Robaszynski, 2005; Iba, 2009) (Fig. 3C). Land vertebrates started to migrate from Asia to North America at the time of the Albian-Cenomanian boundary (Cifelli et al., 1997). This latter migration indicates a closure of the Bering Strait and the establishment of a land bridge around the Albian-Cenomanian boundary. This closure persisted until the latest Miocene, when it opened again, until the present (Marincovich and Gladenkov, 1999). The closure thus prevented belemnites from migrating from the Boreal seas, the then hotspot of belemnite radiation, into the North Pacific (Fig. 3D). The belemnite-free North Pacific Ocean then allowed for the evolution of the modern types of cephalopods.

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