Ammonoid biodiversity changes across the Cenomanian–Turonian boundary in the Yezo Group, Hokkaido, Japan

KEN’ICHI KURIHARA, SEIICHI TOSHIMITSU, and HIROMICHI HIRANO


Ammonoid biodiversity changes from shallow to offshore environments across the Cenomanian–Turonian (C–T) boundary are reconstructed in the Yezo Group, Hokkaido, Japan. This group was probably deposited at approximately 35–45°N along a westward subduction margin in the northeastern Asian continent. Temporal changes in species richness in the Yezo Group, which show persistently high values during the middle Cenomanian and then decline stepwise from near the middle–late Cenomanian boundary, resemble those in Europe, but not those in Tunisia and the Western Interior. These differences suggest that the Cenomanian–Turonian “mass extinction” was not a global event for ammonoids but was restricted to mid-palaeolatitudinal regions (Europe and Japan). Sea level and climate changes probably influenced ammonoid faunas in the Yezo Group as well as those in Europe. However, it is unlikely that a single, simple cause led to the C–T boundary “mass extinction” because various abiotic changes in the Cenomanian–Turonian transition have been detected, and biotic and abiotic change are interrelated.

Key words: Ammonoids, mass extinction, Cenomanian–Turonian (C–T) boundary, Cretaceous, Hokkaido.

Ken’ichi Kurihara [kurihara582@city.mikasa.hokkaido.jp], Mikasa City Museum, 1-212-1 Nishiki-cho, Ikushumbetsu, Mikasa, Hokkaido 068-2111, Japan;
Seiichi Toshimitsu [s.toshimitsu@aist.go.jp], Geological Survey of Japan, AIST, 1-1-1 Higashi, Tsukuba, Ibaraki 305-8567, Japan;
Hiromichi Hirano [hhirano@waseda.jp], Department of Earth Sciences, School of Education and Integrated Arts and Sciences, Waseda University, 1-6-1 Nishiwaseda, Shinjuku-ku, Tokyo 169-8050, Japan.

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Introduction

The mid-Cretaceous period was characterised by one of the warmest climates during the Phanerozoic. The long-term δ¹⁸O data show high sea surface temperatures during the Cenomanian and Turonian and a thermal maximum during the late Turonian (e.g., Jenkyns et al. 1994; Clark and Jenkyns 1999; Wilson et al. 2002; Bornemann et al. 2008). During this interval, there is a conspicuous carbon isotopic event, which indicates perturbations in the global carbon cycle: the Cenomanian–Turonian boundary event (CTBE) (e.g., Voigt et al. 2004; Jarvis et al. 2006). The CTBE is characterised by a major δ¹³C excursion (2–4‰) related to the widespread deposition of organic carbon-rich sediments (“black shale”) known as the oceanic anoxic event 2 (OAE2; Schlanger and Jenkyns 1976). One of the mass extinction events for marine invertebrates has been recognised at the Cenomanian–Turonian (C–T) boundary. At this mass extinction event, 8% of all families, 26% of all genera, and 33–53% of all species went extinct (Sepkoski 1989, 1996). To explain this extinction event, many palaeontological and biostratigraphical studies have been proposed with geochemical and sedimentological data, and several theories have been put forward (Jarvis et al. 1988; Elder 1989; Batt 1993; Kauffman 1995; Kauffman and Hart 1995; Harries and Little 1999; Gale et al. 2000; Smith et al. 2001; Keller et al. 2001; Monnet et al. 2003; Monnet and Bucher 2007; Monnet 2009).

In Japan, Toshimitsu et al. (2003) discussed the relationship between the species diversity changes of Japanese ammonoids and marine environmental changes during the Cretaceous. They noted that the timing of the ammonoid species diversity minimum approximately corresponded to that of the OAE2. Takahashi (2005) revealed that all of the Japanese inoceramid species went extinct at the latest by the Cenomanian. Kurihara and Kawabe (2003) compared molluscan faunal changes (ammonoids and inoceramids) across the
C–T boundary between the Hakkin-zawa River section in Hokkaido, Japan, and the Pueblo section in the Western Interior, USA. They suggested that the timing of the extinction and recovery phases for molluscan faunas was approximately synchronous in both sections. These scholars concluded that the molluscan faunas in Japan were strongly influenced by the OAE2. Their approaches, however, were restricted to events in offshore facies and/or did not examine other factors in sufficient detail. Hence, it is necessary to compare faunal changes in different depositional environments within the Yezo basin to understand truly the C–T mass extinction event in the northwestern Pacific region. In the present paper, ammonoid biodiversity changes from shallow to offshore environments across the C–T boundary in Hokkaido, Japan, are therefore presented.

**Abbreviations.—**CIU, carbon isotopic unit; CTBE, Cenomanian–Turonian boundary event; FAD, first appearance data; OAE, oceanic anoxic event; OMZ, oxygen-minimum zone.

**Geological setting**

The Cretaceous Yezo Group, interpreted as forearc basin sediments (Okada 1983), is widely distributed in central Hokkaido, northern Japan and Sakhalin Island in Far East Russia (e.g., Takashima et al. 2004; Yazykova 2004). This group was probably deposited at approximately 35–45° N along a westward subduction margin in the northeastern Pacific region. In the present paper, ammonoid biodiversity changes from shallow to offshore environments across the C–T boundary in Hokkaido, Japan, are therefore presented.

**Material and methods**

Ammonoid faunas across the Cenomanian–Turonian boundary were examined in the Mikasa, Obira, and Oyubari areas. There is an abundance of megafossil data in the Cenomanian–Turonian transition of all areas (e.g., Hirano et al. 1977; Tanabe et al. 1977; Futakami 1986; Kurihara and Kawabe 2006; Funaki and Hirano 2004; Takahashi 2005). In the present paper, the stratigraphical ranges from these published and original data are used for the examination of ammonoid biodiversity changes in each area.

To compare the ammonoid biodiversity changes among intra- and interregional basins (e.g., Europe, the Western Interior, and Tunisia), we use carbon isotope \((\delta^{13}C)\) stratigraphy (Fig. 2) because the available intra- and interregional
correlation of Cretaceous δ¹³C stratigraphy between terrestrial organic materials and marine carbonates is widely accepted (e.g., Hasegawa and Saito 1993; Hasegawa 1997; Uramoto et al. 2007, 2009; Takashima et al. 2010). The δ¹³C stratigraphy has already been documented in the successions studied. The ammonoid biodiversity, then, is counted as the number of species (species richness) occurring within a carbon isotopic unit (CIU) based on correlations from previous studies (Fig. 2). The extinction (E) and origination (O) rates are defined as follows:
E rate = (number of preexisting species absent above each CIU)/(total number of species below each CIU)×100 (%)  
O rate = (number of successor species not present below each CIU)/(total number of species above each CIU)×100 (%)

Results

In the present study, six carbon isotopic units (CIUs) across the Cenomanian–Turonian (C–T) boundary were used (Fig. 3): (i) CIU1, correlated to the Cunningtoniceras inerme–lower part of the Acanthoceras rhotomagense zones in Europe (early middle Cenomanian); (ii) CIU2, correlated to the upper part of the A. rhotomagense–lower part of the Acanthoceras jukesbrownei zones (late middle Cenomanian); (iii) CIU3, correlated to the upper part of the A. jukesbrownei–lower part of the Metoicoceras geslinianum zones (late middle Cenomanian–early late Cenomanian); (iv) CIU4, correlated to the upper part of the M. geslinianum–upper part of the Watinoceras devonense zones (near the C–T boundary); (v) CIU5, correlated to the upper part of the W. devonense–lower part of the Mammites nodosoides zones (middle early Turonian); and (vi) CIU6, correlated to the upper part of the M. nodosoides Zone (late early Turonian).

None of the CIUs in the Mikasa area were recognised except CIU4. However, as the timing of the first appearance data (FADs) of Cunningtoniceras spp., Calycoceras spp. (ammonoids), Actinoceramus nipponicus, Inoceramus kamuy, and I. hobetsensis nonsulcatus (inoceramids) was recognised within CIUs 1, 2, 3, 5, and 6 in the Obira and Oyubari areas, respectively (Fig. 3), the FADs of these species were used as proxy datum planes in this study, and the boundaries of each CIU were defined as the middle portion of each species in the Mikasa area. The ammonoid biodiversity patterns within each CIU in the Mikasa, Obira, and Oyubari areas are shown in Fig. 4.

Mikasa area.—The ammonoid species richness showed persistent high values (12–13 species) in CIU1 and CIU2, then gradually decreased (6–7 species), finally reaching a minimum (4 species) at CIU5. In CIU6, the species richness increased again (9 species).

The extinction (E rate) and origination (O rate) rates recorded high values between the CIU1 and CIU2 intervals (E rate, 67%; O rate, 69%) and the CIU2 and CIU3 intervals (E rate, 69%; O rate, 75%).
rate, 85%; O rate, 71%), respectively. Although the highest values of E and O rates were recorded between the CIU4 and CIU5 intervals, the cause of the high values is interpreted to be the low species richness.

**Obira area.**—The species richness showed moderate values (7–9 species) in CIU1 and CIU2; it then abruptly decreased (2 species), reaching a minimum (1 species) at CIU4. Subsequently, the species richness increased again at CIU5 (8 species) and persisted with a moderate value (9 species) in CIU6.

The E rate showed a high value between the CIU2 and CIU3 intervals (77%) and the CIU3 and CIU4 intervals (50%), respectively. The highest value of E and O rates during the CIU4 and CIU5 intervals is interpreted to be due to the low species richness. Comparatively high values of E and O rates were recorded between the CIU5 and CIU6 intervals (E rate, 63%; O rate, 67%).

**Oyubari area.**—Species richness showed persistent moderate values (6–7 species) during the interval of CIU1 to CIU3 and then decreased at CIU4 (4 species). Subsequently, species richness increased abruptly at CIU5 (13 species) and persisted with a high value (11 species) in CIU6.

The E and O rates were relatively low compared to those in the Mikasa and Oyubari areas. A high O rate (85%) was recorded between the CIU4 and CIU5 intervals.

**Discussion**

**Taphonomy.**—Before comparing the ammonoid faunas among the Mikasa, Obira, and Oyubari areas, we should note the taphonomic attributes of the ammonoid fossils. Ammonoid shells may have been prone to post-mortem drift, just as modern *Nautilus* shells sometimes appear in areas outside of their original habitat area because of ocean currents (e.g., Stenzel 1964). For instance, Maeda et al. (2003) demonstrated that Late Palaeozoic ammonoids were transported from one or more distant offshore biotopes in Texas, USA. Kawabe (2003) examined the taphonomic attributes of ammonoids in late Albian–Cenomanian strata in the Mikasa and Oyubari areas and pointed out the following: (i) encrustation by organisms and corroded outer surfaces, which are indicative of shells that have floated, are absent from small to moderate-sized (1–30 cm in diameter) ammonoids; and (ii) the attributes of shell breakage indicate that the shells did not endure long-distance transport out of their original habitat. The preservational features of the ammonoid shells collected in the present study were almost coincident with those illustrated by Kawabe (2003). Consequently, we assume that the molluscan fossils in the present study did not undergo long-distance transport except for brief post-mortem movement.

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Ammonoid biodiversity changes in the Yezo Group.—

The temporal changes of ammonoid species richness across the Cenomanian–Turonian (C–T) boundary indicate the following (Fig. 4): (i) persistently high values during the middle Cenomanian (the carbon isotopic unit 1 (CIU1) and CIU2 intervals); (ii) a gradual decline from near the middle–late Cenomanian boundary (the CIU3 and CIU4 intervals), especially in inshore areas (Mikasa and Obira areas); and (iii) abrupt recovery just above the Cenomanian–Turonian boundary event (CTBE) (the CIU5 interval), especially in offshore areas (Obira and Oyubari areas).

Monnet (2009) demonstrated the temporal changes of ammonoid species richness during the late Albian to early Turonian in Europe, Tunisia, and the Western Interior, where are all type regions (old stratotypes and recent boundary stratotypes) for the Cenomanian and Turonian stages. Although his data are of a much higher resolution than the ones in the present study, thus making it difficult to compare directly the biodiversity changes, there are to be some similarities and contrasts between the Yezo Group and other regions. The temporal changes in species richness in the Yezo Group, which show persistently high values during the middle Cenomanian and a subsequent decline stepwise from near the middle–late Cenomanian boundary, resemble those in Europe (Monnet et al. 2003; Monnet and Bucher 2007; Monnet 2009) (Fig. 4). This resemblance indicates that the ammonoid faunas in Japan are characterised by a sustained diversity drop similar to those in Europe, showing that the mass extinction at the C–T boundary, therefore, did take place. In contrast, species richness in Tunisia and the Western Interior increases or remains relatively high across the C–T boundary despite the synchronous deposition of organic-rich sediments correlated to the OAE2; therefore, no ammonoid crisis occurred (Monnet 2009). Hence, these differences suggest that the Cenomanian–Turonian “mass extinction” is not a global event for ammonoids as Monnet (2009) (Fig. 4). Moreover, offshore mudstones are dominant in CIU3 to CIU4. The disappearance of acanthoceratid and kossmaticeratid ammonoids, therefore, may have been affected by shallow to offshore facies changes with transgression. In the Western Interior, Batt (1989) inferred ammonoid habitats in the Cenomanian and Turonian stages based on the relationship between morphotypes and distribution patterns. Within his interpretation, Acanthoceras and Cunningtoniceras (Group 1 in Batt’s study) were dominant and diverse in shallower areas, Calycoceras (Group 2) inhabited shoreface to distal offshore areas, and desmoceratids (Group7) were most abundant in proximal to medial offshore mud facies. Our data, therefore, conform to his hypothesis. However, in Hokkaido, the frequency of acanthoceratid ammonoids is much lower than that of less ornate ammonoids (i.e., desmoceratids, gaudryceratids) in various depositional environments during the late Albian to Cenomanian (Kawabe 2003). It is therefore necessary to investigate the relationship between species diversity and frequency of the ammonoid species in further research.

Species richness still decreased near the C–T boundary (CIU4) in all areas. Laminated or weakly laminated facies were dominant in the Yezo Group. In an open ocean such as the Pacific region, high surface productivity, which is promoted by coastal upwelling and an inflow of nutrients, develops the mid-water oxygen-minimum zone (OMZ) (Arthur et al. 1987; Erbacher et al. 1996). In a continental margin such as the Yezo basin, there were high coastal upwellings and an inflow of nutrients by a major widespread transgression near the C–T boundary (Arthur et al. 1987; Kruis and Barron 1990). The conspicuous abundance of dinoflagellate cysts supports
Ammonoid biodiversity changes from shallow to offshore environments across the C–T boundary are reconstructed in the Yezo Group, Hokkaido, Japan, which was probably deposited at approximately 35–45° N along a westward subduction margin in the northeastern Asian continent. The following conclusions are reached:

(i) Temporal changes in species richness in the Yezo Group, which show persistently high values during the middle Cenomanian, then decline stepwise from near the middle–late Cenomanian boundary, resemble those in Europe, but not those in Tunisia and the Western Interior. Hence, these differences suggest that the Cenomanian–Turonian “mass extinction” is not a global event for ammonoids and that the “mass extinction” was restricted to mid-palaeolatitudinal regions (Europe and Japan).

(ii) Species richness still decreased near the C–T boundary in the Yezo Group. Laminated or weakly laminated facies were dominant, and oxygen-depleted conditions spread. However, ammonoid species richness had already decreased from near the middle–late Cenomanian boundary, resembling those in Europe, but not those in Tunisia and the Western Interior. Hence, these differences suggest that the Cenomanian–Turonian “mass extinction” was restricted to mid-palaeolatitudinal regions (Europe and Japan).

Conclusions
cates that the decrease in ammonoid diversity in the Yezo Group was not solely caused by the OAE2.

(iii) In the Yezo Group, sea level and climate changes probably influenced ammonoid faunas as well as those in Europe. However, it is unlikely that a single, simple cause led to the C–T boundary “mass extinction” because various abiotic changes in the Cenomanian–Turonian transition have been detected, and there are interrelations between biotic and abiotic changes.

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