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Ammonoid Biodiversity Changes Across the Cenomanian—Turonian Boundary in the Yezo Group, Hokkaido, Japan

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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.

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Introduction

The mid-Cretaceous period was characterised by one of the warmest climates during the Phanerozoic. The long-term $\delta^{18}O$ 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 $\delta^{13}C$ 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
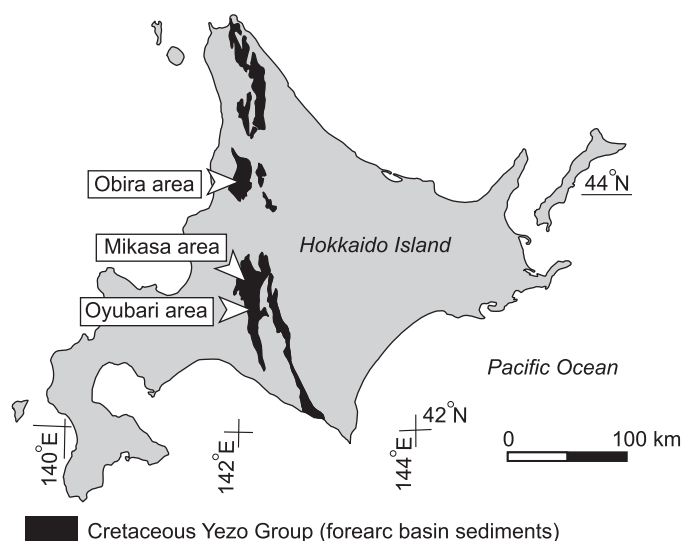
Fig. 1. Map of the study areas (Mikasa, Obira, and Oyubari areas in Hokkaido, Japan).

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 Asian continent (Kodama et al. 2002). The strata yield abundant, well-preserved macro- and microfossils and they show conspicuous west-to-east facies changes (e.g., Takashima et al. 2004). For the present paper, the following three areas were investigated (Fig. 1): the Mikasa area (shelf–coastal

plain setting), the Obira area (incised valley–outer shelf setting), and the Oyubari area (continental slope setting).

Mikasa area.—The succession across the Cenomanian–Turonian (C–T) boundary is composed mainly of shallow marine sandy facies (Mikasa Formation), of which the depositional environments are inferred to have ranged from shoreface to outer shelf (Fig. 2). The Cenomanian–Turonian boundary event (CTBE) is in the middle portion of the Mikasa Formation (Kurihara 2006). Weakly laminated mudstone is only observed just below the C–T boundary.

Obira area.—The succession across the C–T boundary is composed of sandy mudstone, mudstone, and alternating beds of sandstone and mudstone (Fig. 2). The CTBE is in the lower portion of the Saku Formation (Hasegawa and Saito 1993; Uramoto et al. 2007, 2009). Laminated mudstone is dominant within the CTBE. Greenish bioturbated mudstone with *Planolites*-like burrows is dominant above the CTBE. The depositional environment is inferred to have been outer shelf because of the predominance of offshore mudstone (Takashima et al. 2004).

Oyubari area.—The succession through the Cenomanian–Turonian is continuously exposed. Thus, many palaeontological studies concerning faunal turnover in various taxa have been proposed (Kaiho and Hasegawa 1994; Hirano 1995; Hasegawa 1999; Kurihara and Kawabe 2003; Takahashi 2005). The lithofacies across the C–T boundary is composed mainly of alternating beds of turbiditic sandstone and mudstone (Saku Formation). The CTBE is in the lower portion of the Saku Formation (Hasegawa and Saito 1993; Hasegawa 1997). Weakly laminated mudstone and greenish bioturbated mudstone with *Planolites*-like burrows are dominant within and just above the CTBE, respectively. The depositional environment is inferred to have been continental slope based on facies analysis and the morphology of calcareous benthic foraminifera (Kaiho et al. 1993; Takashima et al. 2004).

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 2003; Funaki and Hirano 2004; Takahashi 2005; Kurihara et al. 2007). In the present study, 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 (δ^{13}C) stratigraphy (Fig. 2) because the available intra- and interregional
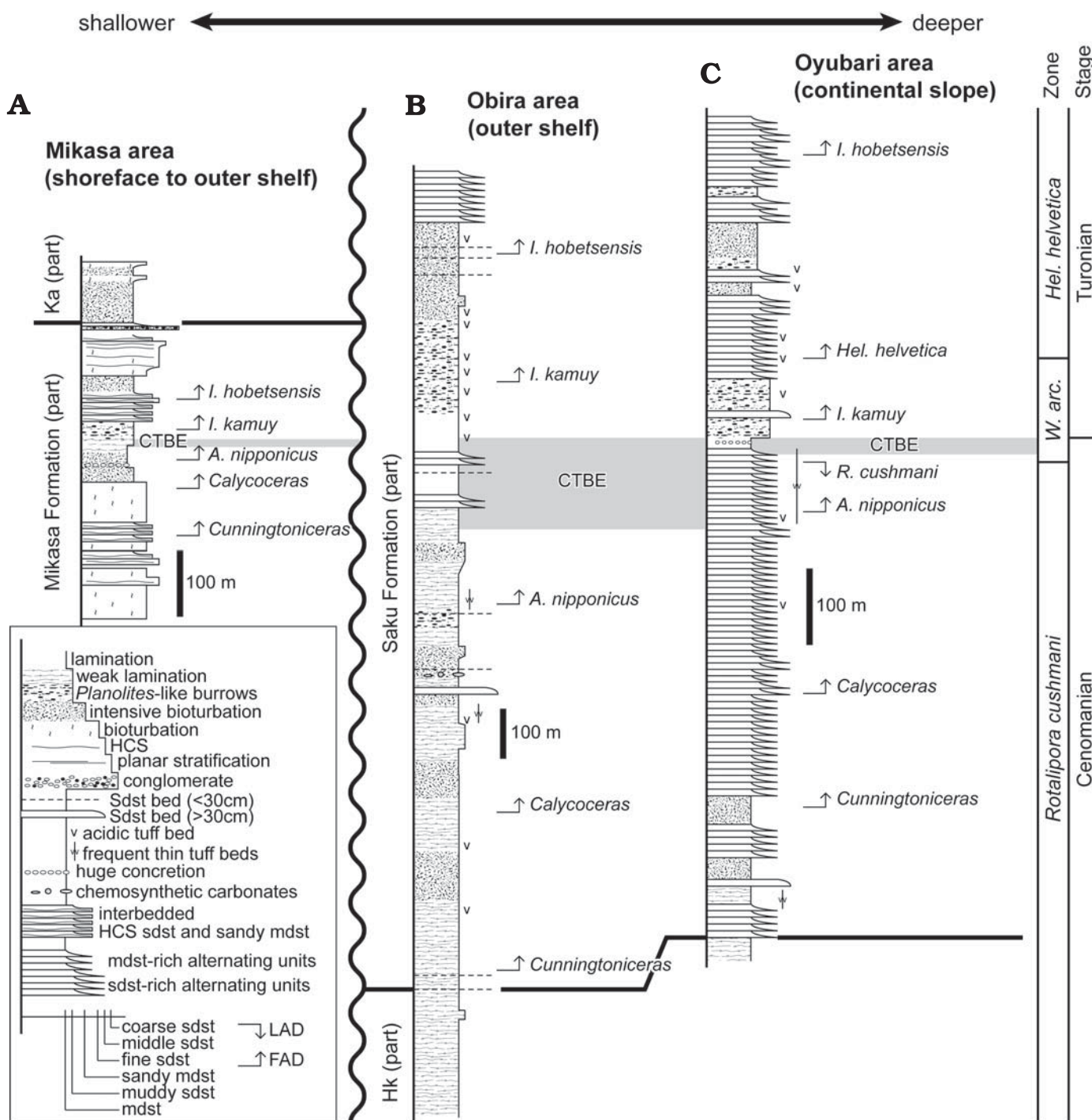
Fig. 2. Composite columnar sections in the Mikasa (**A**), Obira (**B**), and Oyubari (**C**) areas and the stratigraphical levels of macrofossil datum planes used in the present study. The shaded portion shows the Cenomanian–Turonian boundary event (CTBE). The molluscan fossil data are from Tanabe et al. (1977), Futakami (1986), Kurihara and Kawabe (2003), Funaki and Hirano (2004), Kurihara et al. (2007) and unpublished original data. The planktonic foraminiferal zonation and the CTBE are from Hasegawa (1997, 1999), Nishi et al. (2003), Kurihara (2006), and Uramoto et al. (2007, 2009). Abbreviations: Ka, Katsurazawa Formation; Hk, Hikagenosawa Formation; mdst, mudstone; sdst, sandstone; *A. nipponicus*, *Actinoceramus nipponicus*; *Hel. helvetica*, *Helvetoglobotruncana helvetica*; *I. hobetsensis*, *Inoceramus hobetsensis nonsulcatus*; *I. kamuy*, *Inoceramus kamuy*; *W. arc.*, *Whiteinella archaeocretacea*.

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 $\delta^{13}C$ 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:
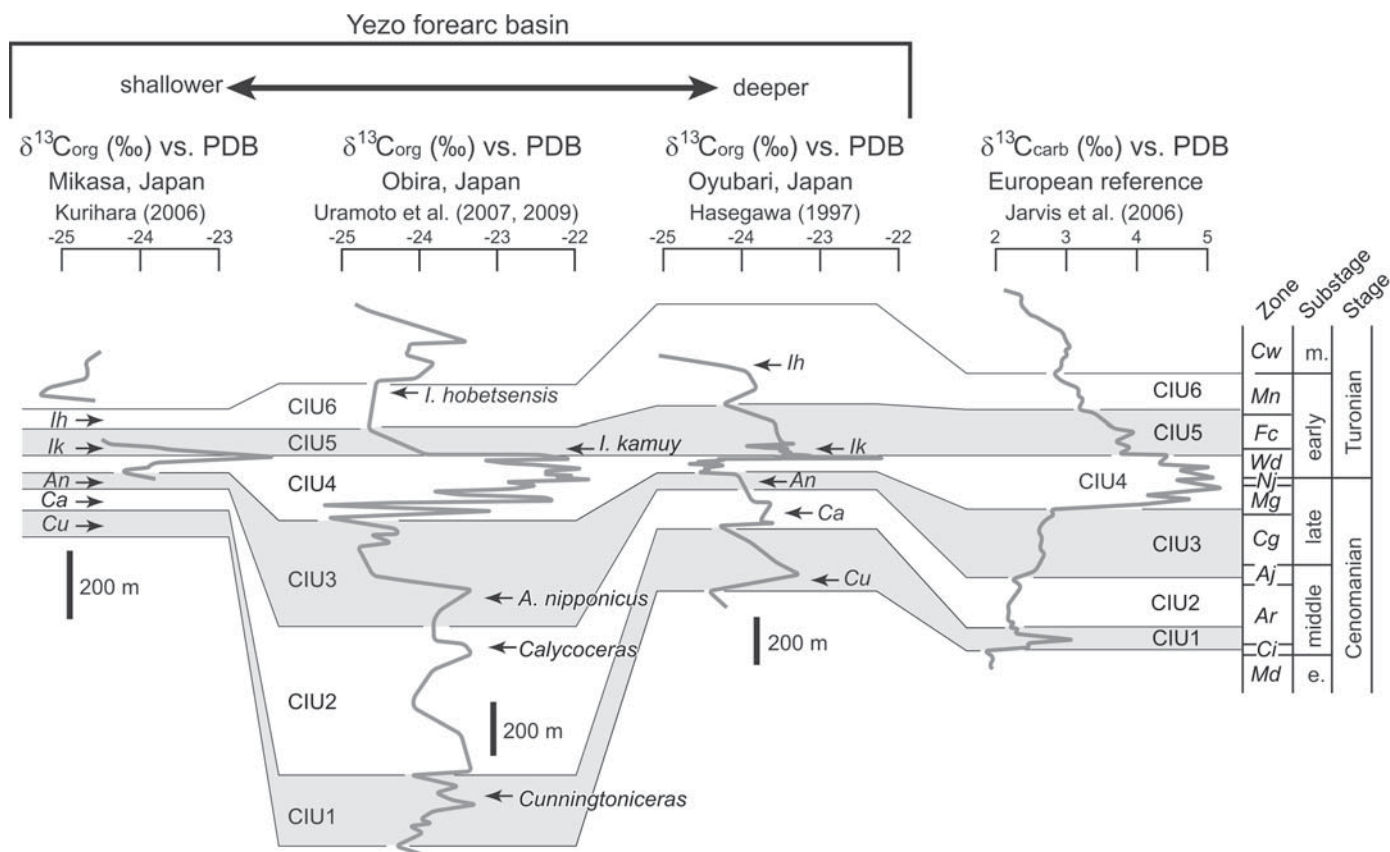
Fig. 3. Correlation of Upper Cretaceous δ^{13}C stratigraphy of terrestrial organic materials in the Mikasa, Obira, and Oyubari areas, Japan and reference δ^{13}C stratigraphy of carbonates in Europe (after Jarvis et al. 2006). Six carbon isotopic units (CIUs) were identified in the present study. Abbreviations: e., early; m., middle; PDB, Pee Dee Belemnite Standard; *Aj, Acanthoceras jukesbrownei*; *An, Actinoceramus nipponicus*; *Ar, Acanthoceras rhotomagense*; *Ca, Calycoceras* spp.; *Cg, Calycoceras guerangeri*; *Ci, Cunningtoniceras inertme*; *Cu, Cunningtoniceras* spp.; *Cw, Collignoniceras woollgari*; *Fc, Fagesia catinus*; *Ih, Inoceramus hobetsensis*; *Ik, Inoceramus kamuy*; *Md, Mantelliceras dixoni*; *Mg, Metoicoceras geslinianum*; *Mn, Mammites nodosoides*; *Nj, Neocardioceras juddii*; *Wd, Watinoceras devonense*.

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 *A. jukesbrownei* zones (late middle Cenomanian); (iii) CIU3, correlated to the upper part of the *A. jukesbrownei*–lower part of the *Metoicoceras geslinianum* zones (latest 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
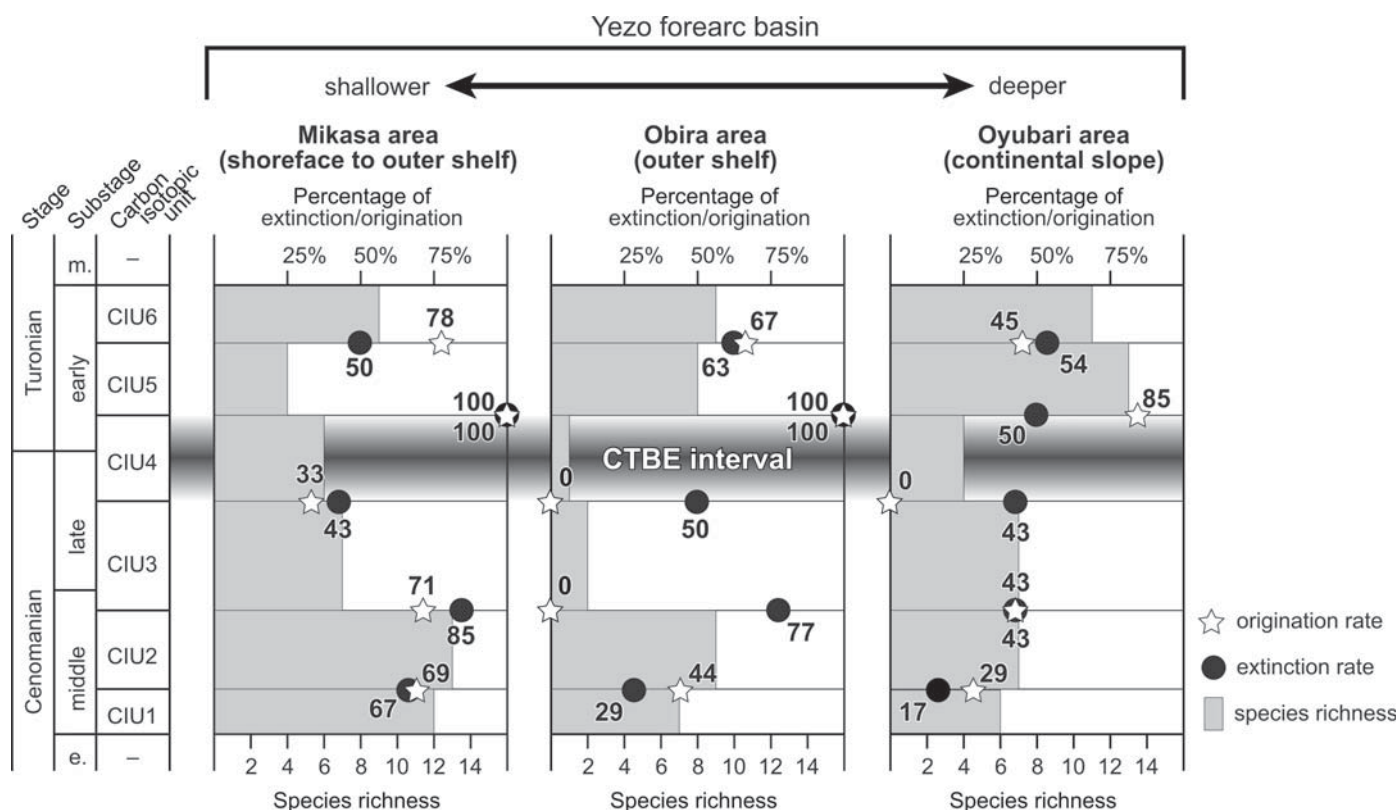
Fig. 4. Temporal changes in ammonoid species richness, extinction, and origination rates in the Mikasa, Obira, and Oyubari areas. Abbreviations: CIUs, carbon isotopic units; CTBE, Cenomanian–Turonian boundary event; e., early; m., middle.

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 fol-
lowing (Fig. 4): (i) persistently high values during the middle
Cenomanian (the carbon isotopic unit 1 (CIU1) and CIU2 in-
tervals); (ii) a gradual decline from near the middle–late
Cenomanian boundary (the CIU3 and CIU4 intervals), espe-
cially in inshore areas (Mikasa and Obira areas); and (iii)
abrupt recovery just above the Cenomanian–Turonian boun-
dary event (CTBE) (the CIU5 interval), especially in off-
shore 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. Al-
though his data are of a much higher resolution than the ones
in the present study, thus making it difficult to compare di-
rectly the biodiversity changes, there seem to be some simi-
larities and contrasts between the Yezo Group and other re-
gions. The temporal changes in species richness in the Yezo
Group, which show persistently high values during the mid-
dle 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 dropdown 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 West-
ern Interior increases or remains relatively high across the
C–T boundary despite the synchronous deposition of or-
ganic-rich sediments correlated to the OAE2; therefore, no
ammonoid crisis occurred (Monnet 2009). Hence, these dif-
ferences suggest that the Cenomanian–Turonian "mass ex-
tinction" is not a global event for ammonoids as Monnet
(2009) pointed out, and moreover, the "mass extinction" was
restricted to mid-palaeolatitudinal regions (Europe and Ja-
pan).

**Possible cause of ammonoid mass extinction in the Yezo
Group.**—In the Mikasa area, high values of extinction (E
rate) and origination (O rate) rates were noted for the middle
Cenomanian (CIU1–CIU2 boundary), even though high val-
ues of species richness persisted (Fig. 4). This observation
implies that a major faunal turnover took place within a short
time span in inshore areas of the Yezo Group. At that time,
ammonoid faunas were replaced at the genus level; for in-
stance, the acanthoceratids *Acanthoceras* and *Cunningtoni-
ceras* in CIU1 were replaced by *Calycoceras* in CIU2, and
the kossmaticeratid *Eogunnarites* in CIU1 by *Marshallites*
and *Mikasaites* in CIU2 (Kurihara et al. 2007). Subsequently,
acanthoceratids and kossmaticeratids, which so far com-
prised the main components of ammonoid species richness,
disappeared within the CIU2 interval (Fig. 5). As a result,
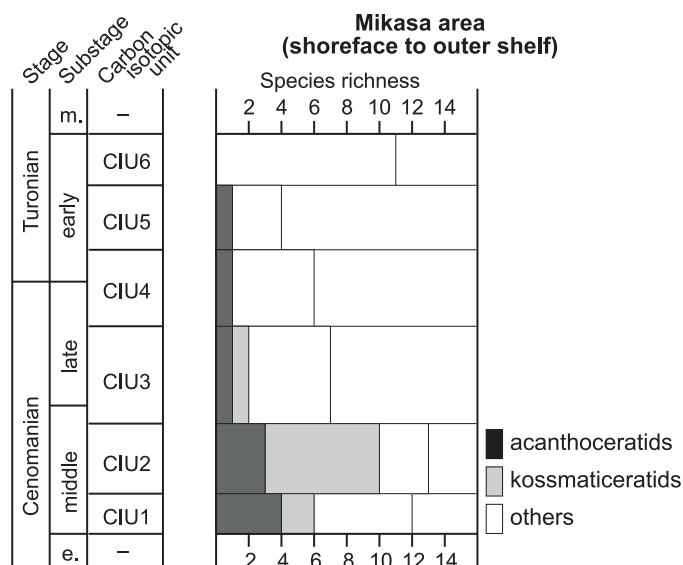desmoceratid species dominated during the CIU3 to CIU4

Fig. 5. Temporal changes in faunal components of ammonoid species rich-
ness in the Mikasa area. Abbreviations: CIUs, carbon isotopic units; e.,
early; m., middle.

interval. The lithofacies in the Mikasa area represents inter-
bedded fine-grained sandstone with hummocky cross-strati-
fication in CIU1 and bioturbated muddy sandstone in CIU2
(Fig. 2). Moreover, offshore mudstones are dominant in
CIU3 to CIU4. The disappearance of acanthoceratid and
kossmaticeratid ammonoids, therefore, may have been af-
fected by shallow to offshore facies changes with transgres-
sion. 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 *Cunningtoni-
ceras* (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., desmo-
ceratids, gaudryceratids) in various depositional environ-
ments during the late Albian to Cenomanian (Kawabe 2003).
It is therefore necessary to investigate the relationship be-
tween species diversity and frequency of the ammonoid spe-
cies 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 pro-
moted by coastal upwelling and an inflow of nutrients, devel-
ops 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 in-
flow of nutrients by a major widespread transgression near the
C–T boundary (Arthur et al. 1987; Kruijs and Barron 1990).
The conspicuous abundance of dinoflagellate cysts supports

high productivity near the C–T boundary in the Yezo basin (Kaneko and Hirano 2005), and the predominance of offshore mudstone towards the C–T boundary in the Mikasa area reflects sea level rise (Fig. 2). These phenomena, therefore, suggest that the mid-water OMZ was expanded and intensified up and down the water column near the C–T boundary in the Yezo basin. Calcareous benthic foraminiferal morphology in the Oyubari area supports the appearance of a low oxygen environment near the C–T boundary (Kaiho and Hasegawa 1994). However, as mentioned above, ammonoid species richness had already decreased from near the middle–late Cenomanian boundary, prior to the expansion of the OMZ. This fact does not deny the influence of the OAE2 on the ammonoid species diversity, rather it means that the decrease of diversity of ammonoids in the Yezo Group was not solely caused by the OAE2.

There is a question, then, as to primary cause of the reduction of diversity in ammonoids in the Yezo Group. Given the various abiotic changes during the Cenomanian–Turonian transition (e.g., Haq et al. 1987; Jenkyns et al. 1994; Erbacher et al. 1996; Bralower et al. 1997; Clark and Jenkyns 1999), it is unlikely that a single, simple cause led to the C–T boundary "mass extinction" (Monnet 2009). However, a major transgression may be a key factor in ammonoid diversity reduction in the Yezo Group because species richness declined stepwise from near the middle–late Cenomanian boundary with changes of faunal components, especially in inshore areas, and the timing of the diversity drop is coincident with the onset of the transgression in the Yezo Group.

The Albian to Turonian interval is characterised by a global 2nd order transgressive trend, and the unusual transgression peaked in the earliest Turonian, which records the most marked highstand of the Mesozoic (Hancock and Kauffman 1979; Haq et al. 1987). Sea level change can severely alter the surface area of ecologically critical zones over the continental shelves and oceanographic circulation patterns (Smith et al. 2001). The unusual highstand induced a shift toward deeper-water environments during the late Cenomanian, causing a reduced partitioning of epicontinental seas (Monnet 2009). Moreover, long-term $\delta^{18}O$ data show high sea surface temperatures during the Cenomanian and Turonian (e.g., Jenkyns et al. 1994; Clark and Jenkyns 1999; Wilson et al. 2002; Bornemann et al. 2008). This global warming is also characterised by a reduction of the equator-to-pole sea surface temperature gradient (Bice and Norris 2002). The reduced partitioning of epicontinental seas and the more equable climate contributed to the homogenisation of marine habitats during the late Cenomanian, which in turn caused a decreasing endemism and decreasing species richness (Monnet 2009). In the Yezo Group, there is a discrepancy in long-term $\delta^{13}C$ stratigraphy between terrestrial organic materials and marine carbonates during the Cenomanian to middle Turonian (Hasegawa 2003; Takashima et al. 2010). The cause of the discrepancy is understood as a driving force for a climatic optimum. Hence, sea level and climate changes probably influenced

the ammonoid faunas in Japan as well as those in Europe. This conclusion is presumably supported by the fact that the "mass extinction" was restricted to mid-palaeolatitudinal regions because marine faunas at mid-palaeolatitudinal regions must be more sensitive to climate changes (i.e., transitional realm).

Several phases of large-scale volcanic activity are known in the late Cenomanian or Turonian, including the Caribbean–Colombian oceanic plateau, the Kerguelen (Broken Ridge) plateau, and the Ontong-Java plateau (e.g., Kerr 1998). The eruption of these large igneous provinces was responsible for the disruption of the biosphere at the C–T boundary both directly (due to volatile and trace metal-enriched hydrothermal fluid release, sea level transgression and disrupted circulation patterns) and indirectly (due to elevated temperatures from increased CO_2) (Kerr 1998). In the Yezo Group, frequent felsic tuff beds, which were generally altered to bentonites, are indeed observable near the C–T boundary (especially in the early Turonian; Takashima et al. 2004), presumably implying flourishing volcanic activity. However, no detailed analysis of volcanic activity has been demonstrated in the Yezo Group, and thus, the influence of volcanic activity on the changes of ammonoid biodiversity is still unknown. However, one of the most obvious physical effects of mantle plume-related volcanism in the oceans will be the rise in sea level (Larson 1991), and the sea level rise probably predates the onset of significant volcanism (Kerr 1998). The possibility that large-scale volcanic activity indirectly affected ammonoid biodiversity in the Yezo Group, therefore, is at least incontrovertible.

Conclusions

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 widespread. However, ammonoid species richness had already decreased from near the middle–late Cenomanian boundary, prior to the expansion of the oxygen minimum zone. This fact does not deny the influence of the OAE2, but rather indi-

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.

Acknowledgements

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