

**Responses of inoceramid bivalves to
Cretaceous marine environmental changes in Japan**

本邦白亜紀の海洋環境変動に対する
イノセラムス類二枚貝の応答様式

by

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Abstract

In Chapter 1, temporal species diversity changes of inoceramid bivalves in Japan are analyzed from an extensive literature survey. The following results and discussions are presented. (1) There is no correlation between the ammonoid and inoceramid diversity changes in Japan. This fact must reflect their different vertical distribution in water column, different ecology and trophic levels in both taxa. (2) High extinction rates are detected at the Albian/Cenomanian (A/C), Cenomanian/Turonian (C/T), Turonian/Coniacian (T/C) and Lower/Upper Campanian (LC/UC) boundaries. The extinction events at the A/C, C/T and T/C boundaries would be caused by Oceanic Anoxic Event (OAE) 1d, OAE2 and OAE3, respectively. The drastic diversity decrease at the LC/UC boundary must result from the abrupt relative sea-level fall in the Yezo forearc basin. (3) The pattern of diversity changes is similar to that of the long-term (2nd order) eustatic sea-level changes. Three possibilities can be presented as a cause of this phenomenon: [1] the changes of shelf area controlled the inoceramid diversity, [2] the changes of the Cretaceous outcrop area (rock volume) associated with the sea-level changes controlled the diversity changes, and [3] combined factor of [1] and [2] affected.

Chapter 2 describes the responses of inoceramid bivalves to environmental disturbances across the Cenomanian/Turonian boundary (C/T boundary). It also focuses on the submarine environments inferred from those responses within the Yezo forearc basin, Hokkaido, northern Japan, based on examination of newly collected specimens and a literature survey. All Late Cenomanian inoceramid species became extinct by the C/T boundary and were replaced by newly originated Early Turonian species mainly composed of *Mytiloides*, as shown in Chapter 1. This drastic change in generic composition, accompanied by stunting, decrease in inter-specific size variation, and dominance by cosmopolitan species evidently took place immediately after the C/T boundary. Based on those results and previous studies, inoceramids would have been affected by oxygen-depleted conditions associated with OAE 2. Consequently, niches became vacant in the Yezo forearc basin just after the C/T boundary, and small, cosmopolitan species invaded those niches in Early Turonian time. Faunal stunting suggests that oligotrophic conditions spread into that basin immediately after the C/T boundary.

In Chapter 3, the above-mentioned results and discussions are summarized, and further consideration is given. As clarified in Chapter 1 and 2, inoceramids showed the sensitive responses to a variety of environmental changes. Many responses are decipherable even from fossil records. Whereas, the results clarified in the present paper strongly imply that the recovery of diversity from mass extinction events and the recovery of size distribution from stunting due to oligotrophic conditions were extremely rapid from a viewpoint of the geological time scale. Thriving of inoceramids throughout Late Cretaceous time is probably derived from such ability of rapid recovery. The number of occurring species is used as the criterion of “diversity” in Chapter 1. However, since various problems on the inoceramid systematics have been pointed

out from the past, it is essential to use distributed areas on morphospace as the criterion of “diversity”, in order to appreciate the veritable “morphological” diversity.

Key words: species diversity; inoceramids; Cretaceous; Japan; oxygen-depleted condition; oligotrophic condition; mass extinction; Cenomanian/Turonian boundary; Oceanic Anoxic Events; Hokkaido; Yezo forearc basin, morphospace

Chapter 1. Species diversity changes of the Cretaceous inoceramid bivalves in Japan

1. Introduction

The Cretaceous marine sediments are widely distributed in Japanese Islands, and yield many ammonoids, inoceramid bivalves and other invertebrate organisms. Many taxonomic, systematic and biostratigraphic studies on inoceramids from Japan have been carried out since Nagao & Matsumoto (1939) (e.g. Toshimitsu, 1985; Matsumoto & Asai, 1989; Noda & Matsumoto, 1998; Takahashi et al, 2003). Whereas, evolutionary, paleoecological and paleobiogeographic studies are scarce compared with those studies. Inoceramids must have been strongly affected by marine environmental changes because most of their adults were immobile epibenthos. Therefore, they are considered the very effective taxa for evaluating the connection between the chronological environmental changes and molluscan diversity changes. Up to now, however, temporal diversity changes in inoceramids from Japan and responses of inoceramid diversity to environmental changes are absolutely not elucidated.

Toshimitsu & Hirano (2000) and Toshimitsu et al. (2003) conducted the survey of the chronological species diversity changes on ammonoids in Japan. Toshimitsu et al. (2003) revealed that the timing of ammonoid species diversity minima approximately corresponds to that of Oceanic Anoxic Events, and claimed the diversity was strongly influenced by Oceanic Anoxic Events and Subevents. Zonova & Yazykova (1998) illustrated that ammonoid and inoceramid species diversity in Far East Russia during Late Cenomanian to Late Coniacian extremely correlated each other ($r = 0.963$; r : correlation coefficient based on calculation by the author). This result suggests that same environmental factors controlled both of the diversities. However, as the vertical distribution in water column, ecology and trophic level of inoceramids were different from those of ammonoids, it is required to investigate the relation of both the diversities in Japan.

The main intension of this chapter is to clarify the aspect of Japanese inoceramid rise and fall, and what factors controlled Japanese inoceramid diversity on the basis of an extensive literature survey and calculations.

2. Material and Methods

Ten genera and 96 species occurred from Japan are utilized and analyzed for the present study, in order to clarify the temporal diversity changes, rates of extinction, origination and turnover, and generic composition (the ratios of species belonging to each genus) changes in inoceramids.

Generally, the concept of “species diversity” includes the elements of “species richness” and “evenness”. However, taking a wide area like Japan as a target, it is difficult to evaluate evenness. Therefore, species diversity in the present paper means species richness, namely the number of species.

I counted the number of species (species diversity) for inoceramids from Japan for each substage of the Cretaceous (younger than the Upper Albian), based on previously published biostratigraphic and taxonomic studies (see Appendix). Although an innominable species such as “aff.” was not counted as one species basically, species given systematic description in published papers and index species assigned by Toshimitsu et al. (1995) were treated as independent species in the present study. *Inoceramus* aff. *concentricus*, which is collected by the author (see Takahashi et al., 2003), is counted as one species exceptionally. The rates of extinction, origination and turnover across each stage/substage boundary, and the generic composition for each substage, were calculated from these results. The ammonoid species diversity in Japan was re-counted and tallied up based on the database of Toshimitsu & Hirano (2000).

Extinction rate (ER) and origination rate (OR) are expressed by the following equations in the present study.

ER = (Number of pre-existing species not present above each boundary) / (Total number of species below each boundary)

OR = (Number of successor species not present below each boundary) / (Total number of species above each boundary)

The following formula has been devised in the present study, in order to calculate turnover rate (TR).

$$TR = \frac{FN - PN}{\sqrt{FN \cdot PN}}$$

Where FN is the number of species in a following age of each boundary and PN is the number of species in a previous age of each boundary. Basically, the criteria for correlation in the present study are based on Toshimitsu et al. (1995). Japanese domestic substages (e.g. K5b2, K6a3; Toshimitsu et al., 1995) are utilized in addition to the European standard stages and substages.

3. Results

Occurrence of Japanese inoceramids has been confirmed in the strata younger than the Upper Albian. Lists of inoceramid species and their stratigraphic distribution are shown in Tables 1-1, 2, 3. Species diversity increases steeply from the Upper Albian to Middle Cenomanian, and then fluctuates during the Middle Cenomanian to Middle Coniacian. Subsequently, it increases suddenly from the Middle Coniacian to Lower Campanian and drops suddenly across the Lower/Upper Campanian boundary (Fig. 1-1). The species diversity did not decrease abruptly

Table 1-3. List of inoceramid species and their stratigraphic distribution.

species	Albian		Cenomanian			Turonian			Coniacian			Santonian	Campanian				Maastrichtian	
	U.	L.	M.	U.	L.	M.	U.	L.	M.	U.		L.	U.	L.	U.	L.	U.	
	K3b3	K4a1-2	K4a3	K4a4-6	K4b1	K4b2	K4b3	K5a1		K5a2	K5b1	K5b2	K6a1-2	K6a3	K6a4	K6b1	K6b2	
<i>Platyceramus alaeformis</i>														?	?	?	?	
<i>Platyceramus chicoensis</i>													1					
<i>Platyceramus comfertim-annulatus</i>													1					
<i>Platyceramus cycloides</i>											1	1	1					
<i>Platyceramus ezoensis</i>											1	1	1					
<i>Platyceramus higoensis</i>												1						
<i>Platyceramus japonicus</i>												1						
<i>Platyceramus mantelli</i>										1	1	?						
<i>Platyceramus miyahisai</i>													1	1				
<i>Platyceramus pacificus</i>													1					
<i>Platyceramus rhomboides</i>											1							
<i>Platyceramus szaszi</i>										1								
<i>Platyceramus tappuensis</i>								1										
<i>Platyceramus vanuxemi</i>																1	1	
<i>Sphenoceramus africanus</i>											1		1					
<i>Sphenoceramus cristatus</i>												1	1					
<i>Sphenoceramus elegans</i>													1					
<i>Sphenoceramus haboroensis</i>												1	?					
<i>Sphenoceramus hetoaianus</i>																1	1	
<i>Sphenoceramus kiritachiensis</i>												1	1					
<i>Sphenoceramus lobatus</i>											1							
<i>Sphenoceramus nagaoi</i>											1	1	1	1	1	1	1	
<i>Sphenoceramus naumanni</i>								1	1	1	1	1	1					
<i>Sphenoceramus ordinatus</i>													1					
<i>Sphenoceramus orientalis</i>													1					
<i>Sphenoceramus sachalinensis</i>													1					
<i>Sphenoceramus sanrikuensis</i>													1					
<i>Sphenoceramus schmidti</i>													1					
<i>Sphenoceramus yokoyamai</i>										1	1	1	1					
<i>Volviceramus koeneni</i>										1								

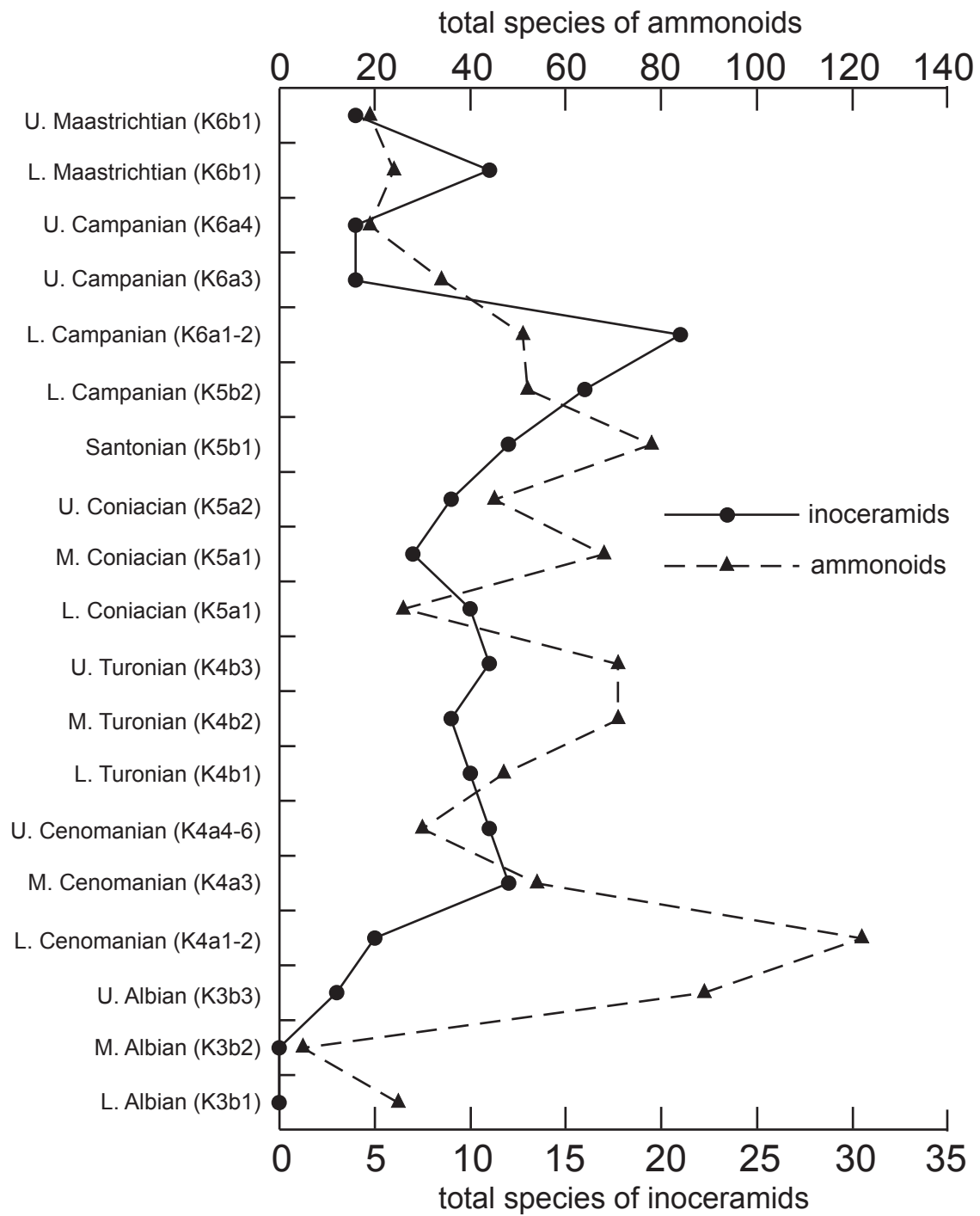


Fig.1-1. Temporal species diversity change of inoceramids and ammonoids in Japan. Ammonoid data are adopted from Toshimitsu & Hirano (2000).

across the horizon, at which Oceanic Anoxic Events (OAEs) prevailed (the most upper Albian: OAE1d, the most upper Cenomanian: OAE2 and the lowest Coniacian: OAE3). The number of inoceramid species is approximately at a quarter of that of ammonoids (Fig. 1-1). There is no correlation between the ammonoid and inoceramid diversity changes in Japan ($r = 0.177$; r : correlation coefficient).

High extinction rates are detected at the Albian/Cenomanian (A/C) (100%), Cenomanian/Turonian (C/T) (100%), Turonian/Coniacian (T/C) (81.8%) and Lower/Upper Campanian (LC/UC) (85.7%) boundaries (Fig. 1-2). Above all, the turnover rate at the Lower/Upper Campanian boundary is the lowest (Fig. 1-3). In other words, a high extinction rate associated with a low origination rate is observed at that boundary (Fig. 1-2). The generic composition changed drastically at the above-mentioned all boundaries (Fig. 1-4). Although the diversity increased ($TR = 0.516$ at the A/C boundary) or did not decrease abruptly ($TR = -0.095$ at the C/T boundary), no Late Albian and Late Cenomanian inoceramid species survived across those boundaries (i.e. the extinction rate is 100%) (Figs. 1-2, 3).

The diversity changes are comparable with the long-term (2nd order) eustatic sea-level changes shown by Haq et al. (1987, 1988) on the whole (Fig. 1-5).

4. Discussion

4. 1. Patterns of species diversity changes between ammonoids and inoceramids in Japan

Since the fluctuation pattern of ammonoid and inoceramid diversities is completely different, it became clear that the factors which controlled the ammonoid and inoceramid diversities were distinct in Japan. It suggests that the Japanese ammonoid diversity was neutral to the eustatic sea-level changes, because the inoceramid diversity changes should have been controlled by the long-term (2nd order) eustasy on the whole, as stated in section 4.3. (below). Different vertical distribution in water column, different ecology and trophic level in ammonoids and inoceramids would be responsible for the different patterns of both diversities in Japan. Therefore, the well correlated diversities between ammonoids and inoceramids shown by Zonova & Yazykova (1998) in Far East Russia must be biased data.

4. 2. Effects of the Oceanic Anoxic Events

The A/C, C/T and T/C boundaries roughly correspond with the timing of occurrence of OAE1d, OAE2 and OAE3, respectively. The high extinction rates detected at those boundaries may be caused by OAEs.

It is well-known that mighty environmental disturbances took place during the latest Cenomanian (e.g. Jenkyns, 1980; Jarvis et al., 1988; Elder, 1989). As a result of those

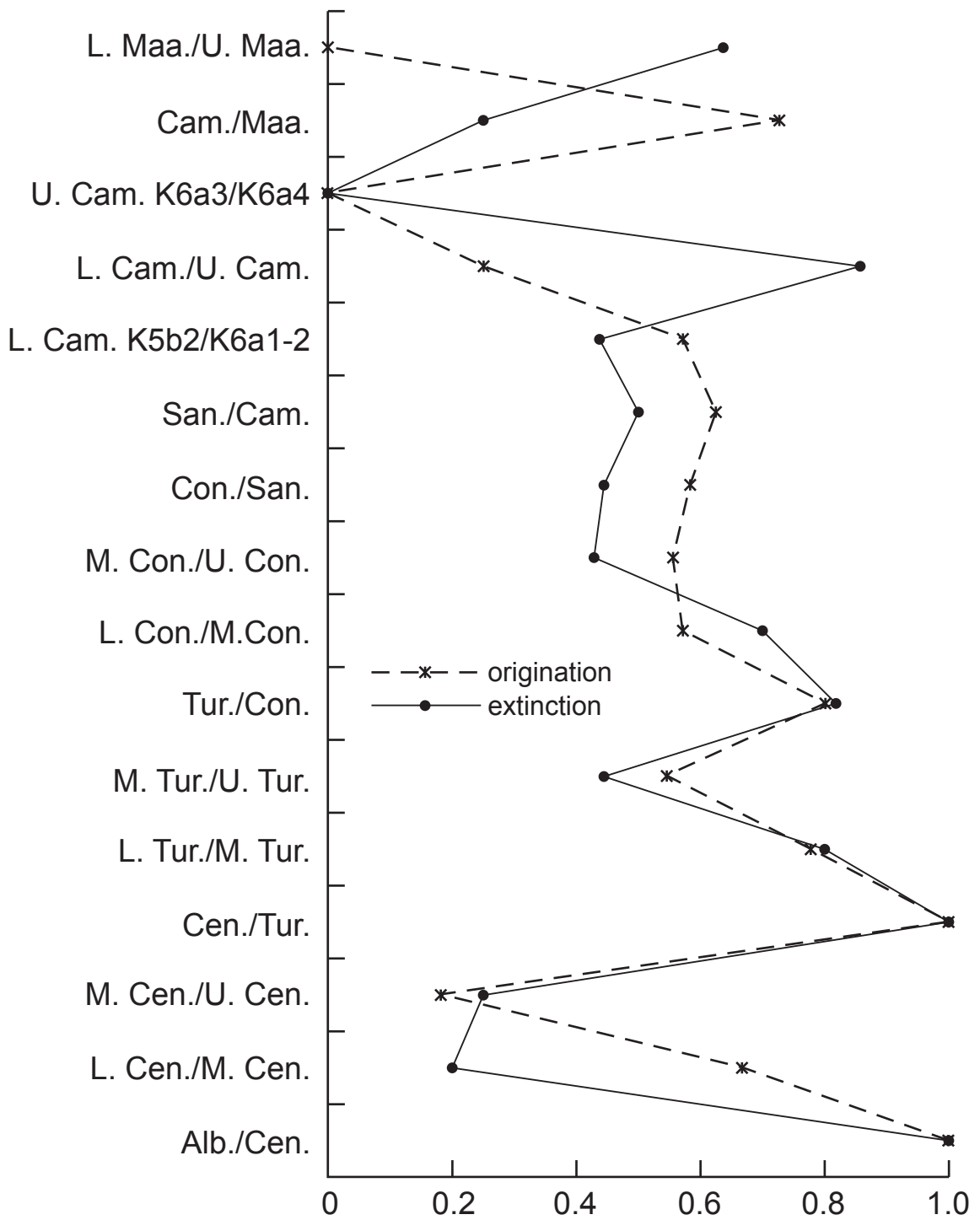


Fig. 1-2. Rates of extinction and origination for Cretaceous inoceramid species in Japan at stage and substage boundaries.

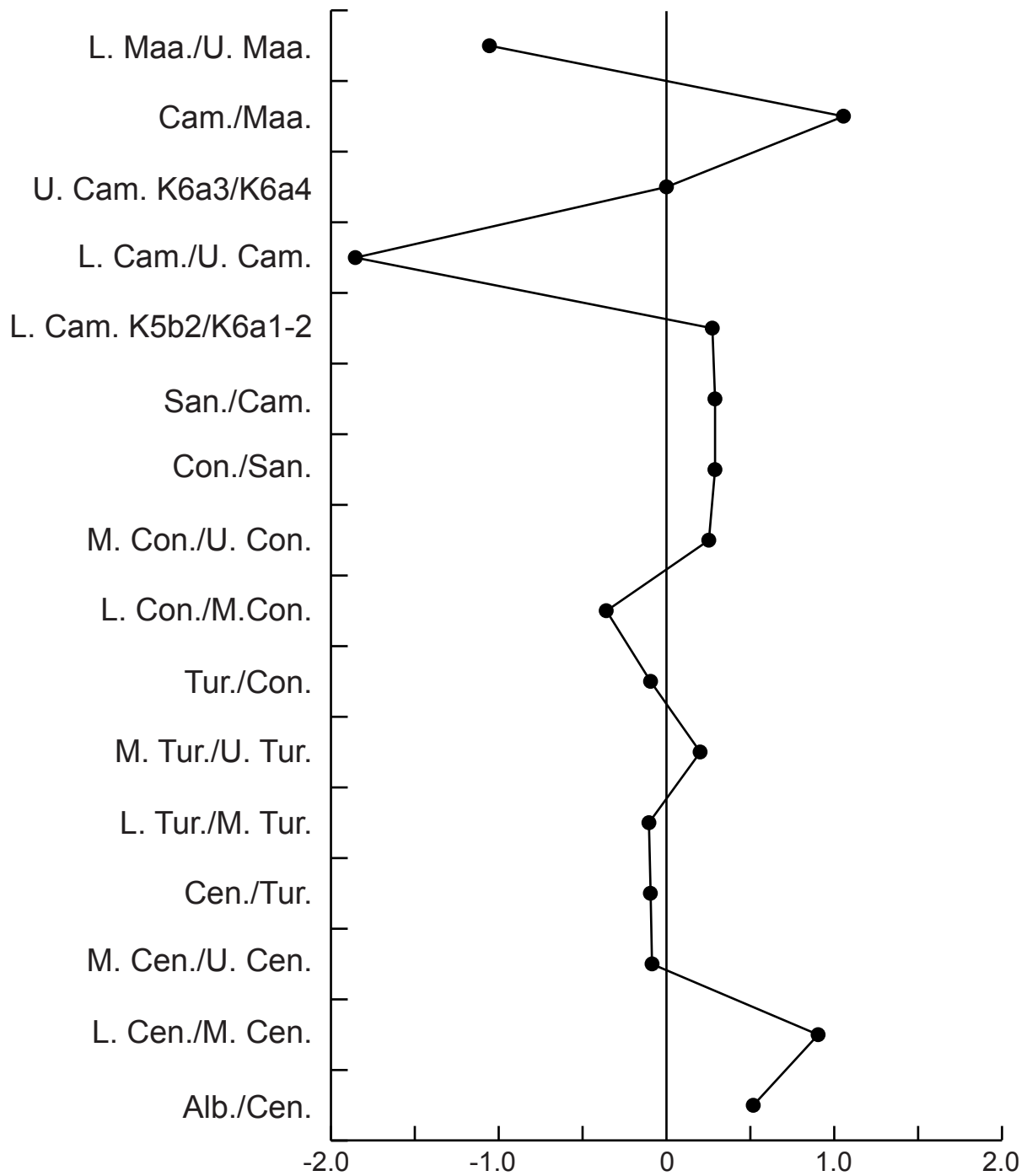


Fig. 1-3. Turnover rate of Cretaceous inoceramid species in Japan.

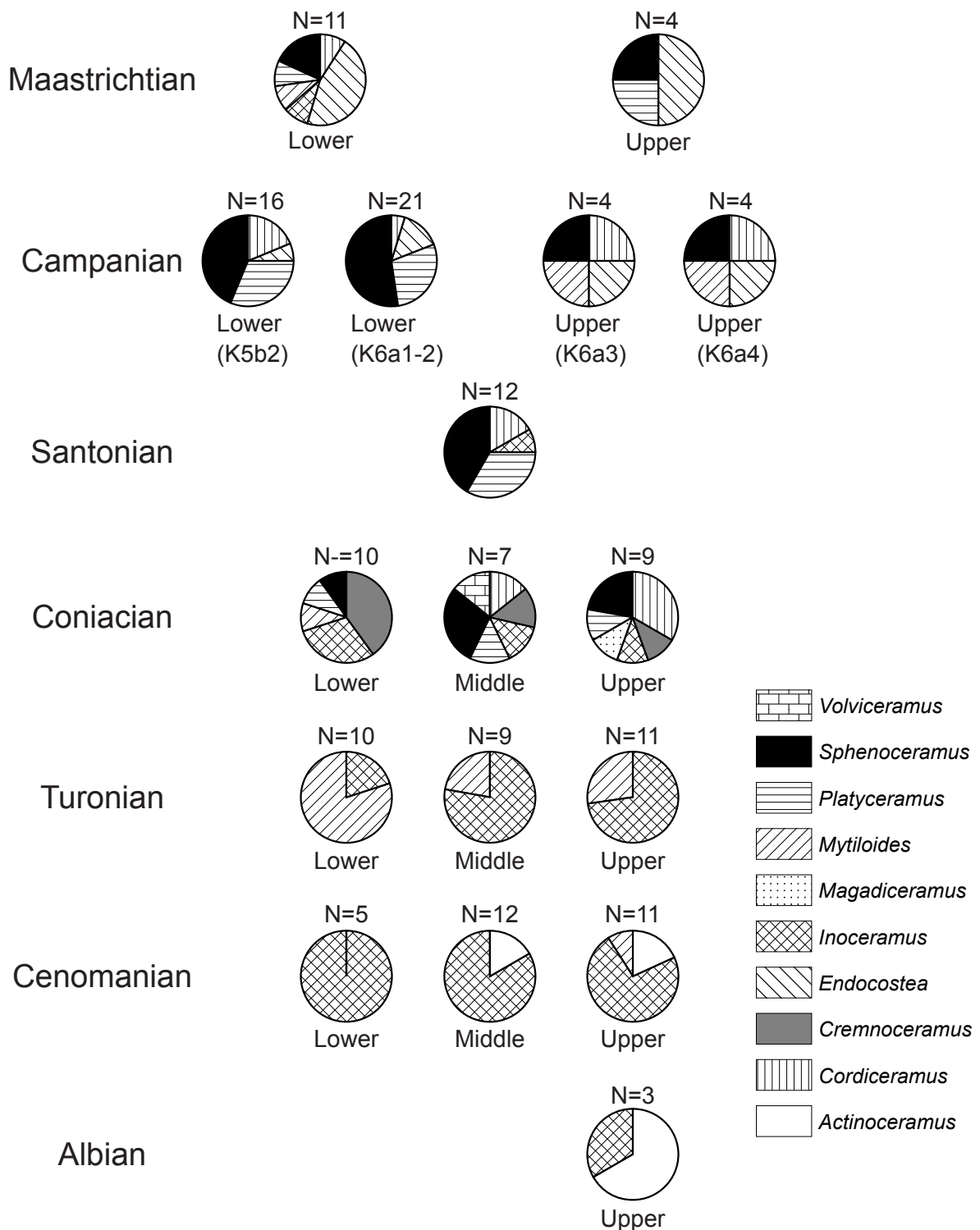


Fig. 1-4. Ratios of species belonging to each genus for each substage in Japan.
N: number of species.

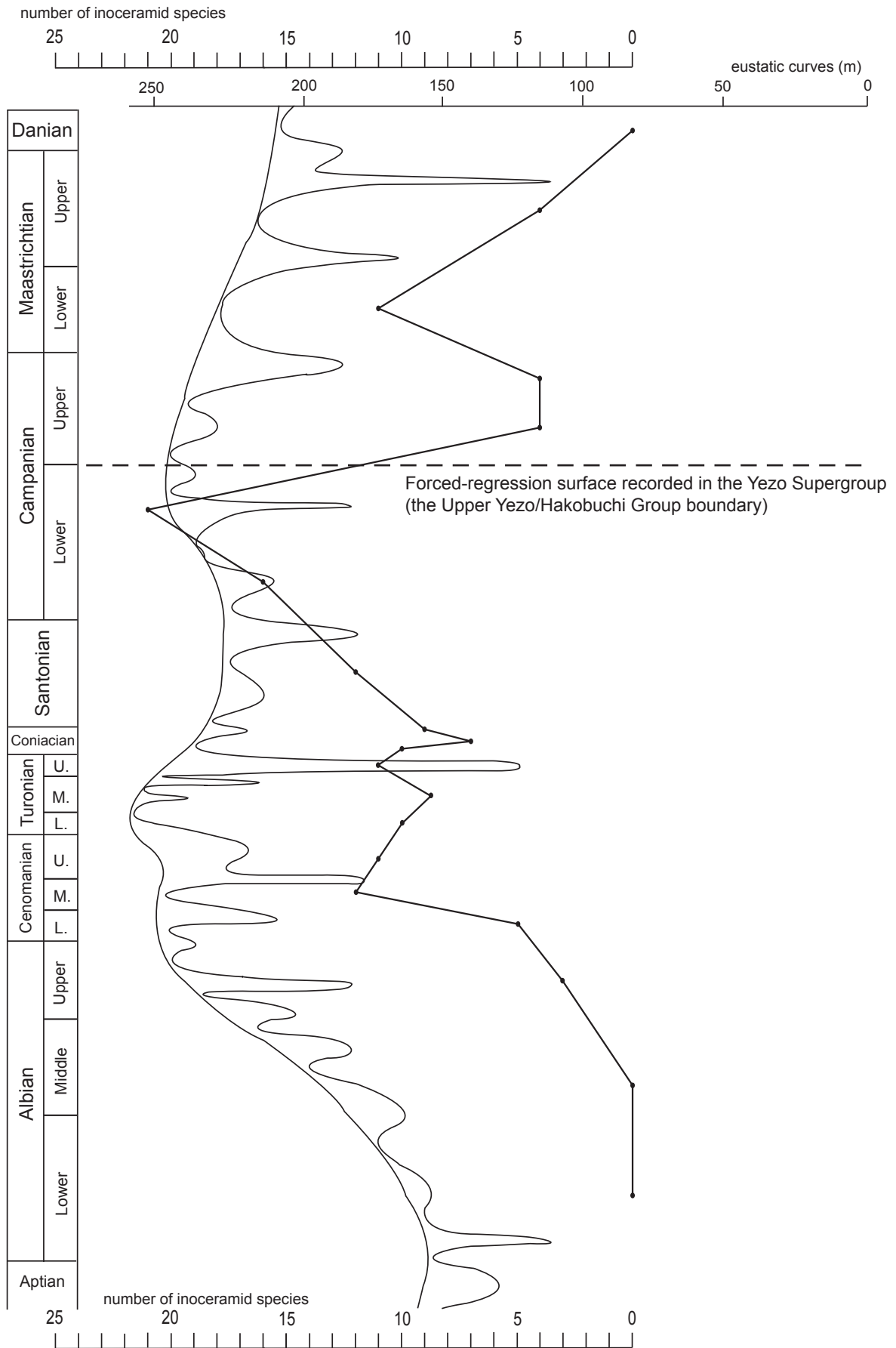


Fig. 1-5. Relationship between inoceramid diversity change in Japan and the eustacy. Eustatic curves are adopted from Haq et al. (1987,1988)

environmental disturbances, high extinction rates for many marine molluscs are detected at the C/T boundary (e.g. Elder, 1989; Sepkoski, 1989, 1996; Harries & Little, 1999). The results demonstrated in the present study suggest that inoceramids from Japan were also damaged dramatically by the environmental disturbances occurred during the latest Cenomanian (I will analyze in Chapter 2 in detail). Accordingly, many *Mytiloides* species originated in Early Turonian. As a result, a drastic change in generic composition is detected across the C/T boundary. Same tendencies (the diversity did not decrease abruptly, extinction rate is high, and generic composition changed drastically) are observed at the A/C and T/C boundaries.

Although many inoceramid species became extinct at the A/C, C/T and T/C boundaries, many species also originated and evolved rapidly across those boundaries as detected in the high origination rates at those boundaries. Such rapid recovery ability seems to be characteristic of inoceramids, and probably ammonoids did not have such ability. Therefore, low diversities in inoceramids were not observed across the horizons at which OAEs occurred. Such an aspect of the inoceramid diversity is different from that of the ammonoid diversity which drastically decreased at the time of OAEs (Toshimitsu et al., 2003).

4. 3. Interrelation between the sea-level changes and inoceramid diversity

The pattern of diversity changes is similar to that of the long-term (2nd order) eustatic sea-level changes (Fig. 1-5). Signor & Lipps (1982) illustrated that major peaks and valleys between ammonoid generic diversity and sedimentary rock area through the Mesozoic generally correspond. Based on that study and the fact verified in the present study, three possibilities can be presented as the cause: (1) the changes of shelf area, which is main habitats of inoceramids, controlled the inoceramid diversity (i.e. species-area relationships), (2) the changes of the Cretaceous outcrop area (rock volume) associated with the sea-level changes controlled the changes of diversity and fossil abundance, (3) combined factor of (1) and (2) affected. Henceforth, estimation of exposure area in each age is essential to elucidate what possibility is true.

While, as the sea-level fall during the latest Cretaceous time was gradual, the sudden diversity decrease at the LC/UC boundary is not inexplicable from a eustatic viewpoint. This result is concordant with the supposition that the relationship between the sea-level changes and paleobiodiversity may be obscured by regional or local tectonic effects in datasets derived from tectonically active margins (Crampton et al., 2003).

The Cretaceous deposits younger than the Albian are mainly exposed in the Yezo Supergroup, Hokkaido, northern Japan. An abrupt relative sea-level fall is recorded near the LC/UC boundary in the Yezo Supergroup. In other words, the Hakobuchi Group (Upper Campanian–Paleocene), mainly composed of inner shelf to foreshore sandstone, overlays the Upper Yezo Group (Albian–Lower Campanian), mainly composed of outer shelf to basin plain

mudstone and turbiditic sandstone. In the Teshionakagawa area, the northern part of the distribution of the Yezo Supergroup, the situation that the Hakobuchi Group overlays conformably the Upper Yezo Group is observable (Takahashi et al., 2003). The boundary of the both groups can be interpreted as the forced-regression surface. In brief, the abrupt and large-scale relative sea-level fall not being harmonious with eustasy must have occurred in the Yezo forearc basin near the LC/UC boundary. It is quite likely that the abrupt relative sea-level fall is responsible for the sudden inoceramid diversity drop at the LC/UC boundary.

5. Conclusions

The species diversity changes, and aspects of replacement and turnover on inoceramid bivalves are analyzed based on the records of previous biostratigraphic and taxonomic literature. The following results are demonstrated:

(1) There is no correlation between the ammonoid and inoceramid diversity changes in Japan. It suggests that the factors which controlled the Japanese ammonoid and inoceramid diversities were completely distinct. This must be a reflection of their different vertical distribution in water column, different ecology and trophic levels in both taxa.

(2) High extinction rates are detected at the Albian/Cenomanian (A/C), Cenomanian/Turonian (C/T), Turonian/Coniacian (T/C) and Lower/Upper Campanian (LC/UC) boundaries. Accordingly, generic composition changed drastically across those boundaries. The extinction events at the A/C, C/T and T/C boundaries would be caused by OAE1d, OAE2 and OAE3, respectively. The drastic diversity decrease at the LC/UC boundary must be derived from an abrupt and large-scale relative sea-level fall recorded in the Yezo Supergroup, Hokkaido.

(3) The pattern of diversity changes is similar to that of the long-term (2nd order) eustatic sea-level changes. Three possibilities can be given as a cause of this phenomenon: (1) the changes of shelf area controlled the inoceramid diversity, (2) the changes of the Cretaceous outcrop area (rock volume) associated with the sea-level changes controlled the changes of diversity and fossil abundance, and (3) combined factor of (1) and (2) affected. Henceforth, it is necessary to estimate the exposure area of the Cretaceous for each age in Japan, in order to examine three possibilities.

Chapter 2. Responses of inoceramid bivalves to environmental disturbances across the Cenomanian/Turonian boundary in the Yezo forearc basin, Hokkaido, Japan

1. Introduction

Mid-Cretaceous time is well-known as a green-house interval of global importance (e.g. Larson, 1991; Clarke & Jenkyns, 1999; Frakes, 1999). Among the effects of this green-house event were Oceanic Anoxic Events (OAEs), which intermittently prevailed during the mid-Cretaceous (120–80 Ma), and which have been studied by a wide range of researchers beginning with Schlanger & Jenkyns (1976). OAEs resulted in a vast amount of organic carbon burial (black shales) in the western Tethys and Atlantic areas, especially at the Cenomanian/Turonian boundary (C/T boundary: 93.5Ma; Gradstein et al., 1995), which suggests that Oceanic Anoxic Event 2 (OAE2) prevailed over a wide area during the latest Cenomanian. OAE2 caused major changes in the marine biota, as evidenced by an estimated global extinction rate of 26% at the genus level and 33–53% at the species level for the C/T boundary (Sepkoski, 1989, 1996). Although biotic responses to OAE2 are well documented by microfossils (Jarvis et al., 1988; Leary et al., 1989; Peryt & Wyrwicka, 1991; Kaiho et al., 1993; Kaiho & Hasegawa, 1994; Fitzpatrick, 1996; Hart, 1996; Wang et al., 2001), studies based upon invertebrate marine macrofossils are few, other than pioneering research done in the Western Interior of North America (Elder, 1989; Harries, 1993; Kauffman & Harries, 1996). In particular, the influence of environmental disturbances across the C/T boundary on invertebrate marine macrofossils along the northwestern margin of the Pacific Ocean has hardly been studied. Understanding bioevents in the Pacific is essential for discussing the global environments, since the paleo-Pacific Ocean was the largest open ocean of the Cretaceous.

Inoceramids, which make up a family of marine bivalves, thrived in the Jurassic and Cretaceous and became extinct approximately 1.5 m.y. prior to the Cretaceous/Tertiary boundary, except for the enigmatic genus *Tenuipteria* (e.g. Ward et al., 1991; Kauffman et al., 1993; Marshall & Ward, 1996). Given their abundance and widespread occurrence, Cretaceous inoceramids are useful for evaluating biotic responses to environmental disturbances. The fact that most adults were immobile epibenthos also implies that inoceramids must have been strongly affected by marine environmental changes. Therefore, inoceramids are appropriate for evaluating the relationship between marine environmental changes and the attendant molluscan responses. Until now, however, there has been little detailed research on the influence of environmental disturbances, which caused the C/T mass extinction events, upon inoceramids (excluding the above-mentioned researches in the Western Interior).

The purpose of this chapter is to describe the responses of inoceramid bivalves to environmental disturbances across the C/T boundary, and to infer submarine environments from those responses, within the Yezo forearc basin, Hokkaido, northern Japan.

2. Inoceramid responses to environmental disturbances across the C/T boundary in the Western Interior of North America

2. 1. Magnitude and patterns of extinction, and examination of stepwise extinction

Kauffman & Harries (1996) and Harries & Little (1999) divided the extinction and recovery processes of marine molluscs into four intervals: extinction interval (extinction rate \gg origination rate), survival interval (extinction rate \approx origination rate) and early, late recovery intervals (extinction rate \ll origination rate) (Fig. 2-1).

Elder (1989) claimed the environmental disturbances occurring during the latest Cenomanian have made an mighty impact on epibenthic bivalves next to ammonoids, and estimated the species level extinction rate of epibenthic bivalves at 61% and that of inoceramids at 92%. While, Harries & Little (1999) estimated the extinction rate at 69% on epibenthic bivalves and at 75% on inoceramids, respectively. As shown in both papers, inoceramids, which showed intercontinental distribution, became extinct more than the other epibenthic bivalves.

Elder (1989) distinguished six steps in extinction process of marine molluscs, and Kauffman et al. (1993) distinguished eight steps. The C/T boundary corresponds to extinction step 5 of Elder (1989) and 7th step (MX5) of Kauffman et al. (1993). Harries & Little (1999) distinguished nine steps, and the C/T boundary corresponds to extinction step 7. Although most epifaunal bivalves had last occurrences at extinction steps 1 (base of the *Eoumphaloceras septemseriatum* zone) and 3 (base of the *Neocardioceras juddi* zone) of Elder (1989), extinction of many inoceramid species took place later than those steps (Elder, 1989; Harries & Little, 1999). Based on this fact, Elder (1989) speculates that inoceramids had a greater tolerance to the latest Cenomanian environmental stresses than many other epifaunal taxa. Therefore, inoceramids occurred continuously up to just below the C/T boundary, and were predominant no less than buchiids and posidoniids.

Stepwise recognized by Elder (1989), Kauffman et al. (1993) and Harries & Little (1999) in the C/T boundary extinction event would merely be pretension due to the Signor-Lipps effect shown by Signor & Lipps (1982). Species occurring with frequency have high possibilities found from higher horizons (i.e. near the true extinct horizon), whereas species occurring with infrequency have lower chances found near the true extinct horizon. As a result, catastrophic extinction is regarded as gradual or stepwise extinction (see Fig. 5 of Williams, 1994). Equally,

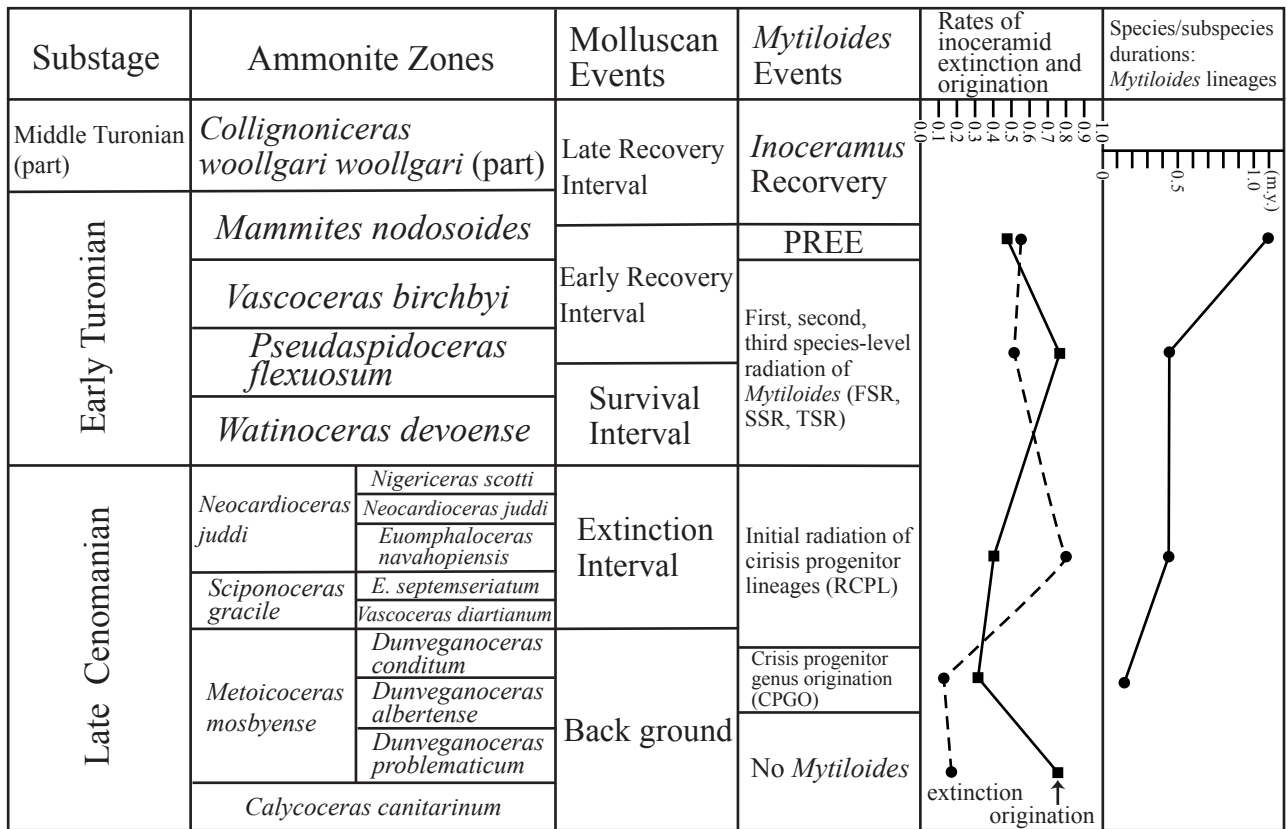


Fig. 2-1. Correlation of ammonoid biozones, molluscan events and *Mytiloides* events in the Western Interior of North America. Rates of inoceramid extinction and origination, species/subspecies durations of *Mytiloides* lineage for each *Mytiloides* event are also shown. Ammonod zones, *Mytiloides* events and species/subspecies durations are adopted from Kauffman & Harries (1996), and molluscan events are adopted from Harries & Little (1999). Rates of extinction and origination are calculated by the author based on Kauffman et al. (1993). When rates of extinction and origination for each *Mytiloides* event cannot be determined as a single value due to uncertain stratigraphic ranges of some species/subspecies, an average value is shown. PREE: post-radiation evolution and extinction of *Mytiloides* spp.

the phenomenon that last occurrence horizons of inoceramids are higher than other epibenthos may reflect the Signor-Lipps effect.

Marshall & Ward (1996) utilized the confidence interval developed by Strauss & Sadler (1989), Marshall (1990) and Springer (1990) for the last occurrences of ammonoids from the most upper Maastrichtian, in order to resolve whether the Cretaceous/Tertiary (K/T) extinction event was catastrophic or not. Meldahl (1990) revealed that the catastrophic, stepwise and gradual extinction can be distinguished respectively by plotting the relationships between the last occurrence horizons and occurrence abundance. Range charts shown in the previous papers on the C/T boundary of the Western Interior were illustrated only the stratigraphic range of fossil occurrence, not shown each occurrence horizon of each specimen. Accordingly, readers cannot calculate confidence intervals by referring to those range charts. It is essential to illustrate the occurrence horizon of each specimen and to show the confidence intervals in the future, in order to examine whether the C/T extinction event were stepwise or not and confirm whether inoceramid extinction took place later than other epifaunal extinction, with the above-mentioned methods.

2. 2. *Process of extinction and recovery in each Mytiloides event*

The process of inoceramid extinction and recovery across the C/T boundary in the Western Interior is divided into six *Mytiloides* events (Kauffman & Harries, 1996), as follows: (1) no *Mytiloides*, (2) crisis progenitor genus origination, (3) initial radiation of crisis progenitor lineages, (4) first–third species-level radiation of *Mytiloides*, (5) post-radiation evolution and extinction of *Mytiloides*, and (6) *Inoceramus* recovery. *Mytiloides* expanded their offshore habitats into shallow areas with passing each interval (Kauffman & Harries, 1996). The below-described rates of extinction and origination are calculated by the author based on a range chart shown in Kauffman et al. (1993). Those are given by the following equations: Extinction rate = (the number of extinct species and subspecies in the interval)/(All species and subspecies in the interval), Origination rate = (the number of originated species and subspecies in the interval)/(All species and subspecies in the interval). The below descriptions are mainly based on Kauffman & Harries (1996).

(1) No *Mytiloides*: This interval corresponds with the *Calycoceras canitaurium* Zone – the middle part of the *Dunveganoceras albertense* Zone of the lower Upper Cenomanian (Fig. 2-1). *Mytiloides* does not occur and only the genus *Inoceramus* occurs from this interval. This interval was under background conditions for marine molluscs, and there should be little environmental stresses for organisms. Twelve species and subspecies of *Inoceramus* occurred in this interval based on Kauffman et al. (1993). The extinction rate is 0.17 and the origination rate is 0.75.

(2) Crisis progenitor genus origination (CPGO): This interval corresponds with the middle part of the *Dunveganoceras albertense* Zone – the middle part of the *Dunveganoceras conditum*

Zone of the middle Upper Cenomanian (Fig. 2-1). The base is defined by origination of a species of *Mytiloides* (*Mytiloides* cf. '*latus*'). This interval was under background conditions for marine molluscs (Fig. 2-1). *M.* cf. '*latus*' was originated within the black shale associated with the Hartland Regional Oxygen Event, which is a local anoxic to dysoxic event. Fourteen–fifteen inoceramid species and subspecies occurred in this interval based on Kauffman et al (1993). The extinction rate is about 0.13–0.14 and the origination rate is about 0.27–0.36. The subsistence duration of *M.* cf. '*latus*' (i.e. duration of this interval) is approximately 0.15 m.y.

(3) Initial radiation of crisis progenitor lineages (RCPL): This interval corresponds with the middle part of the *Dunveganoceras conditum* Zone – *Nigericeras scotti* Zone (the upper limit is the C/T boundary; Fig. 2-1). The base is defined by initiation of the *Mytiloides* lineage radiation. This interval corresponds with the interval of background conditions to the extinction interval for marine molluscs. First, stock of *Mytiloides* cf. '*latus*' speciated into *M.* aff. *submytiloides* in the *Dunveganoceras conditum* Zone (upper part of the *Metoicoceras mosbyense* Zone; Fig. 2-1). Second, stock of *M.* cf. '*latus*' speciated into *M.* aff. *hattini* at the base of the *Neocardioceras juddi* Zone. *M.* aff. *hattini* originated in the extinction interval suggesting existence of intensity environmental stresses for marine molluscs. Common morphological characters of *M.* cf. '*latus*' and *M.* aff. *submytiloides* are thin shells and small (mainly less than 50mm). Twenty inoceramid species and subspecies occurred in this interval based on Kauffman et al. (1993). The extinction rate is 0.80 and the origination rate is 0.38–0.44. The extinction rate is the highest in this interval (Fig. 2-1). The average subsistence duration of *Mytiloides* species and subspecies is a little less than 0.45 m.y.

(4) First–third species-level radiation of *Mytiloides* (FSR, SSR and TSR): This interval corresponds with the *Watinoceras devoense* Zone – *Vascoceras birchby* Zone (the base is the C/T boundary), and the survival interval to the early recovery interval for marine molluscs (Fig. 2-1). Basically, only *Mytiloides* occurs and *Inoceramus* does not occur from this interval. Three *Mytiloides* species in RCPL exploded. The lineage which showed remarkably speciation is the *M.* aff. *hattini* lineage. Sixteen–seventeen inoceramid species and subspecies occurred in this interval based on Kauffman et al. (1993). The extinction rate is 0.47–0.56 and the origination rate is 0.71–0.81. The origination rate is the highest in this interval except for no *Mytiloides* interval (Fig. 2-1). The average subsistence duration of *Mytiloides* species and subspecies is a little less than 0.45 m.y., which were calculated by the author based on Fig. 6 in Kauffman & Harries (1996).

(5) Post-radiation evolution and extinction of *Mytiloides* (PREE): This interval corresponds with the lower part of the *Mammites nodosoides* Zone of the middle–upper Lower Turonian, and the late part of the early recovery interval for marine molluscs (Fig. 2-1). Marine ecosystem began to recover to background conditions in this interval. Fifteen–sixteen species and subspecies occurred in this interval based on Kauffman et al. (1993). The extinction rate is 0.50–0.60 and the origination rate is 0.44–0.53. The average subsistence duration of *Mytiloides* species

and subspecies is approximately 1.10 m.y., which is the longest overwhelmingly among all intervals (Fig. 2-1).

(6) *Inoceramus* recovery: This interval corresponds with the upper part of the *Mammites nodosoides* Zone – the lower part of the *Collignonicerias woollgari woollgari* Zone, of the most upper part of the Lower Turonian to Middle Turonian, and the late recovery interval for marine molluscs. Seven species and subspecies occurred in this interval and did not speciated. The genus *Inoceramus* occurred dominantly.

2. 3. Survival strategy of inoceramids across the C/T boundary

Harries (1993) and Harries et al. (1996) discussed the survival strategy of each taxon of marine invertebrates across the C/T boundary. They stated that inoceramid bivalves showed a variety of different mechanisms to survive the C/T mass extinction event.

One of the hypothesized mechanisms for surviving through mass extinction is rapid evolution (Harries, 1993; Harries et al., 1996). If a lineage was able to show speciation rate which enable it to continuously adapt to changing environments, that lineage can survive the environmental stresses and disturbances. The genus *Mytiloides* displayed the remarkable rate of evolution mainly during the survival interval. Generally, it is considered that the evolutionary rate becomes more rapid under the environments which bring high selective pressure if mutation rate being uniform, because a little variation causes great distinction of the fitness (an adaptive value). In fact, a progenitor of *Mytiloides* species appeared in the black shale associated with a local anoxic to dysoxic event (the Hartland Regional Oxygen Event), and then it lineage speciated into *M. aff. hattini* in the extinction interval within which marine biota was stressed (Kauffman & Harries, 1996). Moreover, many *Mytiloides* species showed rapid evolution and speciation remarkably within the survival interval in which environmental disturbances must stress the marine biota, and which ecological niches were vacant. Elder (1989) called this phenomenon the ‘*Mytiloides* flood event’. Inoceramids showed the evolutionary rate of approximately 5.1 spp./m.y. in the Cenomanian, 4.7 spp./m.y. in the Late Cenomanian, and 11.2 spp./m.y. in the Early Turonian (Harries, 1993). This high evolutionary rate in the Early Turonian is primarily attributable to the high speciation rate of the *Mytilodes* lineage (Harries, 1993).

Dispersal ability associated with long-lived planktotrophic larvae is given as another cause of inoceramid survival factor across the C/T boundary. Personal communication of Kauffman in Harries (1993) referred that inoceramid larvae had a long planktotrophic duration (10–25 weeks) judging from the prodissoconch of well-preserved inoceramid specimens. In fact, Knight & Morries (1996) clarified that inoceramids had a planktotrophic stage of more than 50 days based on observation of growth lines preserved on the Albian inoceramid specimens from England. Wide paleobiogeographic distribution of many inoceramid species (Dhondt, 1992) supports the presumption that inocermids had long planktotrophic duration.

Harries (1993) stated that one of the ubiquitous features of all mass extinction boundaries is the presence of Lazarus taxa (Jablonski, 1986). The *Inoceramus* lineage had the Lazarus nature (Harries, 1993). This nature is thought to an important factor of surviving the C/T mass extinction event. Harries (1993) and Harries et al. (1996) claimed that the *Inoceramus* lineage must migrate to either refugia or a secondary habitat, or form small populations that the probability found as the fossil record is negligible. This supposition is based on the fact that the first-appearing *Inoceramus* did not appear until the late Early Turonian (absence duration of that lineage is 0.75 m.y.).

3. Material

Although the term “horizon” should correspond to a surface, as noted in the latest version of the International Stratigraphic Guide (Salvador, 1994), in this chapter I use this term to refer to a stratigraphic section with a certain thickness; examples of my usage include the lower Upper Cenomanian, upper Upper Cenomanian, lower Lower Turonian and basal Middle Turonian. The following abbreviations are used herein: IUC, lower Upper Cenomanian; uUC, upper Upper Cenomanian; ILT, lower Lower Turonian; bMT, basal Middle Turonian.

Most inoceramid species are thought to have been suspension-feeding epibenthos (Kauffman & Harries, 1996), excluding their larval stages, although MacLeod & Hoppe (1992) hypothesized that one or more inoceramids were chemosynthetic symbionts. Furthermore, Tanabe (1973, 1983) speculated that the life-style of the adult stages of certain inoceramids was pseudoplanktonic. Since inoceramid species treated in the present study do not show the characters of chemosynthetic symbionts or pseudoplankton, they are inferred to have been suspension-feeding epibenthos.

3. 1. Material

Ninety-three inoceramid specimens from the Oyubari, Tappu and Teshionakagawa areas of Hokkaido (Fig. 2-2) were analyzed for the present study, in order to recognize temporal changes in size-frequency distribution and size variation (Tables 2-1, 2). All 19 bMT specimens, 11 uUC specimens and five ILT specimens from the Oyubari area (Table 2-2) have been documented by Hirano et al. (1981, 1990) and Kawabe (2000). The stratigraphic ranges of inoceramid species in the present study are shown in Fig. 2-3.

The IUC specimens were collected only from the Tappu area, the uUC specimens from the Oyubari and Tappu areas, and the ILT specimens from all areas. The bMT specimens were collected only from the Oyubari area (sample level Y070061 shown in Hirano et al., 1989, and Kawabe, 2000) (Fig. 2-3). All individuals were collected randomly, and all measured specimens are housed at Waseda University, Tokyo (WE. P328Y-334Y, 401-413, 501-558), Japan (Tables

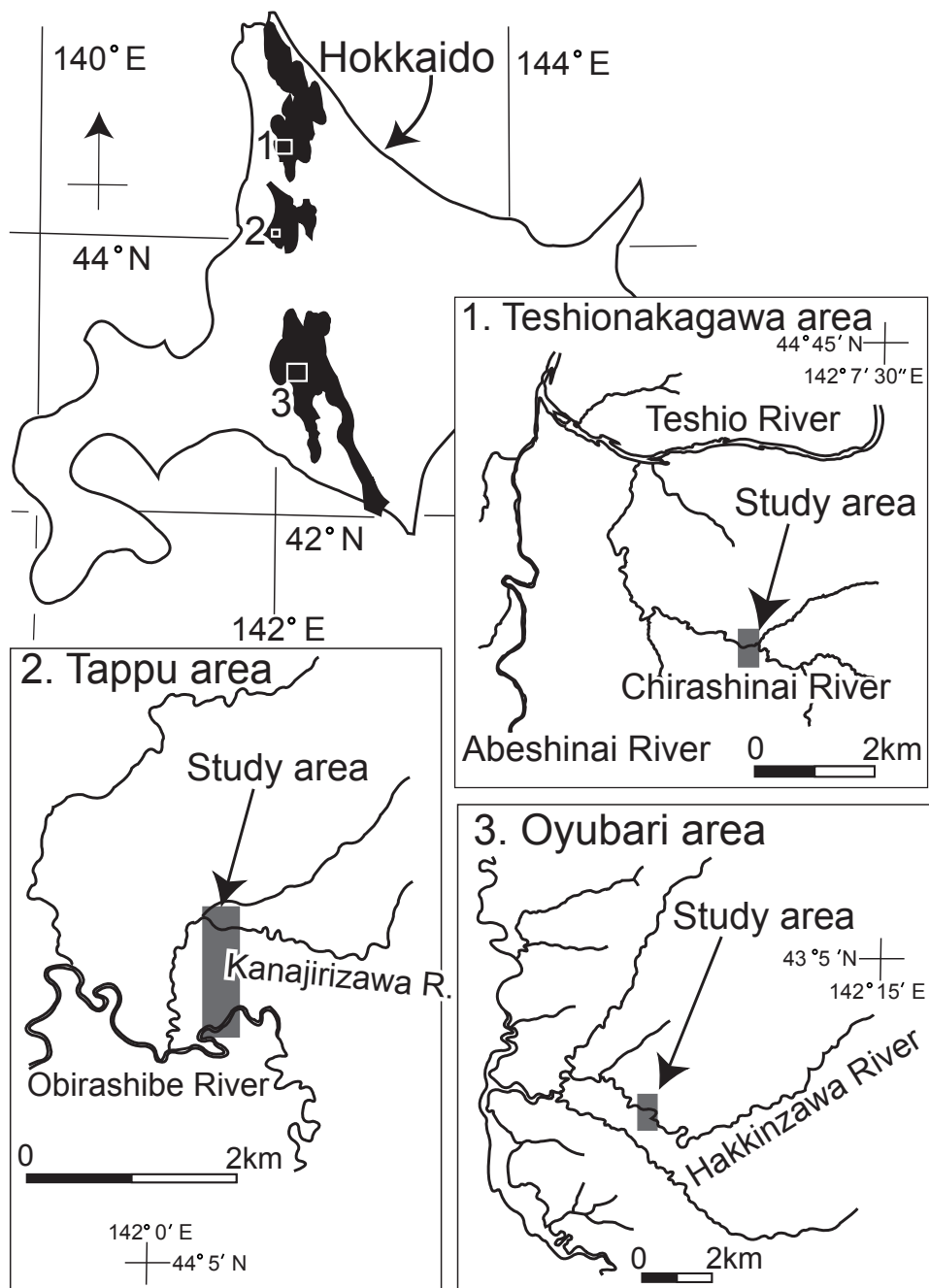


Fig. 2-2. Distribution of the Yezo Supergroup and index map showing study areas.

Table 2-1. List of the measured inoceramid specimens from the Teshionakagawa and Tappu areas.

sample number	area	species	right or left valve	horizon	H (mm)
WE. P501	Teshionakagawa	<i>Inoceramus kamuy</i>	RV	lower Lower Turonian	56.10
WE. P502		<i>Inoceramus</i> sp.	?	lower Lower Turonian	18.40
WE. P503		<i>Inoceramus</i> sp.	RV	lower Lower Turonian	25.05
WE. P504		<i>Mytiloides sackensis</i>	RV	lower Lower Turonian	16.95
WE. P505		<i>Mytiloides sackensis</i>	RV ?	lower Lower Turonian	19.15
WE. P506		<i>Mytiloides</i> sp.	RV	lower Lower Turonian	36.45
WE. P507	Tappu (Obirashibegawa River)	<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	23.60
WE. P508		<i>Inoceramus</i> sp.	RV	lower Lower Turonian	9.45
WE. P509		<i>Mytiloides</i> sp.	RV	lower Lower Turonian	19.10
WE. P510		<i>Inoceramus</i> ex gr. <i>pennatulus</i>	?	upper Upper Cenomanian	107.30
WE. P511		<i>Inoceramus</i> ex gr. <i>pennatulus</i>	?	upper Upper Cenomanian	140.65
WE. P512		<i>Inoceramus</i> ex gr. <i>pennatulus</i>	LV	upper Upper Cenomanian	180.25
WE. P513		<i>Inoceramus ginterensis</i>	LV	upper Upper Cenomanian	82.70
WE. P514		<i>Inoceramus ginterensis</i>	RV	upper Upper Cenomanian	101.55
WE. P515		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	32.55
WE. P516		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	43.20
WE. P517		<i>Inoceramus</i> cf. <i>nodai</i>	RV	lower Upper Cenomanian	47.30
WE. P518		<i>Inoceramus</i> cf. <i>pictus minus</i>	LV?	lower Upper Cenomanian	35.85
WE. P519		<i>Inoceramus</i> cf. <i>pictus minus</i>	RV	lower Upper Cenomanian	46.05
WE. P520		<i>Inoceramus</i> ex gr. <i>pennatulus</i>	LV	lower Upper Cenomanian	74.10
WE. P521		<i>Inoceramus ginterensis</i>	LV	lower Upper Cenomanian	112.10
WE. P522	Tappu (Kanajirizawa River)	<i>Inoceramus kamuy</i>	?	lower Lower Turonian	22.50
WE. P523		<i>Inoceramus kamuy</i>	RV	lower Lower Turonian	27.00
WE. P524		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	28.30
WE. P525		<i>Inoceramus kamuy</i>	RV	lower Lower Turonian	32.35
WE. P526		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	32.55
WE. P527		<i>Mytiloides</i> sp.	LV?	lower Lower Turonian	36.15
WE. P528		<i>Inoceramus</i> cf. <i>pictus minus</i>	?	upper Upper Cenomanian	28.05
WE. P529		<i>Inoceramus</i> sp.	?	upper Upper Cenomanian	97.95
WE. P530		<i>Inoceramus</i> sp.	?	upper Upper Cenomanian	124.70
WE. P531		<i>Inoceramus</i> sp.	?	upper Upper Cenomanian	210.15
WE. P532		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	31.85
WE. P533		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	32.20
WE. P534		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	32.75
WE. P535		<i>Actinoceramus nipponicus</i>	LV	lower Upper Cenomanian	34.30
WE. P536		<i>Actinoceramus nipponicus</i>	RV	lower Upper Cenomanian	37.60
WE. P537		<i>Inoceramus nodai</i>	RV	lower Upper Cenomanian	20.45
WE. P538		<i>Inoceramus nodai</i>	LV	lower Upper Cenomanian	22.50
WE. P539		<i>Inoceramus nodai</i>	RV	lower Upper Cenomanian	32.30
WE. P540		<i>Inoceramus nodai</i>	RV	lower Upper Cenomanian	55.00
WE. P541		<i>Inoceramus pennatulus</i>	LV	lower Upper Cenomanian	112.35
WE. P542		<i>Inoceramus pictus minus</i>	?	lower Upper Cenomanian	36.90
WE. P543		<i>Inoceramus pictus minus</i>	LV?	lower Upper Cenomanian	53.65
WE. P544		<i>Inoceramus pictus minus</i>	RV	lower Upper Cenomanian	57.65
WE. P545		<i>Inoceramus pictus minus</i>	LV	lower Upper Cenomanian	75.00
WE. P546		<i>Inoceramus</i> sp.	RV	lower Upper Cenomanian	23.25

Table 2-2. List of the measured inoceramid specimens from the Oyubari area.

sample number	area	species	right or left valve	horizon	H (mm)	References
WE. P330Y	Oyubari	<i>Inoceramus cf. hobetsensis</i>	LV?	basal Middle Turonian	31.35	Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV?	basal Middle Turonian	16.65	Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV	basal Middle Turonian	20.30	Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV	basal Middle Turonian	28.45	Kawabe(2000)
WE. P401		<i>Inoceramus hobetsensis</i>	RV	basal Middle Turonian	29.10	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV?	basal Middle Turonian	29.15	Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV	basal Middle Turonian	35.90	Kawabe(2000)
WE. P402		<i>Inoceramus hobetsensis</i>	LV	basal Middle Turonian	36.00	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	RV	basal Middle Turonian	37.70	Kawabe(2000)
WE. P328Y		<i>Inoceramus hobetsensis</i>	LV	basal Middle Turonian	40.35	Kawabe(2000)
WE. P403		<i>Inoceramus obiraensis</i>	LV	basal Middle Turonian	39.70	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P404		<i>Inoceramus obiraensis</i>	LV?	basal Middle Turonian	48.75	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P405		<i>Inoceramus sp.</i>	?	basal Middle Turonian	18.20	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P329Y		<i>Inoceramus sp.</i>	?	basal Middle Turonian	25.20	Kawabe(2000)
WE. P329Y		<i>Inoceramus sp.</i>	?	basal Middle Turonian	25.90	Kawabe(2000)
WE. P329Y		<i>Inoceramus sp.</i>	LV	basal Middle Turonian	26.85	Kawabe(2000)
WE. P406		<i>Inoceramus sp.</i>	RV?	basal Middle Turonian	35.30	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P407		<i>Inoceramus sp.</i>	LV	basal Middle Turonian	61.70	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P408		<i>Inoceramus sp.</i>	RV	basal Middle Turonian	79.80	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P547		<i>Inoceramus cf. kamuy</i>	RV	lower Lower Turonian	18.45	
WE. P409		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	14.40	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P410		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	15.45	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P411		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	23.80	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P412		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	26.80	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P548		<i>Inoceramus kamuy</i>	LV	lower Lower Turonian	28.25	
WE. P331Y		<i>Mytiloides labiatus</i>	LV?	lower Lower Turonian	31.30	Kawabe(2000)
WE. P549		<i>Mytiloides labiatus</i>	LV	lower Lower Turonian	36.40	
WE. P550		<i>Mytiloides labiatus</i>	RV	lower Lower Turonian	45.00	
WE. P551		<i>Mytiloides sackensis</i>	LV	lower Lower Turonian	24.25	
WE. P333Y		<i>Actinoceramus nipponicus</i>	?	upper Upper Cenomanian	42.85	Kawabe(2000)
WE. P333Y		<i>Actinoceramus nipponicus</i>	LV	upper Upper Cenomanian	44.35	Kawabe(2000)
WE. P552		<i>Inoceramus ex gr. pennatulus</i>	RV	upper Upper Cenomanian	55.50	
WE. P413		<i>Inoceramus ex gr. pennatulus</i>	LV	upper Upper Cenomanian	111.10	Hirano et al.(1981, 1990), Kawabe(2000)
WE. P553		<i>Inoceramus ex gr. pennatulus</i>	LV?	upper Upper Cenomanian	132.80	
WE. P334Y		<i>Inoceramus ginterensis</i>	RV	upper Upper Cenomanian	42.00	Kawabe(2000)
WE. P334Y		<i>Inoceramus ginterensis</i>	RV?	upper Upper Cenomanian	47.15	Kawabe(2000)
WE. P334Y		<i>Inoceramus ginterensis</i>	RV?	upper Upper Cenomanian	47.20	Kawabe(2000)
WE. P334Y		<i>Inoceramus ginterensis</i>	RV	upper Upper Cenomanian	49.15	Kawabe(2000)
WE. P332Y		<i>Inoceramus ginterensis</i>	LV	upper Upper Cenomanian	55.80	Kawabe(2000)
WE. P332Y		<i>Inoceramus ginterensis</i>	RV?	upper Upper Cenomanian	74.85	Kawabe(2000)
WE. P335Y		<i>Inoceramus gradilis</i>	LV?	upper Upper Cenomanian	30.40	Kawabe(2000)
WE. P554		<i>Inoceramus pennatulus</i>	RV	upper Upper Cenomanian	178.20	
WE. P555		<i>Inoceramus pictus minus</i>	LV	upper Upper Cenomanian	9.20	
WE. P556		<i>Inoceramus pictus minus</i>	LV?	upper Upper Cenomanian	22.50	
WE. P334Y		<i>Inoceramus sp.</i>	RV	upper Upper Cenomanian	32.50	Kawabe(2000)
WE. P557		<i>Inoceramus sp.</i>	?	upper Upper Cenomanian	40.65	
WE. P558		<i>Inoceramus sp.</i>	?	upper Upper Cenomanian	73.70	

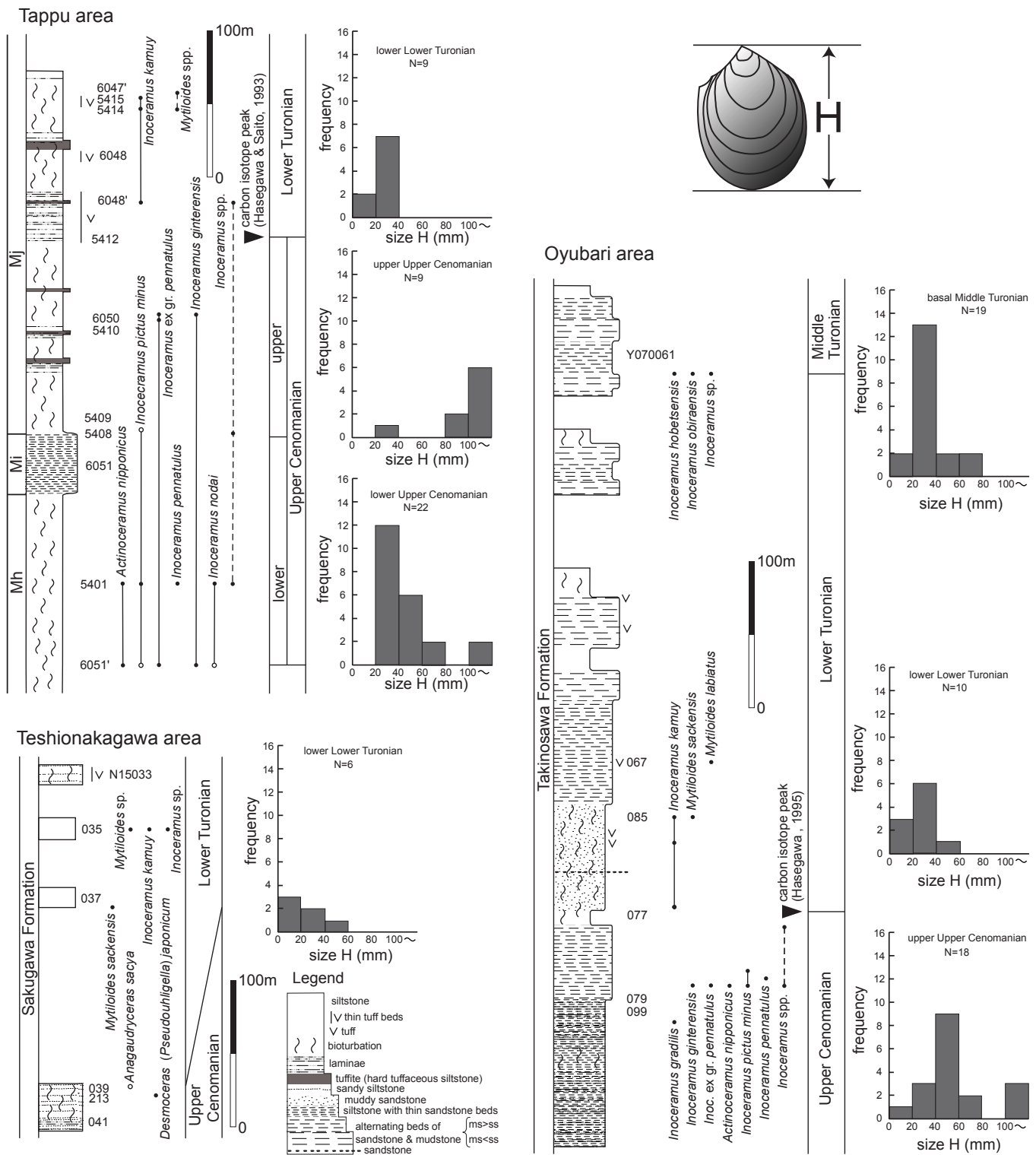


Fig. 2-3. Stratigraphic distribution of measured inoceramids in the Teshionakagawa area (the Chirashinai River section), the Tappu area (the Obirashibe and Kanajirizawa river sections) and the Oyubari area (the Hakkinzawa River section), and the size-frequency distribution at each horizon. *Anagaudryceras sacya* and *Desmoceras (Pseudouhligella) japonicum* from the Teshionakagawa area are ammonoid species that identify the Cenomanian stage. Solid circles: identified specimens. Open circles: specimens compared to these species

2-1, 2). I utilized three genera and 30 species reported in earlier papers in order to document paleogeographic distribution (Table 2-3).

3. 2. *Geological setting*

The Yezo Supergroup is made up of Cretaceous forearc-basin sediments (Okada, 1983) and is widely distributed to the north to south from central Hokkaido and in western Sakhalin. The supergroup is divided into four groups: the Lower Yezo, Middle Yezo, Upper Yezo, and Hakobuchi groups, in ascending stratigraphic order (e.g. Matsumoto, 1951; Okada, 1983). The Middle Yezo Group includes C/T boundary sequences, which is well exposed along the Chirashinai River in the Teshionakagawa area, the Obirashibe and Kanajirizawa rivers in the Tappu area, and the Hakkinzawa (= Shirakin) River in the Oyubari area.

The Middle Yezo Group, ranging from the Albian to Turonian stages, is present in the Teshionakagawa area and is divided into the Moehoro, Shirataki, Sakotandake, Sakugawa and Saku formations, in ascending stratigraphic order (Nagao, 1962). Takahashi et al. (2003) showed that the C/T boundary is present between sample levels N15037 and N15039 in the Sakugawa Formation, based on macrofossil biostratigraphy (Fig. 2-3). The Sakugawa Formation that encompasses the C/T boundary consists of massive to well-bioturbated, pelagic siltstone to sandy siltstone.

The Middle Yezo Group is divided into fifteen lithologic units (Ma to Mo) in the Tappu area (Tsushima et al., 1958). The C/T boundary is recognized between sample levels 6048' and 6050 along the Obirashibe River section (see Sekine et al., 1985; Hirano et al., 1997), within the Mj lithologic unit, based on age-indicative inoceramid species (Hirano et al., 1997). Hasegawa & Saito (1993) showed that the C/T boundary lies at sample level 5412 of Tanabe et al. (1977) in the Kanajirizawa River section, based on carbon-isotope stratigraphy (Fig. 2-3). The lithology around the C/T boundary consists of laminated to weakly bioturbated, pelagic siltstone with intercalations of tuffite (hard, tuffaceous siltstone).

The Middle Yezo Group in the Oyubari area is divided into the Maruyama, Hikagenosawa, Takinosawa, and Shirogane formations, in ascending stratigraphic order (Motoyama et al., 1991). The C/T boundary has been assigned to the middle part of the Takinosawa Formation (sample level Y070077 of Hirano et al., 1989; Kawabe, 2000) along the Hakkinzawa River, based on macro- and microfossil biostratigraphy and carbon-isotope stratigraphy (e.g. Hirano et al., 1990; Motoyama et al., 1991; Hasegawa & Saito, 1993; Hirano, 1995; Hasegawa, 1995, 1997; Kawabe, 2000; Kurihara & Kawabe, 2003; Fig. 2-3). The Takinosawa Formation that encompasses the C/T boundary consists mainly of gray to greenish gray, pelagic siltstone to muddy sandstone with intercalations of turbidite sandstone. Motoyama et al. (1991), Hasegawa (1997) and Kurihara & Kawabe (2003) have described the detailed lithology of the Cenomanian-Turonian sequence represented by the Hikagenosawa, Takinosawa and Shirogane formations.

Table 2-3. List of endemic and cosmopolitan species.

<u>endemic species</u>	<u>cosmopolitan species</u>
<i>Actinoceramus nipponicus</i>	<i>Inoceramus crippsi</i>
<i>Actinoceramus tamurai</i>	<i>Inoceramus flaccidus</i>
<i>Inoceramus aff. concentricus</i>	<i>Inoceramus ginterensis</i>
<i>Inoceramus aff. reachensis</i>	<i>Inoceramus gradilis</i>
<i>Inoceramus costatus</i>	<i>Inoceramus heinzi</i>
<i>Inoceramus iburiensis</i>	<i>Inoceramus hobetsensis</i>
<i>Inoceramus kamuy</i>	<i>Inoceramus nodai</i>
<i>Inoceramus obiraensis</i>	<i>Inoceramus pictus minus</i>
<i>Inoceramus pennatulus</i>	<i>Inoceramus virgatus</i>
<i>Inoceramus reduncus</i>	<i>Mytiloides aff. colombianus</i>
<i>Inoceramus tenuis</i>	<i>Mytiloides aff. sackensis</i>
<i>Mytiloides mikasaensis</i>	<i>Mytiloides colombianus</i>
	<i>Mytiloides goppelnensis</i>
	<i>Mytiloides labiatus</i>
	<i>Mytiloides mytiloides</i>
	<i>Mytiloides sackensis</i>
	<i>Mytiloides subhercynicus</i>
	<i>Mytiloides taraokai</i>

The criteria for correlation in the present study are based on Toshimitsu et al. (1995), therefore sequences which contain *Actinoceramus nipponicus* (Nagao & Matsumoto) and *Inoceramus pictus minus* Matsumoto are assigned to the Upper Cenomanian. The first appearance of *I. hobetsensis* Nagao & Matsumoto indicates the base of the Middle Turonian. Criteria for determining the C/T boundary position in the Oyubari and Tappu areas are described in the above-mentioned previous studies.

4. Methods

4. 1. Size-frequency distribution and size-variation changes

In the present study, inoceramid size is defined as maximum height, expressed as H (i.e., maximum length from umbo to ventral margin; see Fig. 2-3).

First, the size-frequency histogram for each horizon in each area was drawn up, and then the Kolmogorov-Smirnov fitness test was used to evaluate the normal distribution. Second, the Mann-Whitney U test was performed to evaluate whether two samples belong to the same size universe. The above-mentioned null hypothesis (two samples belong to the same size universe) was examined by the U test for possible pairs. The frequency of relatively large individuals (more than 60mm in size) at all horizons was also calculated.

A coefficient of variation is calculated for each horizon, in order to evaluate differences in size variation. Because the number of species and the ratio of individuals belonging to each species in each horizon probably affect the coefficient of variation, the following formula for comparing intra-specific variation has been devised in the present study. Specimens containing more than one individual in a single species can be used to calculate the coefficient of intra-specific variation (CIV).

$$CIV = \frac{100}{N} \sum \frac{n_k}{x_k}$$

Where N is all number of specimens from each horizon, n_k is number of specimens of species k , σ_k is universe standard deviation of species k for size (H) and \bar{x}_k is a mean value of species k for size (H). In addition, a coefficient of inter-specific variation was calculated using a median for each species at each horizon.

4. 2. Ratios of endemic and cosmopolitan species

The ratios of endemic and cosmopolitan species in the Middle and Upper Cenomanian, and the Lower and Middle Turonian were examined from the results of previous biostratigraphic and taxonomic studies: the Western Interior of North America (Harries, 1993; Kauffman et al., 1993; Kauffman, 1995; Harries et al., 1996; Kauffman & Harries, 1996; Sageman & Bina, 1997; Harries & Little, 1999; Walaszczyk & Cobban, 2000), Europe (Uličný, 1997; Lamolda et al., 1997; Voigt & Hilbrecht, 1997; Voigt, 2000; Wiese & Kaplan, 2001; Wilmsen & Niebuhr, 2002) and Japan (Matsumoto & Nishida, 1995).

5. Inoceramid responses to environmental disturbances across the C/T boundary in the Yezo forearc basin

5. 1. Size-frequency distribution and size-variation changes

The size-frequency distribution in each area and the compiled distributions are shown in Figs. 2-3 and 2-4. Based on the Kolmogorov-Smirnov fitness test, the null hypothesis of normal distribution for the uUC in the Oyubari area, and the uUC of the compiled distribution, are rejected at the 1% significant level, and the bMT in the Oyubari area and the IUC in the Tappu area are rejected at the 5% significant level. Therefore, since parametric methods (e.g. the t test) were not suitable for evaluating whether two samples belong to the same size universe, a non-parametric method (i.e. the Mann-Whitney U test) was utilized. The statistical results show that the ILT histograms for the Tappu and Oyubari areas (Fig. 2-3) shift significantly to the left (i.e. the smaller side) compared with other horizons (excluding comparison with the bMT in the Oyubari area), as shown in Fig. 2-5. Moreover, the compiled ILT size histogram shifts to the left significantly, compared with the other horizons (Figs. 2-4, 5). The results of the U test for possible pairs are shown in Fig. 2-5. The proportion of relatively large-size specimens (more than 60mm) at each horizon is about 18% for the IUC, 48% for the uUC, 0% for the ILT and 11% for the bMT (Fig. 2-4).

The size variations of all specimens decrease suddenly across the C/T boundary and become lowest at the ILT (Fig. 2-6). The coefficient of intra-specific variation remains almost constant within a range of 24–35%, while inter-specific variation fluctuates (Fig. 2-6). The values of coefficients for inter-specific variation in the IUC and uUC are approximately 61% and 83%, respectively, with a steep drop in the values of coefficients across the C/T boundary. The values of coefficients reach about 36% in the ILT and 33% in the bMT (Fig. 2-6).

5. 2. Temporal-diversity changes, rates of extinction and origination, and generic-composition changes

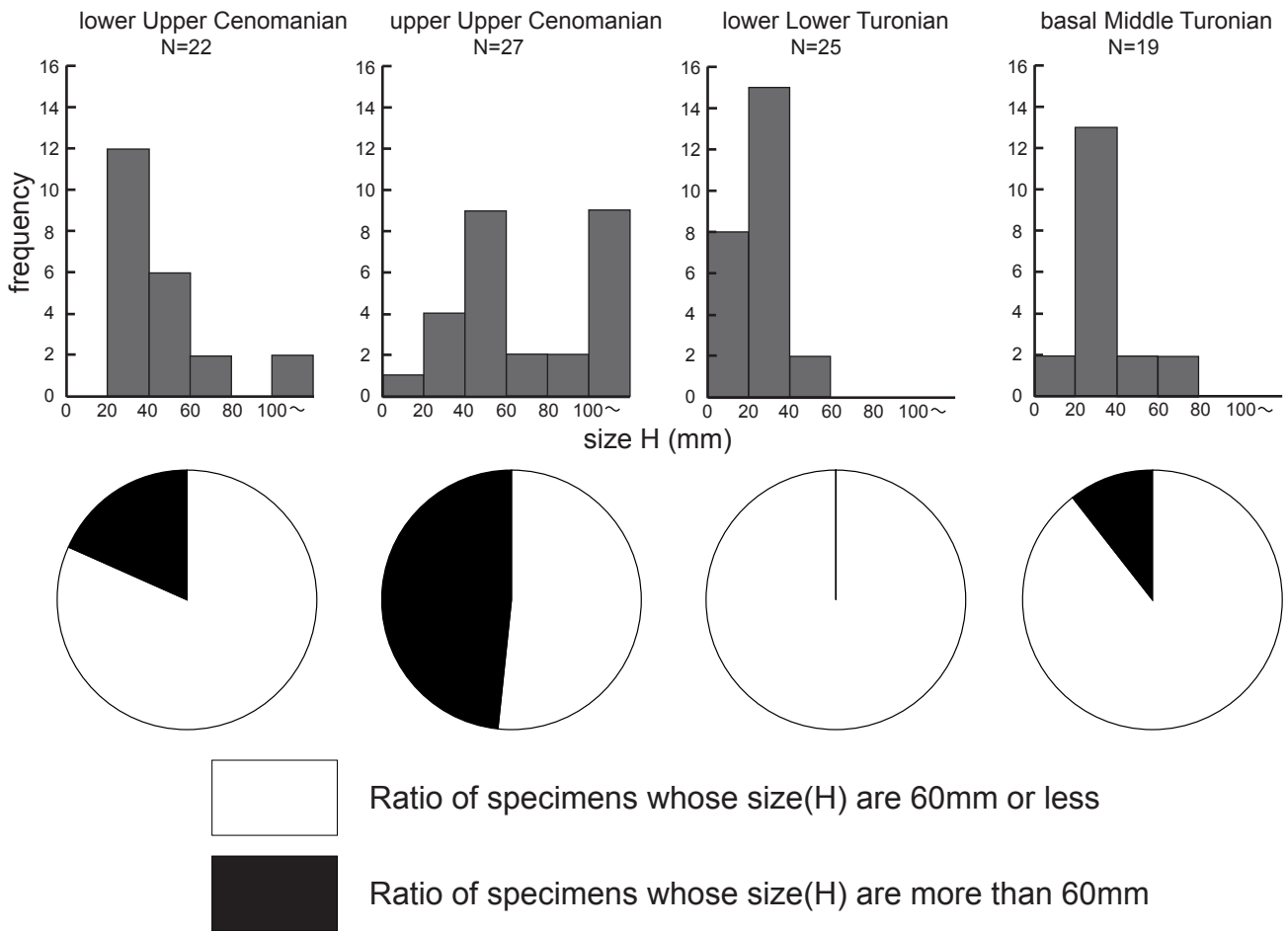


Fig. 2-4. Compiled size-frequency distributions for three areas, and ratios of relatively large-sized specimens at each horizon. N: number of specimens

a. All specimens from three areas

	b. Mid. Tur.	I. Low. Tur.	u. Up. Cen.	I. Up. Cen.
basal Middle Turonian		bMT>ILT	bMT<uUC	bMT<IUC
lower Lower Turonian	△ (1.698)		ILT<uUC	ILT<IUC
upper Upper Cenomanian	× (0.013)	× (0.0001)		uUC>IUC
lower Upper Cenomanian	△ (3.362)	× (0.011)	△ (1.218)	

b. Oyubari area

	b. Mid. Tur.	I. Low. Tur.	u. Up. Cen.
basal Middle Turonian		bMT=ILT	bMT<uUC
lower Lower Turonian	○ (14.564)		ILT<uUC
upper Upper Cenomanian	× (0.284)	× (0.108)	

c. Tappu area

	I. Low. Tur.	u. Up. Cen.	I. Up. Cen.
lower Lower Turonian		ILT<uUC	ILT<IUC
upper Upper Cenomanian	× (0.063)		uUC>IUC
lower Upper Cenomanian	× (0.234)	× (0.086)	

Fig. 2-5. Results of the Mann-Whitney U test. The null hypothesis is that each specimen belongs to the same size-distribution universe. Signs of equality and inequality above the oblique lines illustrate statistical distinctions for each distribution. Circles, triangles and crosses shown below the oblique lines indicate no significance at the 95% confidence level, significance at the 95% confidence level, and significance at the 99% confidence level, respectively. Numbers in parentheses indicate the possibilities in percentages, following the null hypothesis.

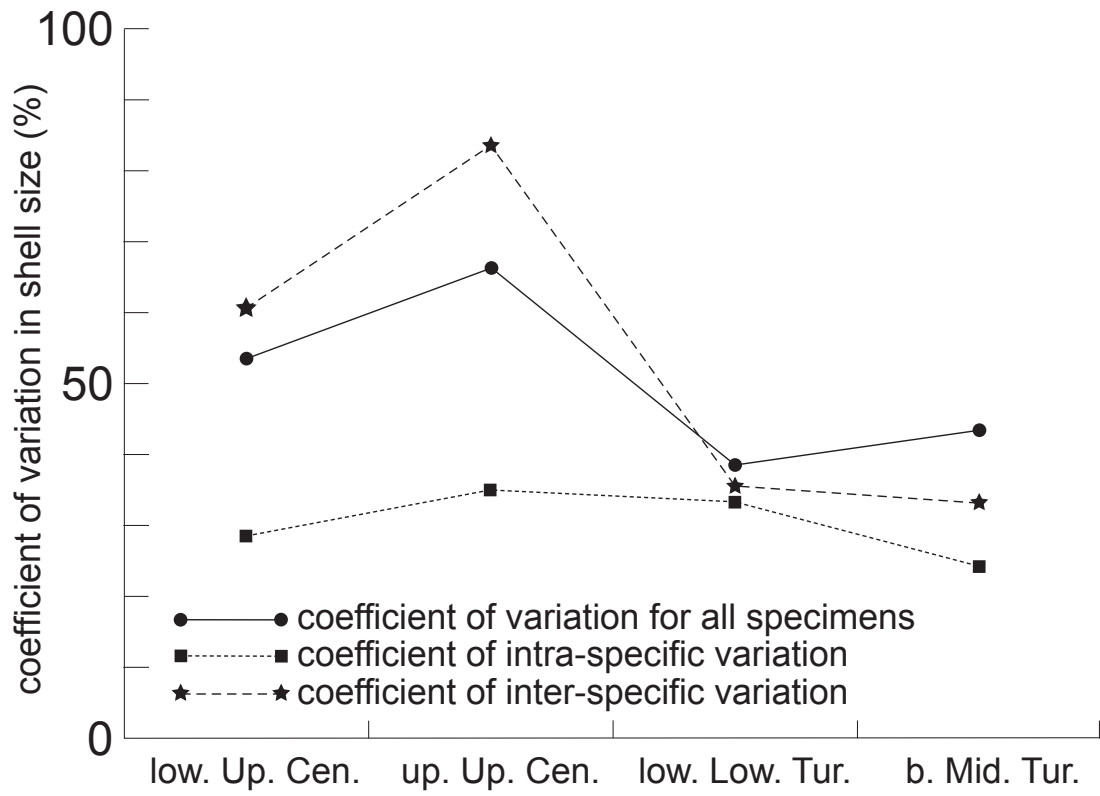


Fig. 2-6. Changes in coefficients of variation for all specimens, and coefficient of intra- and inter-specific variation

Among the Cenomanian and Turonian substages, species diversity in the Lower Cenomanian was low (5 species), while species diversities for the other substages were stable within a range of 9 to 12 species (Fig. 1-1) as demonstrated in Chapter 1. Species diversity did not decrease abruptly across the C/T boundary. However, the rates of extinction and origination across the C/T boundary were 100% (Fig. 1-2). In other words, all Late Cenomanian inoceramid species became extinct prior to the C/T boundary and were replaced by newly originated Early Turonian species. Accordingly, the ratios of species in each genus (= generic composition) changed drastically across the C/T boundary. *Mytiloides*, significantly, originated during Early Turonian time, and then repopulation by *Inoceramus* took place in Middle and Late Turonian time (Fig. 1-4).

5. 3. *Paleobiogeographic change*

A list of endemic and cosmopolitan species is shown in Table 2-3. Endemic species predominated and made up approximately 54–58% of the fauna during Middle Cenomanian to Middle Turonian (but not Early Turonian) time (Fig. 2-7). In comparison, cosmopolitan species predominated only in Early Turonian time and comprised 90% of species (Fig. 2-7).

6. Discussion

6. 1. *Cause of stunting among inoceramids above the C/T boundary*

Most size-frequency histograms for ILT inoceramids show a significant shift to the left (i.e. the smaller side), as described in section 5.1. (above). In addition, individuals with shell sizes greater than 60mm are absent in ILT faunas. In other words, most ILT inoceramid individuals were significantly smaller at death than individuals from the other horizons (Figs. 2-4, 5). Possible causes of this phenomenon are: (1) a significant reduction in adult shell size (stunting) took place just above the C/T boundary, in the ILT, (2) a taphonomic bias led us to collect many small, immature individuals from ILT deposits, or (3) most specimens collected from the ILT are immature individuals, by chance. I use the definition of “stunting” proposed by Ager (1963), in which a retardation of growth is controlled by environmental factors, and under unfavorable conditions produces unusually small individuals within the range of normal size variation. In contrast, “dwarfism” refers to teratological specimens (monstrosities) controlled by heredity, independent of environmental controls.

All inoceramid specimens in the present study were collected from uniform lithofacies of pelagic siltstone to muddy sandstone, so taphonomic factors evidently did not bias the size-frequency distribution. I employed the Mann-Whitney U test to examine for small, immature individuals occurring by chance, assuming that the inoceramids from each horizon belong to the

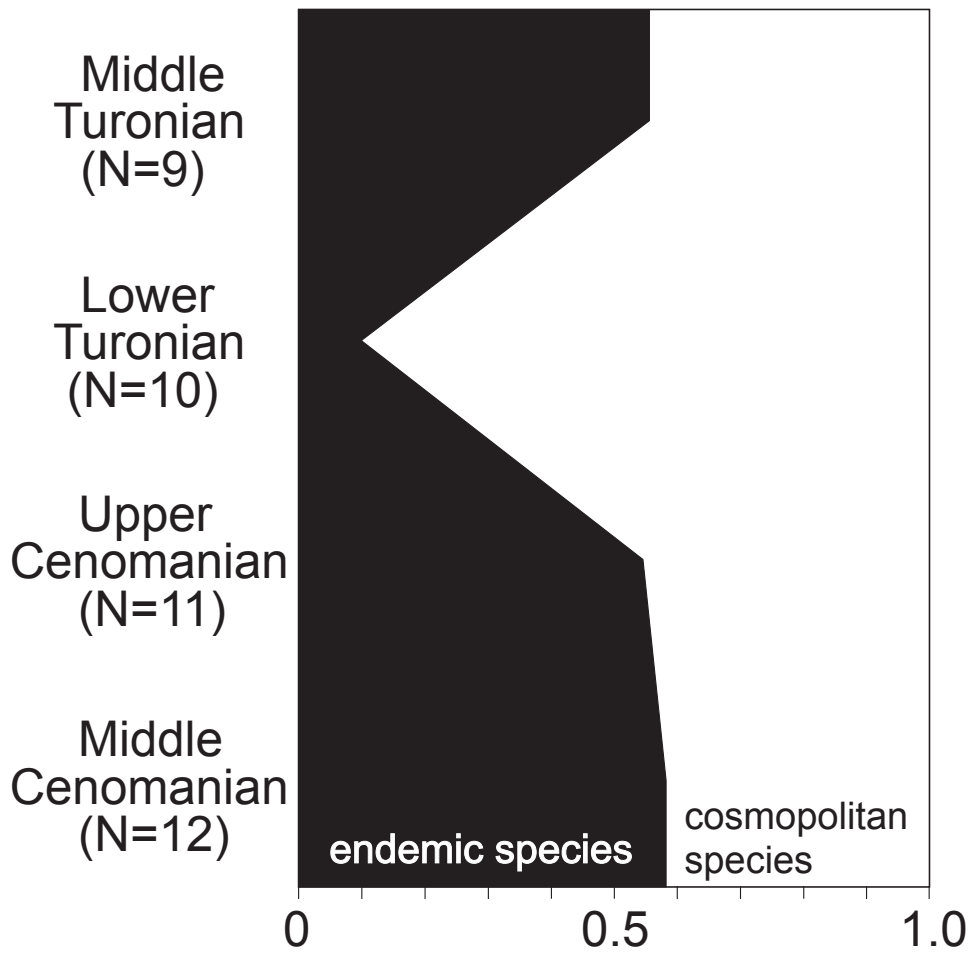


Fig. 2-7. Ratios of endemic and cosmopolitan species for each substage in Hokkaido. N: number of species

same size universe, that is to say a null hypothesis. Results show the probability that chance caused distinction in ILT distributions compared to the IUC and uUC horizons to be below 1%, and below 5% compared to the bMT horizon (Fig. 2-5). Since inoceramid specimens in each horizon were collected at random, the above-mentioned null hypothesis is rejected at the 1% and 5% significant levels. In view of these statistical results, size differences were not related to chance. Overall, it seems quite likely that stunting among adult inoceramids took place just above the C/T boundary.

Environmental factors (e.g. water temperature, salinity, pH, dissolved oxygen and population density) affect the growth of bivalves, and changes in these conditions control the adult sizes of bivalves. However, both species that become smaller and those that became larger must coexist under the same conditions of change, since every species has different conditions for optimal growth. Therefore, modern habitats in which only small bivalves dwell provide clues as to why only small inoceramids lived in the ILT. The following modern environments are ones in which only small bivalves live (see Hayami, 1997): (1) the deep sea (e.g. Knudsen, 1967, 1970; Nicol, 1978), (2) submarine caves (Kase & Hayami, 1992; Hayami & Kase, 1993, 1996; Hayami, 1997), and (3) islands isolated from large continents (Soot-Ryen, 1960; Vermeij, 1990).

Most bivalves inhabiting modern deep-sea environments have sizes of 10mm or less (Knudsen, 1967, 1970; Nicol, 1978). Only chemosynthetic communities include many large-size bivalves in the deep sea (e.g. Corliss et al., 1979; Boss & Turner, 1980). This phenomenon implies that bivalves can grow to a large size even in the deep sea, if sufficiently fed. However, since phytoplankton produced in the euphotic zone, the excrement and carcasses of zooplankton and nekton, and organic matter from continents do not reach the deep sea in abundance, the deep sea is constantly in an oligotrophic condition. Hayami (1997) described in detail the environments within submarine caves with bivalves and documented that more than 90% of the bivalve species there have shell lengths of 8mm or less. The temperature, salinity and oxygenation of seawater in submarine caves do not differ from those of the open sea (Hayami, 1997). Compared with the open sea, submarine caves characteristically are impoverished in nutrients (Hayami & Kase, 1993; Hayami, 1997), because primary producers are nearly absent. Vermeij (1990) investigated bivalves inhabiting islands isolated from large continents and observed that the ratio of small-size bivalves in shallow-marine increased eastward in Micronesia and Polynesia. In other words, the shell sizes of shallow-marine bivalves become smaller as separation increased from the continent and the large islands to the west. Vermeij (1990) proposed that this phenomenon resulted from a progressive decrease in terrestrial-sourced nutrients for suspension feeders. The one condition common to the above-mentioned habitats in the deep sea, submarine caves and islands isolated from large continents is oligotrophy.

The major primary producers in Cretaceous time were dinoflagellates and calcareous nannoplankton (Hart, 1996). In the Oyubari area, calcareous nannofossils do not occur immediately above the C/T boundary (Motoyama et al, 1991). In northwestern Europe,

dinoflagellate cyst species scarcely occur near the C/T boundary, and the number of individuals and species diversity drop steeply after the boundary (Jarvis et al., 1988; FitzPatrick, 1996; Hart, 1996). It is known that nannoplankton diversity also decreased remarkably across the C/T boundary (Hart, 1996). In addition, planktonic foraminifers, which are low-level consumers, are rare just across the C/T boundary along the Hakkinzawa River in the Oyubari area (Motoyama et al., 1991; Hasegawa, 1995). A decrease in primary productivity would have reduced the amount of zooplankton and nekton. Because primary producers, as well as excrement and the carcasses of zooplankton and nekton, are major nutrients for suspension-feeding bivalves, the results of the above-mentioned research imply that oligotrophic conditions for suspension-feeding bivalves expanded into the Yezo forearc basin just after the C/T boundary.

In sum, the stunting of inoceramids evidently reflects the spread of oligotrophic conditions into the Yezo forearc basin just above the C/T boundary. The larger size-frequency distribution in the bMT, compared to the ILT, strongly implies that the spread of oligotrophic conditions in the Early Turonian ameliorated in the late Early Turonian to Middle Turonian.

6. 2. Environmental disturbances inferred from inoceramid responses near the C/T boundary, and other considerations

As stated above in Chapter 1 and section 5.2., the extinction rate across the C/T boundary was 100% (Fig. 1-2). In addition, the generic composition changed drastically above the C/T boundary and *Mytiloides* dominated only in Early Turonian time (Fig. 1-4). Furthermore, faunal stunting, the abrupt decrease of inter-specific variation and the dominance of cosmopolitan species took place after the C/T boundary (Figs. 2-4, 5, 6, 7). As Foote (1996) demonstrated, a morphological decrease in disparity (which corresponds to inter-specific size variation in the present study) associated with stable or increasing diversity would be a consequence of environmental stresses and selective extinction. This implies that major environmental disturbances occurred around the C/T boundary in the Yezo forearc basin, and that they had a significant effect on epibenthic inoceramid bivalves.

Well-laminated black mudstone or shale is unknown in the present study sections, and high total organic carbon (TOC) values have not been detected around the C/T boundary in the Yezo Supergroup (e.g. Hasegawa & Saito, 1993; Hasegawa & Hatsugai, 2000). Thus, unequivocal evidence that dysoxic or anoxic conditions spread into the Yezo forearc basin have not been hitherto recognized in both the lithology and geochemistry. Kaiho & Hasegawa (1994) examined the amount of dissolved oxygen, using a dissolved-oxygen index based on calcareous benthic foraminiferal wall thickness, size, and morphology. They inferred that minimum oxygen conditions prevailed twice prior to and 1.5 m.y. after the C/T boundary, and that benthic foraminiferal extinctions coincided with initiation of the two oxygen-minimum levels. This study suggests that the principal disturbance that spread into the Yezo forearc basin near the C/T

boundary probably was oxygen-depletion. This oxygen-depleted condition is inferred to reflect the global OAE2.

The data presented here suggest the following scenario: Inoceramids in the Yezo forearc basin became extinct by the C/T boundary because they were strongly affected by oxygen depletion associated with OAE2. Consequently, vacant niches during Early Turonian time were filled by cosmopolitan taxa, mainly *Mytiloides*. As the oligotrophic environment spread, invaders were restricted to small-size species. Ameliorating oligotrophic conditions from the late Early Turonian to early Middle Turonian allowed repopulation of the Yezo forearc basin by moderate- to large-sized inoceramid species, such as *I. hobetsensis* and *I. obiraensis* Noda & Matsumoto (Fig. 2-3).

A variety of inoceramid responses to environmental disturbances near the C/T boundary are given in the present study. Other researchers (Elder, 1989; Harries, 1993; Kauffman & Harries, 1996; Harries & Little, 1999) have also reported inoceramid responses to C/T mass-extinction events in the Western Interior Seaway. The inoceramid extinction rate at the C/T boundary has been estimated at 92% (Elder, 1989) or 75% (Harries & Little, 1999), after which *Mytiloides* radiated dramatically within the Western Interior Seaway. In contrast, *Inoceramus kamuy* Matsumoto & Asai was the progenitor (i.e. the first-appearing taxon following a mass extinction) above the C/T boundary in the Yezo forearc basin, where it appears 2.5m above the boundary in the Hakkinzawa River section of the Oyubari area (Fig. 2-3). The time represented by 2.5m of sediments above the C/T boundary is estimated at 0.03 m.y., using calculations based on the work of Kaiho & Hasegawa (1994). This fact contrasts with the Western Interior Seaway, where only *Mytiloides* existed for up to 0.75 m.y. after the C/T boundary (Harries, 1993). The present research demonstrates for the first time that an *Inoceramus* species was a crisis progenitor after the C/T mass extinction, as well as inoceramid responses to mighty environmental stresses.

Unfortunately, changes in inoceramid size, inter-specific size variation, and paleobiogeography across the C/T boundary have not been investigated for the Western Interior. Comparing the environmental responses of inoceramids in the Yezo forearc basin with those in the Western Interior Seaway and Tethys will reveal the universal aspects of oxygen-depletion on epibenthic faunas, as well as the faunal extinction and recovery patterns related to mass extinction events. Comparing inoceramid responses in Hokkaido with those in the Western Interior and Tethys will be crucial for elucidating the many aspects of mass-extinction events.

7. Conclusions

The inoceramid responses to environmental disturbances across the C/T boundary in the Yezo forearc basin, Hokkaido, have been investigated by an examination of newly collected specimens and a literature survey. Inoceramid responses imply that major environmental changes took place in submarine environments near that boundary, as reflected in high extinction and

origination rates. In addition, dramatic changes in generic composition, faunal stunting, decreases in inter-specific size variation, and the dominance of cosmopolitan species took place after the C/T boundary. The prevalence of stunting just above the C/T boundary suggests that oligotrophy spread throughout the Yezo forearc basin. The present study and prior investigations imply that inoceramids of the Yezo forearc basin were strongly affected by environmental disturbances related to oxygen depletion associated with OAE2.

It will be necessary in future studies to compare inoceramid responses in Hokkaido with those in the Western Interior and Tethys, in order to elucidate the true aspects of mass extinction events.

Chapter 3. Summary on the inoceramid responses to marine environmental changes and further consideration

As clarified in Chapter 1, the inoceramid diversity responds to the eustatic and relative sea-level changes sensitively. The pattern of the inoceramid diversity changes is similar to that of the long-term (2nd order) eustatic curve, and the steep drop of diversity at the Lower/Upper Campanian boundary should reflect the abrupt relative sea-level fall recorded in the Yezo Supergroup. In addition, as clarified in Chapter 2, inoceramids showed the sensitive responses to changes in the amount of dissolved oxygen and trophic conditions. High extinction rates and decrement of inter-specific variation would result from the oxygen-depleted condition. Moreover, oligotrophic conditions spread just after the C/T boundary throughout the Yezo forearc basin probably caused the faunal stunting of inoceramids. The present paper revealed that many inoceramid responses are decipherable even from fossil records.

While, the results clarified in the present paper strongly imply that the recovery of diversity from mass extinction events and the recovery of size distribution from stunting due to oligotrophic conditions were extremely rapid from a viewpoint of the geological time scale. Thriving of inoceramids throughout Late Cretaceous time was probably derived from such biological ability of rapid recovery. In addition, various survival strategy against environmental disturbances, such as rapid evolution, dispersal ability associated with long-lived planktotrophic larvae, and migration to either refugia or secondary habitats must contribute to inoceramid thriving.

In Chapter 1, the number of occurring species is used as the criterion of “diversity”. However, a variety of problems on the inoceramid systematics have been pointed out from the past. Such problems bring great differences of intra- and inter-specific variation for inoceramids in each age. Therefore, it is essential to use distributed areas on morphospace as the criterion of “diversity” in order to appreciate the veritable “morphological” diversity. Henceforth, it is necessary to elucidate temporal changes for distributed areas on the inoceramid morphospace.

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