Differential preservation of the Upper Cretaceous ammonoid *Anagaudryceras limatum* with corrugated shell in central Hokkaido, Japan

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The taphonomy of the Upper Cretaceous ammonite *Anagaudryceras limatum* differs from associated ammonites in the same horizon. This differential taphonomy is reconstructed based on fragmentation patterns and structural property of the corrugated shells of their body chamber parts. The characteristic preservation of isolated body chamber parts with corrugations is commonly observed in *A. limatum* from the upper Turonian of the Oyubari area, central Hokkaido, Japan. This preservation probably results from the differential internal structural properties of the hollow body chamber and septated phragmocone as well as the peculiar corrugation on body chamber of the present species: (1) fracturing along the corrugations against bending force is easier than flat material, because of the concentration of force on the tops or bottoms of corrugations, and (2) high durability against compressive forces. The separated body chamber parts were resistant to being squashed and broke into pieces due to the durability of corrugations against compressive force. The statistic test on the fossil assemblage suggests that selective destruction did not affect the fidelity of species composition and relative abundance of the studied fossil assemblage. Molluscan death assemblages in marine systems consistently show strong fidelity to relative abundances in the live community, suggesting that there was an *Anagaudryceras*-dominant ammonoid community during the late Turonian in the Oyubari area.

Key words: Ammonoidea, *Anagaudryceras*, corrugation, paleoecology, taphonomy, Cretaceous, Hokkaido.

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Introduction

Recognition of the quality of the fossil record and the sources of bias is particularly significant for high-resolution studies in paleoecology and paleobiogeography (Kidwell and Bosence 1991; Kidwell 2001). One such quality is ecological fidelity, which is the selective destruction of species and morphs that affects relative abundance in a fossil assemblage (Kidwell and Brenchley 1996; Kidwell 2001). Quantifying such differential preservation and taphonomic bias in a fossil assemblage is an important direction of taphonomic research (Kidwell and Flessa 1996; Kidwell and Holland 2002).

The Upper Cretaceous ammonoid, *Anagaudryceras limatum* (Yabe, 1903) (Gaudryceratidae, Lytoceratina), is commonly found in upper Turonian–Coniacian strata in Hokkaido, Japan (Matsumoto 1995; Toshimitsu and Hirano 2000). The principal morphological character is a planispiral, evolute, rounded whorl having restricted radial ribs on the adult body chamber, which become adorally stronger from the slightly adapical position of the last septum (Yabe 1903; Matsumoto 1995). In Hokkaido, the isolated body chamber parts with corrugations are commonly found, unlike those of other Cretaceous ammonoids (compare to Maeda 1987; Wani 2001, 2003; Kawabe 2003).

In the present study, the taphonomic attributes of *A. limatum* and other associated planispiral ammonoids from a fossil horizon in central Hokkaido are quantitatively examined, and then differential preservation of *A. limatum* and their implication for taphonomy and paleoecology are discussed.

Institutional abbreviation.—NSM PCL, National Science Museum, Tokyo, Japan, Paleontological Collection Locality.

Material and method

A total of 118 specimens (73 *Anagaudryceras limatum* and 45 other associated planispiral ammonoids) from two adjacent localities around the Shuparo Lake of the Oyubari area, central Hokkaido, Japan (Fig. 1), have been analyzed for the present study (Table 1). All specimens are housed in the collections of NSM.

Taphonomic attributes were scored on the basis of the patterns of shell fragmentation. These attributes have been first categorized separately for *A. limatum* and then other planispiral ammonoids, and then compared. The size-distribution patterns and mean shell diameter are also depicted and calculated, based on specimens whose diameters can be mea-

Table 1. List of species and number of individuals in each fragmentation category. Categories: a, intact; b, phragmocones with distorted body chamber; c, phragmocones lacking body chambers; d, isolated body chamber parts; e, indeterminate.

species	No. of specimen	fragmentation category				
		a	b	c	d	e
Anagaudryceras limatum	73	7	19	5	37	5
Gaudryceras denseplicatum	4	2		2		
Gaudryceras tenuiliratum	1	1				
Gaudryceras sp.	3	1		1	1	
Tatragonites sp.	5	4		1		
Damesites ainuanus	14	10	1	1		2
Damesites sp.	9	7	2			
Yokoyamaoceras sp.	1		1			
Mesopuzosia yubarensis	4	2	2			
Collignoniceras sp.	1	1				
Subprionocyclus minimus	1	1				
Scaphites sp.	2	1	1			
Total	118					

sured. For deformed specimens, the preserved maximum diameter is measured.

Geological setting

The Yezo Group, which was deposited in the Cretaceous Yezo Forearc Basin, is widely distributed in a north-south direction in central Hokkaido. In the Oyubari area, offshore facies are widely exposed (Kawabe 2000, 2003; Takashima et al. 2004). Many biostratigraphic studies have been undertaken around the Shuparo Lake in the Oyubari area (e.g., Matsumoto 1942; Hirano et al. 1977, 1980; Motoyama et al. 1991; Kaiho et al. 1993; Hasegawa 1999; Ando 2003; Kawabe et al. 2003; Nishi et al. 2003; Takashima et al. 2004), where the Saku, Kashima, and Hakobuchi Formations (see Takashima et al. 2004, for the definitions) crop out, in the ascending order (Fig. 1). These strata strike in a north-south direction and generally young to the west, and are unconformably capped by the Paleogene deposits (Hirano et al. 1980; Takashima et al. 2004). The Saku Formation (2300 m thick in the Oyubari area) is composed mainly of alternating beds of turbiditic sandstone and siltstone. The Kashima Formation (1670 m thick in the Oyubari area) is mainly composed of bioturbated, massive siltstone, with intercalations of volcaniclastic sandstones. The Hakobuchi Formation (450 m thick in the Oyubari area) generally consists of sandstone, with intercalations of conglomerates and alternating beds of sandstone and siltstone.

All specimens used in this study were collected from calcareous concretions embedded in massive, coarse-grained siltstone just below an intercalation of thick greenish volcaniclastic fine-grained sandstone in the lower part of the Kashima Formation (Fig. 2). Although the specimens were
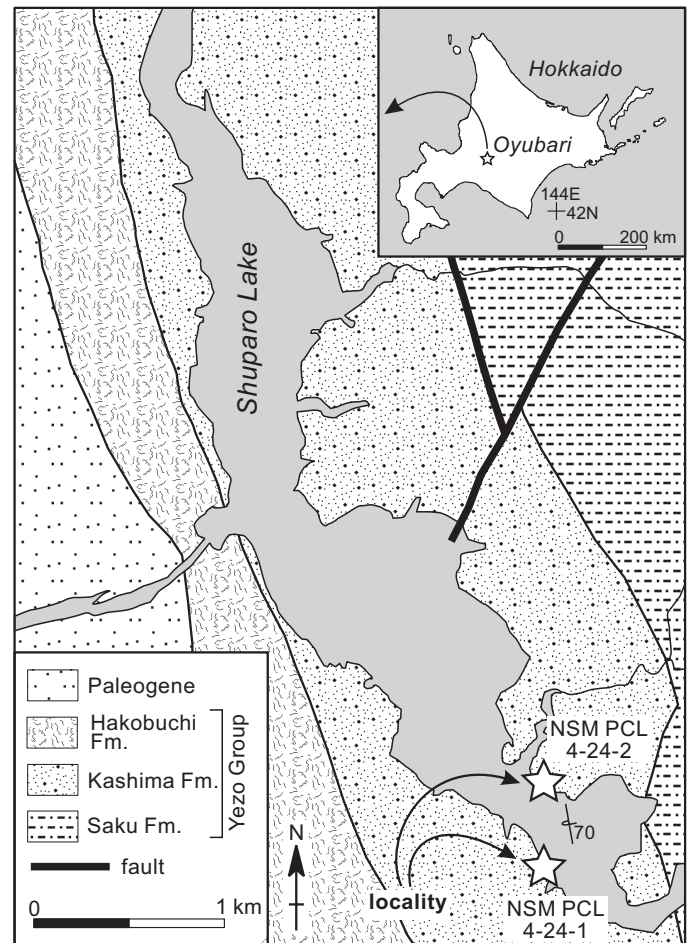

Fig. 1. Geological map of Cretaceous–Paleogene strata around Shuparo Lake in Oyubari area, central Hokkaido, Japan. Modified from Takashima et al. (2004).

collected in two localities, NSM PCL 4-24-1 and 4-24-2, around the Shuparo Lake (Fig. 1), their horizons are the same judging from their stratigraphic position relative to the same intercalation of sandstone (Fig. 2). The age of the horizon is late Turonian according to macro- and micro-fossil data (Nishi et al. 2003; Takashima et al. 2004; see also Table 1, for the associated ammonoid species). The depositional environment is reconstructed as a continental slope (~300 m deep), based on lithology and benthic foraminifers (Kaiho et al. 1993; Kawabe 2000; Takashima et al. 2004).

Taphonomic attributes

Most shells preserve their original three-dimensional morphology, although some were slightly distorted diagenetically. Shell material in all specimens is preserved, although it was recrystallized to calcite due to diagenesis. Shells were found sporadically within calcareous concretions without any preferred orientation, and there is no difference of burial orientations between *Anagaudryceras limatum* and the other species. Shells were commonly fragmented with various types. Five
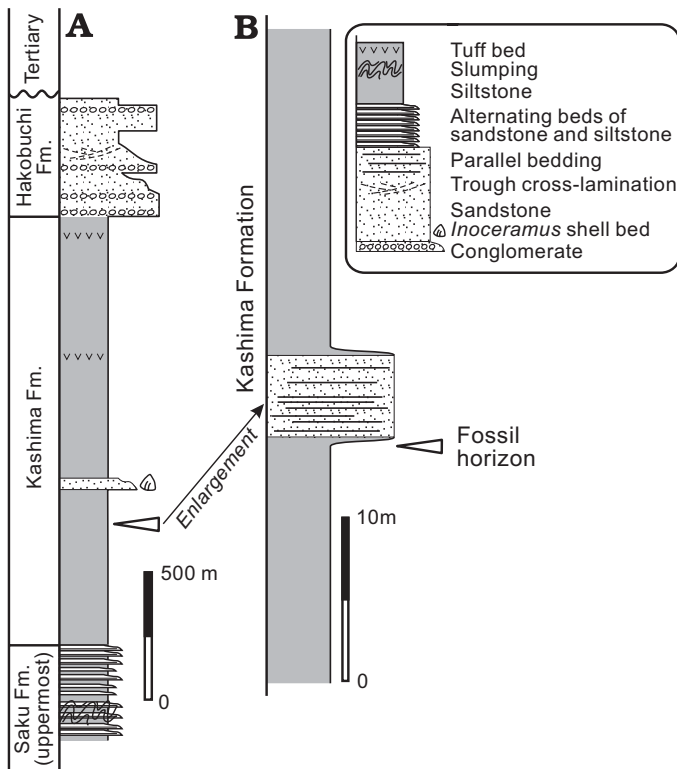
Fig. 2. Columnar sections and fossil horizon. **A**. Composite columnar section around Shuparo Lake. Modified from Takashima et al. (2004). **B**. Enlarged columnar section of fossil horizon. All specimens are collected from calcareous concretions embedded in massive, coarse-grained siltstone just below intercalation of greenish sandstone in the lower part of Kashima Formation.

categories of shell fragmentation have been recognized, as follows: (a) intact shells (Fig. 3A); (b) phragmocones with distorted body chamber with radial edges almost straight along growth lines and ribs, and located just adoral of the last septum, although body chamber parts mostly retain their original morphology (Fig. 3B); (c) phragmocones lacking body chambers, with radial edges almost straight along growth lines and ribs, and located just adoral of the last septum (Fig. 3C); (d) isolated body chamber parts, which are, however, not broken into pieces and retain their original morphology in most specimens (Fig. 3D); and (e) indeterminate due to poor preservation. Epifauna, corrosion, and abrasion have not been noted on any of the shells.

Shell fragmentation rates in *A. limatum* and the other species are summarized in Table 1 and Fig. 4A. The shell fragmentation rates in *A. limatum* for the categories a–e are as follows: 9.6%, 26.0%, 6.8%, 50.7%, and 6.8%, respectively, for a total of 73 specimens. The common occurrence of isolated body chamber parts is characteristic of *A. limatum*, which is different from those of other ammonoids in Hokkaido (compare to Maeda 1987; Wani 2001, 2003; Kawabe 2003). In the other associated species of the study section, their shell fragmentation rates for the categories a–e are: 66.7%, 15.6%, 11.1%, 2.2%, and 4.4%, respectively, for a total of 45 specimens. There is a statistically significant difference between

the fragmentation rates in *A. limatum* and the other planispiral ammonoids (using the Goodness-of-Fit test, p <0.001).

Size-distribution patterns and mean shell diameters of the specimens whose diameters can be measured, are summarized in Fig. 4B. The mean shell diameters are 104 and 49 mm for *A. limatum* and the other species, respectively.

Reconstruction of taphonomic history

These results clearly show that *Anagaudryceras limatum* has been preserved differently from other species in a single fossil assemblage from the same horizon. The two different types of the taphonomic attributes of the fossil assemblage are explained by either (1) the postmortem transport history of *A. limatum* was different from those of the other species (e.g., transport out of life habitat), or (2) the responses to a similar taphonomic history differed between *A. limatum* and the other species (e.g., selective shell destruction according to species and morphs).

The first scenario is unlikely based on the following two facts: (1) A lack of epifauna on the shells suggests that all shells did not float and drift after death for any length of time (see also Boston and Mapes 1991; Maeda and Seilacher 1996). Modern *Nautilus* experiments of postmortem drift also support the model that all shells in this study sank quickly due to low air pressure inside the phragmocones (Wani et al. 2005). (2) The abundance of *A. limatum* (Table 1) suggests that they were not preserved through exceptional taphonomic history and was the same as the other species. Cephalopod shells preserved through exceptional taphonomic history (e.g., floating for a long distance) have low abundance (e.g., a fossil nautiloid *Aturia*, in Chirat 2000).

The characteristic taphonomic attributes of *A. limatum* are derived, therefore, from different responses to the same burial conditions. They are probably related to the internal structural difference between hollow body chamber and septated phragmocone, which is enhanced by corrugated adult body chambers. These ribs become adorally stronger from the slightly adapical position of the last septum with constant shell thickness (i.e., the inside of body chambers is also corrugated at approximately the same degree); such ornamentation is not developed in the phragmocone and juvenile body chamber parts (Fig. 3A, B; Matsumoto 1995). Corrugation of shells increases the shell strength against compressive force and is the most effective means to increase stiffness without increasing the need for additional shell material (Pennington and Currey 1984; Currey 1988). The durability of similar shapes is generally utilized in constructing arches, tunnels, and corrugated cardboard. However, corrugated materials more readily deform along ribs against a bending force (see also Brett 1990), because bending forces do not uniformly act on corrugated materials and instead concentrate on the tops or bottoms of corrugations
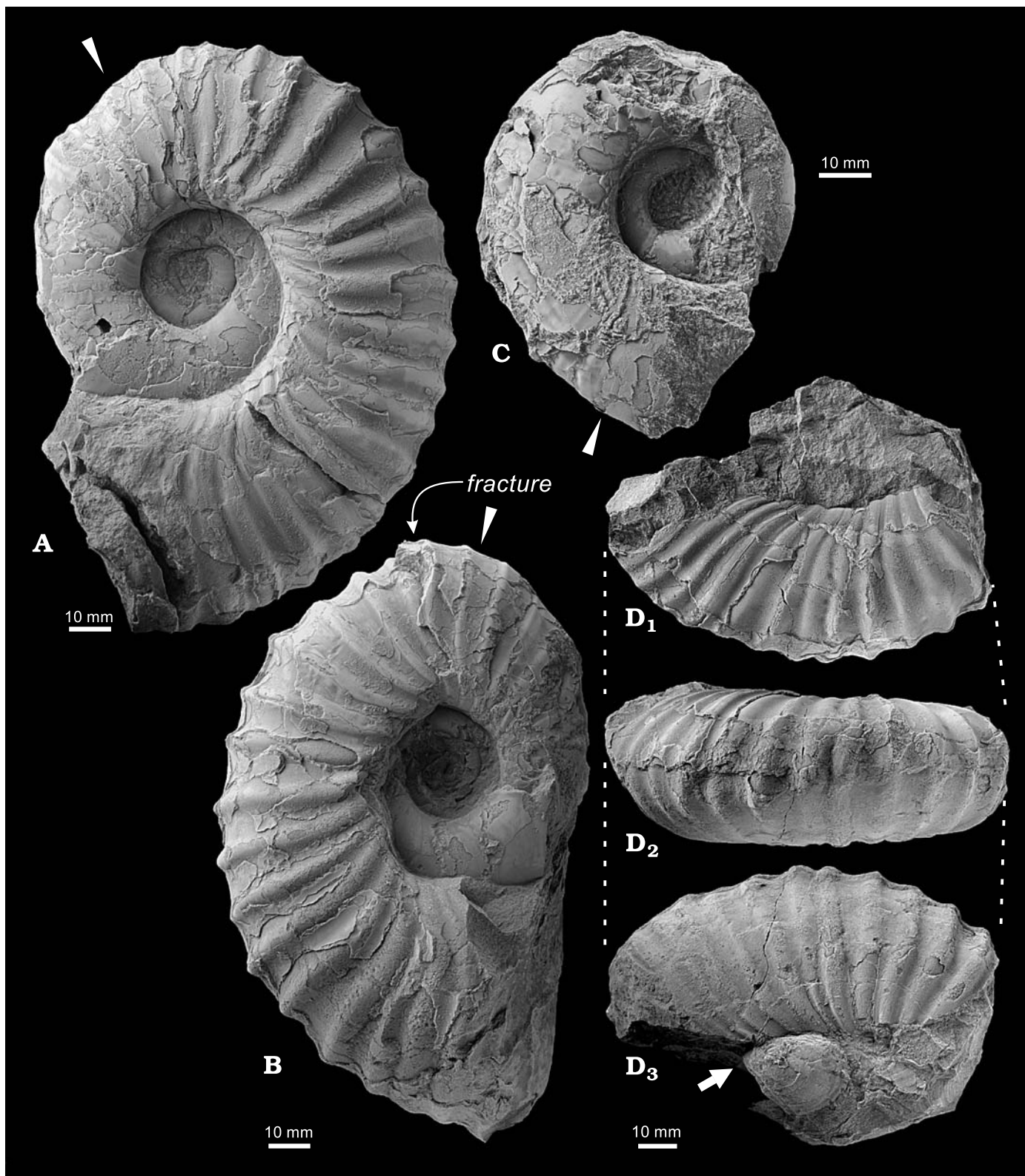
Fig. 3. Categories of shell fragmentation patterns. **A**. Intact, NSM PM 17534. **B**. Phragmocones with distorted body chamber, with radial edges almost straight or paralleling growth lines, and located just adoral of last septum, NSM PM 17535. Note body chamber part retaining their original morphology. **C**. Phragmocones lacking body chambers, with edges almost straight or parallel to growth lines, and located just adoral of last septum, NSM PM 17536. **D**. Isolated body chamber parts, NSM PM 17537, lateral (D₁ and D₃) and ventral (D₂) views. Note lower jaw (arrow) preserved near separated body chamber. All specimens belong to late Turonian (Late Cretaceous) lytoceratid ammonoid *Anagaudryceras limatum* (Yabe, 1903) from the Oyubari area in the central Hokkaido, Japan. Specimen B is from locality NSM PCL 4-24-1, and all the others are from NSM PCL 4-24-2. Triangles indicate position of last septum.
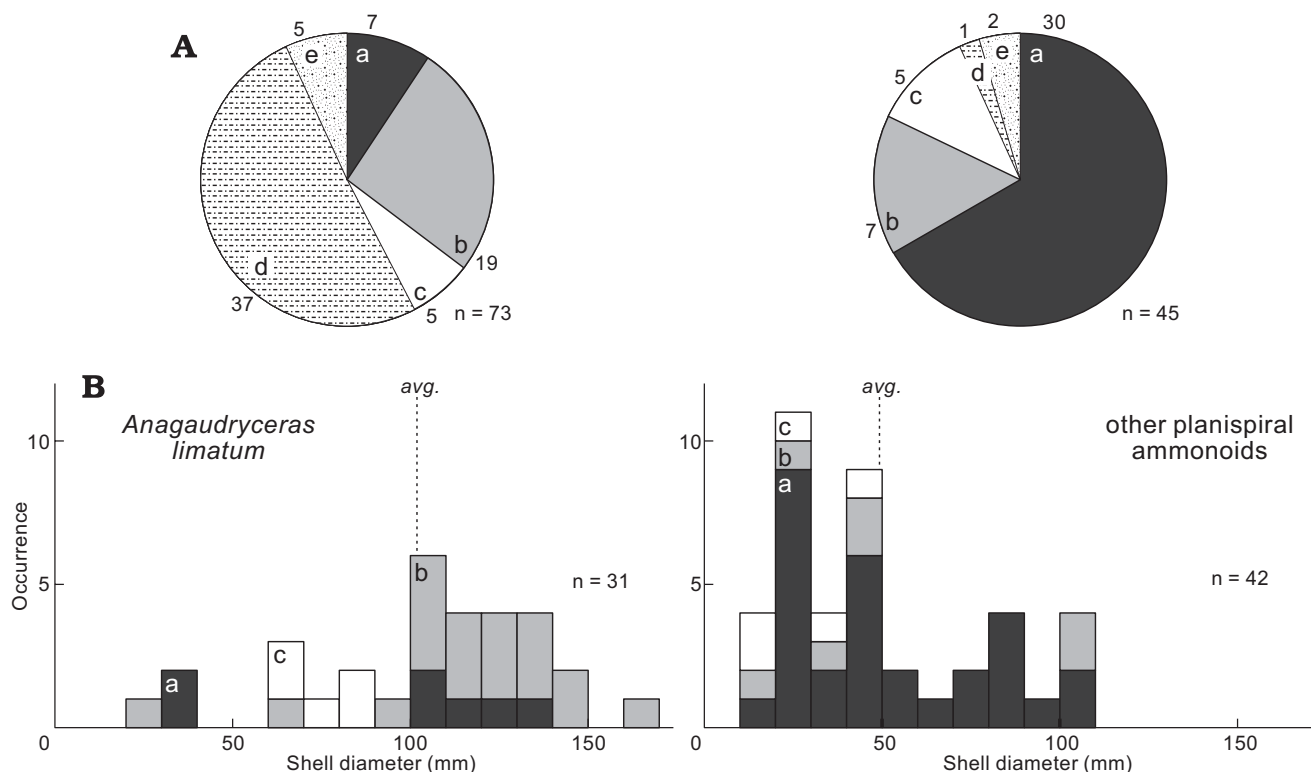
Fig. 4. Comparison of taphonomic attributes between *Anagaudryceras limatum* (Yabe, 1903) and other planispiral ammonoids. **A**. Fragmentation patterns. Numbers around pie diagrams signify number of individuals in each category. **B**. Size-distribution patterns and mean shell diameters of specimens whose diameters can be measured. Categories: a, intact; b, phragmocones with distorted body chamber; c, phragmocones lacking body chambers; d, isolated body chamber parts; e, indeterminate.

(Fig. 5). Indeed, fractured edges on the corrugated body chambers tend to be at tops or bottoms (Fig. 3). This mechanical property is utilized for connecting material (e.g., water and gas pipes, bellows). Such mechanical properties of corrugations are key factors for the characteristic taphonomic attributes of *A. limatum* (i.e., high percentage of isolated body chambers and low percentage of intact shells; Fig. 4).

Collapse patterns of ammonoid shells depend largely on their burial orientation (e.g., Seilacher et al. 1976; Maeda et al. 2003). The collapse pattern in most *Anagaudryceras* shells of the category b (i.e., phragmocones with distorted body chamber; 14 of 19 specimens, Table 1) is that the body chambers exhibit inward bending (Fig. 3B), and those of the others show horizontal flattening of body chambers with minor longitudinal fractures. According to Seilacher et al. (1976) and Maeda et al. (2003), collapse with body chambers bending inward and horizontal flattening are related to vertical–oblique and horizontal burial orientations in relation to the bedding plane, respectively. The coexistence of these collapse patterns is probably due to their burial orientation without preferred orientation within calcareous concretions. Similar coexistence is observed in the other species, which also show similar orientation within calcareous concretions. Therefore, the difference in the burial orientations is not a factor of the preservational difference between *A. limatum* and the other species.

Fragmentation by compaction after final burial can be distinguished from the fact that the shell fragments were not dispersed but generally remained near to the position of the original shell (as seen in the fragmentation category b; Fig. 3B). For fragmentation before final burial, on the other hand, it is difficult to determine the mechanisms from the fossil record alone. However, the experimental reproduction of fragmentation patterns with modern *Nautilus* has shown that the breaking patterns due to various mechanisms are distinct from each other (Wani 2004). The analogy from the study of modern nautilus enables us to reconstruct ammonoid taphonomy as a primary approach (Boston and Mapes 1991; Maeda and Seilacher 1996; Wani 2004); it also suggests that the fragmentation patterns of phragmocones without body chambers in *A. limatum*, the edges of which are almost straight or parallel to the growth line and located just adoral of the last septum in most specimens (Fig. 3C), is derived from sediment loading. There are no associated fragments with host phragmocones in the specimens of the fragmentation categories c and d (Fig. 3C, D), which suggests that the shells were washed away after sediment loading-induced fracture and then reburied, so that fragments and phragmocones were separated (see also Wani 2001, 2003, 2006). These events of washing away and redeposition are possibly related to the deposition of the greenish sandstone, which is at the horizon just above those of the fossil occurrences (Fig. 2). The reason why most separated phragmocones were rarely preserved at the studied localities or horizon
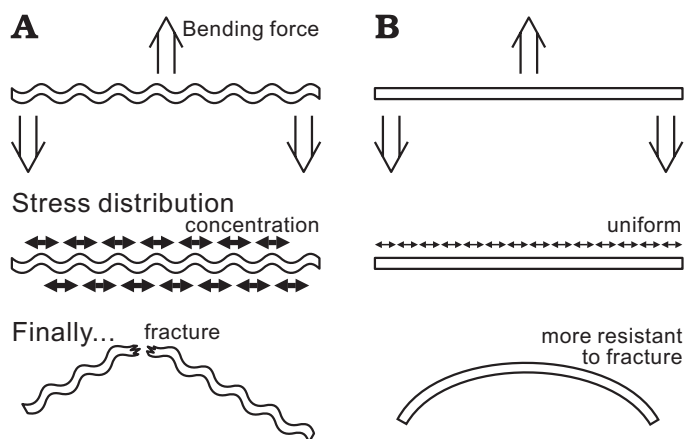
Fig. 5. Bending force on corrugated and flat materials. **A**. Bending force concentrates on tops and bottoms of corrugations, resulting in fracturing easier than flat material. **B**. Bending force uniformly acts on flat material.
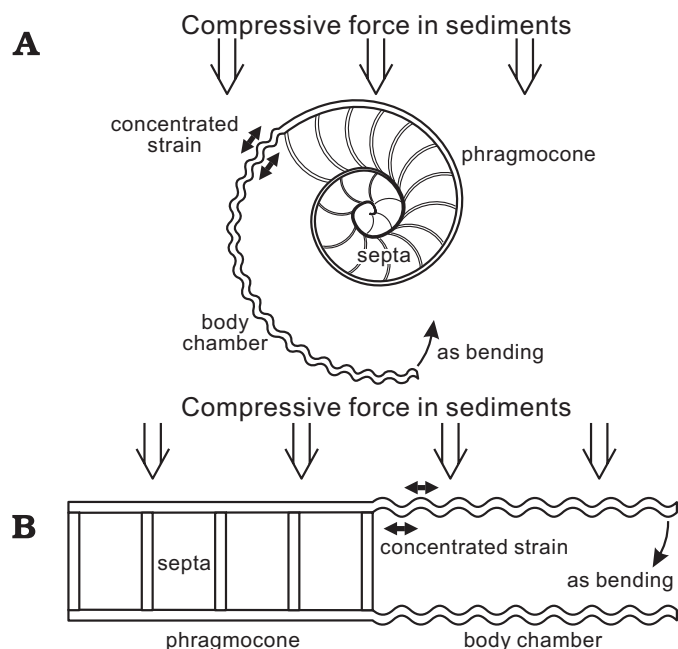

Fig. 6. Schematic drawing of shell cross-section in *Anagaudryceras limatum*. Compressive force in sediments concentrates on just adoral of last septum and acted on corrugated shell material as bending force. Vertical (**A**) and horizontal (**B**) burial orientations.

is possibly explained the following two models, although this is difficult to identify based only on this study. (1) Separated phragmocones were selectively dissolved, although shells of hollow body chambers do not show any trace of dissolution. (2) Separated phragmocones were selectively transported due to lack of body chambers. In modern *Nautilus*, shells without body chambers are transported by bottom current more readily than intact shells (Wani and Ikeda 2006).

Compressive force by sediments was concentrated just adoral to the last septum, at which is almost the boundary between with and without corrugated ornamentation (see Matsu-

moto 1995; Fig. 3A, B). The force acting on the shell just adoral to the last septum was a bending force in both vertical and horizontal burial orientations (Fig. 6), because phragmocones reinforced by septa were rarely compressed, and hollow body chamber parts were easily compressed (Seilacher et al. 1976; Maeda 1987). The diameter difference was unlikely to have had any influence on the fragmentation since analogical experiments with modern *Nautilus* reveal almost uniform breaking load irrespective of shell diameter (Wani 2004). On the other hand, the separated body chamber parts were resistant to being squashed and fragmented due to the durability of corrugations against compressive force (Fig. 3D). After burial, body chambers were also mechanically reinforced by sediment infill (Seilacher et al. 1976; Maeda 1987; Maeda and Seilacher 1996). Body chamber parts of the other ammonoids were squashed and fragmented more easily than those in *A. limatum* due to lack of corrugations, and therefore were rarely preserved in the fossil assemblage (the category d of the other ammonoids in Fig. 4A).

Abundance of *Anagaudryceras limatum*

The selective destruction of *Anagaudryceras limatum* possibly affected the fidelity of species composition and relative abundance of the fossil assemblage in the study area. However, the analysis of the individual numbers in each fragmentation category suggests that the effect of this selective destruction on the fidelity is negligible: overlapping numbers of the fragmentation categories c and d, which complement each other morphologically, are few in the studied fossil assemblage (only five of 73 specimens; Table 1). The balance (68 specimens), probably the true relative abundance of *A. limatum* in the fossil assemblage, still exceeds the individuals of the other associated species (Table 1; see also Matsumoto et al. 1981, for contemporaneous faunal compositions of the shallower environments, Tanabe et al. 1978, for upper Turonian compositions from the subordinate strata in the adjacent areas, and Kawabe 2003 and Tanabe 1979, for compositions of the upper Albian–Cenomanian and middle Turonian in the Oyubari area, respectively). Molluscan death assemblages in marine systems consistently show strong fidelity to relative abundances in the live community (Kidwell and Flessa 1996, and references therein), however those in ammonoids have been uncertain. This study quantitatively illustrates a similar high fidelity also in ammonoids, suggesting that there was an *Anagaudryceras*-dominant ammonoid community in the late Turonian in the study area. Similar dominance of *A. limatum* in the late Turonian has been also reported in the adjacent area with offshore facies of central Hokkaido (Kurihara and Hirano 2003), which clearly contrasts with *Anagaudryceras*-impoverished communities in the contemporaneous shallower environment (Matsumoto et al. 1981). This suggests that the ammonoid communities dur-

ing the late Turonian were laterally different, depending on environment. This is in contrast to those in the upper Albian–Cenomanian of central Hokkaido, where the relative faunal compositions of ammonoids were similar from inshore to offshore facies (Kawabe 2003). Furthermore, the scarcity of intact shells less than 100 mm in diameter (Fig. 4B) is probably not due to the difference in their taphonomy but in their paleoecology, because the other ammonoids of similar size are abundant. This scarcity might be related to the life cycle of *A. limatum* (e.g., migration through growth, reproductive behaviour at adult stage), although this is difficult to argue based only on this study, and therefore should be investigated together with other approaches (e.g., isotopic analysis of shells).

Destructive processes of disarticulation, fragmentation, and corrosion affected different skeletal types in different ways (Brett 1990). Differential durability of invertebrate skeletal materials to destructive processes has been recognized (Chave 1964), which is informative as qualitative indicators of physical environmental parameters (Brett and Baird 1986). Therefore, the factors of selective destruction should be considered for improved paleoecological interpretation. The taphonomic bias similar to those in *A. limatum* of this study might therefore be presumed for other ammonoids with ornamented body chambers (e.g., Cretaceous acanthoceratids), although taphonomic bias varies widely in taxonomic groups, tectonic settings, geological time, geological evolution of Earth's surface, and the cumulative effects of age (Kidwell 2001).

Acknowledgments

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