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Low durophagous predation on Toarcian (Early Jurassic) ammonoids in the northwestern Panthalassa shelf basin

YUSUKE TAKEDA and KAZUSHIGE TANABE



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Predatory shell breakage is known to occur occasionally on the ventrolateral portion of the body chamber in Mesozoic ammonoids. Here we report, for the first time, quantitative data of shell breakage in large ammonoid samples that were recovered from the lower Toarcian (Lower Jurassic) strata in the Toyora area, western Japan. The strata yielding the ammonoid samples consisted mostly of well-laminated, bituminous black shale that was deposited in an oxygen-depleted shelf basin of the northwestern Panthalassa, under the influence of the early Toarcian oceanic anoxic event. Among a total of 1305 specimens from 18 localities, apparent shell breakage was recognised in 35 specimens belonging to 7 genera, resulting in only a 2.7% frequency of occurrence relative to the total number of specimens. The breakage occurs mostly on the ventrolateral side of the body chamber with a complete shell aperture. This fact, as well as the low energy bottom condition suggested for the ammonoid-bearing shale, indicate that the shell breaks observed in the examined ammonoids were not produced by non-biological, post-mortem biostratinomical processes but were lethal injuries inflicted by nektonic predators such as reptiles, jawed fishes, coleoids, nautiloids, and carnivorous ammonoids with calcified rostral tips in their upper and lower jaws. Similar predatory shell breaks on the ventrolateral side of the body chamber have been found in contemporaneous ammonoid assemblages of the Tethys Realm, with a much higher frequency of occurrence than in the examined samples from the northwestern Panthalassa, suggesting a weaker durophagous predation pressure on ammonoids in the latter bioprovince.

Key words: Ammonoidea, predation, ventral bite marks, Jurassic, Toarcian, Panthalassa.

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Introduction

The study of the evolution of predator-prey interactions has contributed much to our understanding of the ecological background of biodiversity change through geological time, because they represent a driving force of natural selection. Many previous researchers have investigated this subject based on analysis of a predator's stomach contents or coprolites (e.g., Cicimurri and Everhart 1991; Richter and Baszio 2001) and lethal/sublethal breakage in a prey's hard tissue made by predators (e.g., Dietl et al. 2000; Kelley et al. 2001). As a result, a hypothesis called the Mesozoic Marine Revolution (MMR) has been proposed for the biotic interactions between predators and prey in the late Mesozoic and younger marine ecosystems (e.g., Vermeij 1977, 1982, 1987; see also the review by Harper 2003). However, most previous studies have focused on the predator-prey interactions in hard tissue-bearing benthic communities (Vermeij 1987). Studies on biotic interactions among predators with higher trophic levels in ancient marine ecosystems have not yet been sufficiently elucidated, although they may provide a reliable basis for a better understanding of MMR.

The Ammonoidea treated in this paper are the extinct cephalopod group with an external chambered shell that flourished in the oceans worldwide from the Devonian to the end of the Cretaceous. Direct evidence of predation on ammonoids is rarely preserved in the fossil record (Ritterbush et al. 2014), except for the case that remains of the predator and prey ammonoid are found in association (e.g., Vullo 2011). Previous researchers have been considered the predation on ammonoids on the basis of various evidence such as (i) analysis of shell and jaw remains preserved in the gut contents of marine reptiles (Brown 1904; Sato and Tanabe 1998) and ammonoids (Lehmann and Weitschat 1973; Riegraf et al. 1984; Jäger and Fraaye 1997), (ii) calcitic lower jaw plates (aptychi) and embryonic and early post-embryonic shells preserved as the coprolite remains of an unknown predator (Mehl 1978; Tanabe et al. 2008a; Keupp 2012), and (iii) predatory

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sublethal injuries on ammonoid shells (e.g., Landman and Waage 1986; Hengsbach 1996; Keupp 2000, 2006; Kröger 2000, 2002, 2011; Klug 2007; Klompmaker et al. 2009; Zatoń 2010; Slotta et al. 2011; Hoffmann and Keupp 2015). Additionally, aligned circular holes preserved on the lateral side of large shells of the Late Cretaceous ammonoids *Placenticeras* (Kauffman and Kesling 1960; Kauffman 1990; Tsujita and Westermann 2001) and *Sphenodiscus* (Odunze and Mapes 2013) were previously interpreted as mosasaur bite marks, but some of them have been reinterpreted as limpet home scars on the basis of *in situ* occurrence of limpet shells on the circular holes on *Placenticeras* and other Late Cretaceous ammonoid shells (Kase et al. 1994, 1995, 1998).

In this paper, we focus on the lethal damage represented by irregular-shaped breakage preserved on the ventrolateral side of the body chamber. Klompmaker et al. (2009) examined large museum ammonoid collections and reported that this type of shell breakage occurs frequently in various Mesozoic ammonoids, but is scarce in Palaeozoic ammonoids. Andrew et al. (2010) examined ammonoid collections recovered from the Lower Lias (Lower Jurassic) of Dorset, England, and reported that up to 20% of small ammonoids possessed such ventral "bite" marks. These previous studies on ammonoid predation were mostly based on materials from the Tethys Realm, while little investigation has been done on the Early Jurassic ammonoids from the Panthalassa, the largest ocean of that time (Fig. 1).

In this paper, we report on shell breakage on the ventrolateral side of the body chamber in large ammonoid samples recovered from the lower Toarcian sequence in the Toyora area, western Japan, deposited in the oxygen-depleted shelf basin in the northwestern Panthalassa. Subsequently, we discuss the nature of the breakage and the causative possibility of predation, by comparing various factors that can produce shell breakage in ammonoids. Furthermore, we compare the frequency of durophagous predation on the Early Jurassic ammonoids from the Panthalassa to those of the contemporaneous ammonoids of the Tethyan Ocean.

Institutional abbreviations.—UMUT, The University Museum, the University of Tokyo, Tokyo, Japan.

Other abbreviations.—AF, assemblage frequency; LTF, lower taxon frequency; SD, standard deviation.

Material and geological setting

Lower to Middle Jurassic (Lower Sinemurian to Bathonian) shallow marine siliciclastic deposits called the Toyora Group are exposed around the Tabe Basin in the Toyora area, southwest Japan (Fig. 2). This group represents shelf basin deposits in the northwestern Panthalassa Ocean during the above mentioned time interval (Fig. 1). The Toyora Group unconformably rests upon pre-Jurassic metamorphic rocks, and is lithostratigraphically divided into three formations

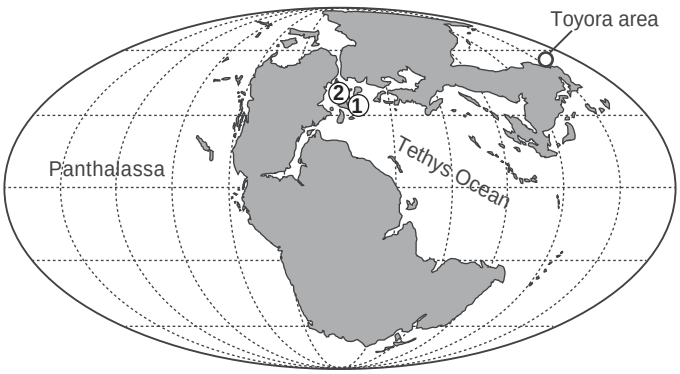


Fig. 1. Early Jurassic map illustrating the previously studied areas for ventrally damaged ammonoids. 1, Dotternhausen, Germany (Taverne 2000; Klompmaker et al. 2009); 2, Lyme Regis, England (Andrew et al. 2010). The Toyora area was located in the northwestern part of the Panthalassa. Palaeogeographical map after Scotese (2001).

showing the major sedimentary cycles, namely, the Higashinagano Formation of an initial transgressive phase, the Nishinakayama Formation of an inundative phase, and the Utano Formation of a regressive phase toward the top of the sequence (Hirano 1971). In the northern part of the Tabe Basin, the Nishinakayama Formation, approximately 300 m in maximum thickness, can be subdivided into three members: Na (silty shale, 90 m thick), Nb (dark grey silty shale and fine-laminated, bituminous black shale with intercalations of fine-grained sandstone, 160 m thick), and Nc (alternating sandstone and mudstone, 20–60 m thick) toward the top of the sequence (Fig. 2; Tanabe et al. 1982; Izumi et al. 2012). The Nishinakayama Formation in the area is rich in macrofossils such as ammonoids, belemnoids, bivalves, and crinoids throughout the lower and middle parts of the sequence (Hirano 1971, 1973a, b; Tanabe et al. 1982; Tanabe 1991). Hirano (1973b) recognised three ammonoid assemblage zones in the formation, namely, the *Fontanelliceras fontanellense*, *Protogrammoceras nipponicum*, and *Dactylioceras helianthoides* zones in ascending order, and correlated them to the late Pliensbachian (Domerian)–early Toarcian (Whitbian). The ammonite biostratigraphy of this formation was recently revised by Nakada and Matsuoka (2011), who recognised four chronostratigraphic zones, namely, the *Canavaria japonica*, *Paltarpites paltus*, *Dactylioceras helianthoides*, and *Harpoceras inouyei* zones toward the upper part of the sequence, which were correlated to the *Pleuroceras spinatum* Zone of late Pliensbachian to the lower part of *Hildoceras bifrons* Zone of early Toarcian in the European Tethyan section. More recently, Izumi et al. (2012) examined carbon isotope ratios of organic carbon, total organic carbon (TOC), and degree of bioturbation from the uppermost Pliensbachian to the lower Toarcian sequence in the Sakuraguchi-dani Valley section and recognised a carbon isotopic trend similar to those in contemporaneous strata in the Tethys and in the eastern and central Panthalassa regions, which are characterised by a distinct negative excursion around the *Dactylioceras tenuicostatum–Harpoceras falciferum* Zone boundary in the lower Toarcian. Based on the analyses of total organic carbon

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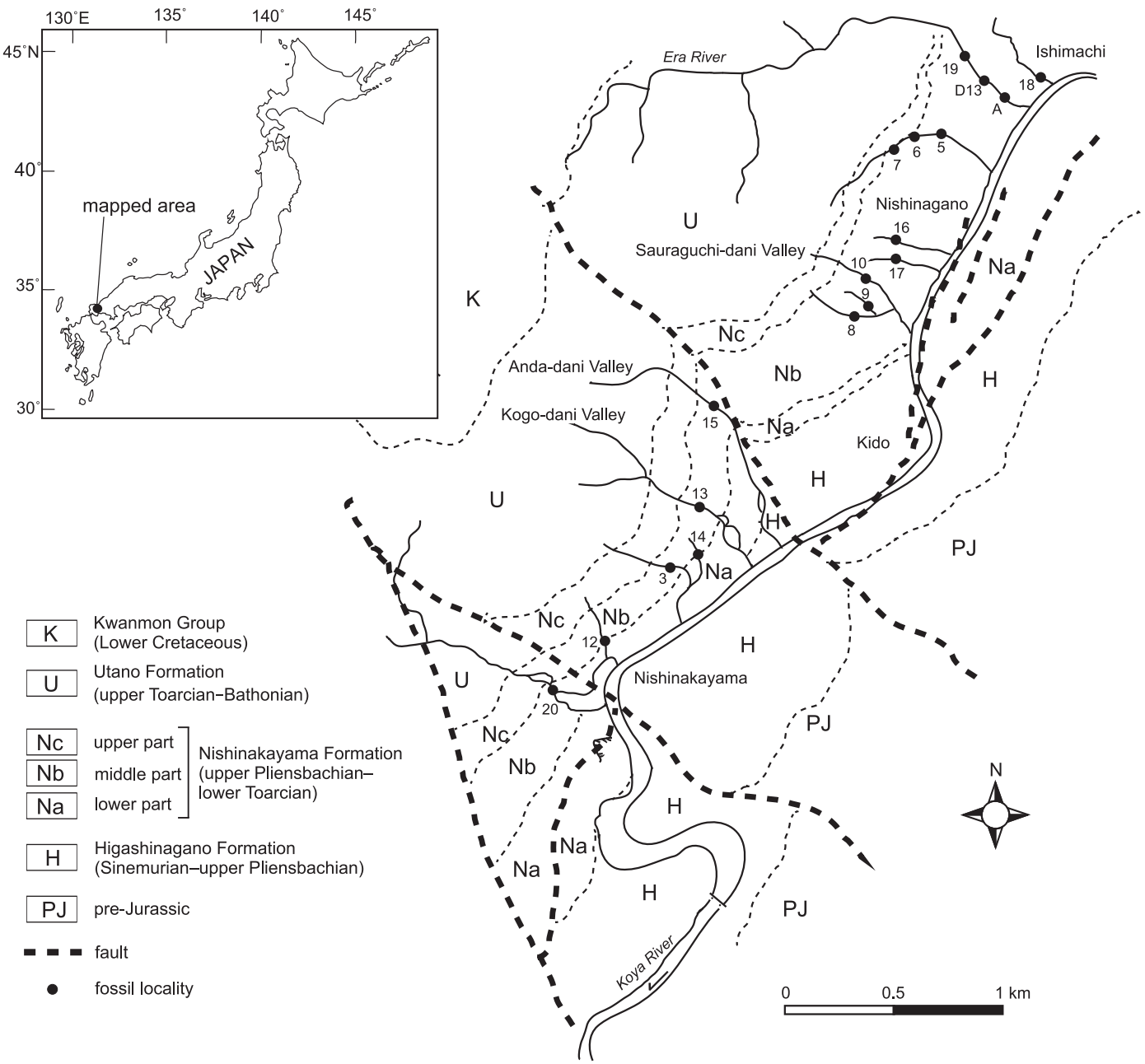


Fig. 2. Geological map of the Toyora area, southwest Japan (modified from Tanabe et al. 1982).

content and degree of bioturbation in the Sakuraguchi-dani Valley section, they further suggested that accumulation of organic carbon occurred, and anoxic bottom-water was prevalent in the northwestern Panthalassa shelf basin during the early Toarcian reflecting the global oceanic anoxic event. However, subsequent multiproxy geochemical analysis in this section by Kemp and Izumi (2014) demonstrated little evidence for the development of pervasive anoxia on the northwestern Panthalassa shelf, although high levels of terrestrial organic matter and intermittent well-laminated horizons support at least ephemeral deoxygenation and high organic carbon preservation potential.

This study is based on an examination of a total of 1305 ammonoid specimens belonging to 16 genera that were collected from 18 localities in the middle part (Nb member) of the Nishinakayama Formation (Fig. 2; Tanabe et al. 1982; Tanabe 1991). These localities are included in the *P. paltus* Zone to the uppermost part of the *H. inouyei* Zone of early Toarcian age (Nakada and Matsuoka 2011). The ammonoid specimens examined were collected from shale slabs at each locality from a unit horizon of about 1 to 2 m thick. The slabs were cut parallel to the laminae and/or bedding plane, and every fossil distinguishable by the naked eye was collected. The ammonoid specimens examined were mostly horizontally embedded in the fine-laminated black to greyish black silty shales, showing two types of preservation; (i) "half" ammonoids without an upper flank of the body chamber, and (ii) complete ammonoids with both lower and upper

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flanks of the shells (Tanabe et al. 1984). Although they have suffered from lateral deformation (less than 40% for the diagenetic decrease of body whorl breadth) during sediment compaction, a shell aperture is preserved in many specimens, some of which retain their jaw apparatus in situ within the body chamber. These modes of occurrence and preservation strongly suggest that the ammonoids from the Nishinakayama Formation have not suffered post-mortem shell breakage, and accordingly are suitable for analysis of shell breakage by biological processes.

Analytical methods

In this paper we followed the methods used in previous studies of ventral shell breakage of ammonoids (Klompmaker et al. 2009; Andrew et al. 2010). Because species level identification is difficult for some juvenile specimens, we have determined the ammonoid specimens at the genus level, as was done on other ammonoid samples by previous researchers. Two indices, Assemblage Frequency (AF) and Lower Taxon Frequency (LTF), formulated by Kowalewski (2002), were calculated to quantify the breakage frequency for the specimens of individual genera. AF is a measure of the overall frequency of breakage in an ammonoid assemblage, and is computed as follows: $AF = \Sigma Di/\Sigma Ni$, where Di is the number of specimens of i-th species with predation traces and Ni is the total number of specimens of i-th species in the sample. LTF aims to estimate the frequency of breakage for a specific ammonoid genus, and is calculated as follows: LTF = DK/NK, where K is a target genus in the analysis, DK is the number of specimens of that genus that contain at least one successful predation trace, and NK is the total number of specimens of that genus in the sample.

To detect the tendency of occurrence of breakage among ammonoid taxa, the Strauss Index was used. This index is obtained by subtracting the percentage of specimens with damage relative to all specimens with damage found in the assemblage, from the percentage of the taxon in the assemblage (Kowalewski 2002; Alexander and Dietl 2003). Positive values indicate that the taxa were preyed on selectively, whereas negative values indicate that the taxa survived predation.

All the specimens with a near-complete aperture were measured for their shell diameter to investigate the body size dependence of breakage. The specimens with shell breakage were photographed, and their digital images were analysed using the freeware ImageJ. The measurement of breakage follows previous studies (Klompmaker et al. 2009; Andrew et al. 2010). Three straight lines from the centre of the shell coiling are used (Fig. 3): A, a line to the shell aperture; B, a line to the apertural margin of the breakage; and C, a line to the adapical margin of the breakage. Line A was used only if the aperture was intact and measurable. Then, the angular distances between A and B (angle where breakage begins towards the aperture), A and C (angle where breakage ends towards the aperture), and B and C (extent of breakage), and the body chamber length (angular distance between A and the last septum) were measured. The length, depth, and area of the breakage were also measured (Fig. 3).

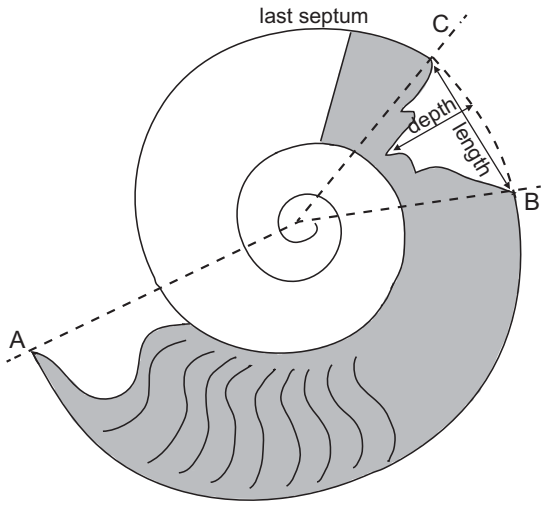


Fig. 3. Measurements for analysing the ventral breakage of ammonoid shells. Lines A, B, and C are the reference lines: A, from the coiling centre to aperture; B, apertural marginal line of damage; C, adapical marginal line of damage. Shaded area indicates body chamber. The length and depth of the breakage were also measured.

The body chamber length should be measured to determine the relative position of breakage in the body chamber (or phragmocone). Since, in many of the examined ammonoid specimens, the aragonitic shell wall has been dissolved away during early diagenesis (Tanabe et al. 1982), and the phragmocone-body chamber boundary has been altered, the body chamber angle of a shell could not be measured in many specimens. Therefore, we estimated the body chamber angle of individual specimens on the basis of the negative relationship between the whorl expansion rate and the body chamber angle, as demonstrated by Saunders and Shapiro (1986) and Klug and Korn (2004) for Palaeozoic ammonoids and by Okamoto (1996) for Mesozoic ammonoids. The body chamber angle of ammonoids would be constrained by the whorl expansion rate of the shells, because the volume ratio of the phragmocone and body chamber must be constant to maintain the neutral buoyancy of a living ammonoid (Trueman 1941). Finally, the position of breakage in the shell in relation to the living posture of the ammonoid shell was determined. The orientation of the aperture of a living and/or fossil planispirally coiled cephalopod might be constrained by the body chamber length (Trueman 1941; Jacobs and Chamberlain 1996). We determined the life orientation of an ammonoid based on the relationship between the length of the body chamber and the orientation of the shell, as estimated by Westermann (1996).

Results

Frequency and taxon-selectivity of ventral shell breakages.—Among the total of 1305 specimens examined, apparent ventral shell breakage was recognised in only 35 specimens

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that belong to the Dactylioceratidae (*Dactylioceras*) and Hildoceratidae (*Cleviceras*, *Fuciniceras*, *Fontanelliceras*, *Harpoceras*, *Paltarpites*, and *Protogrammoceras*) (Table 1; see Figs. 4 and 5 for representative examples). The AF of ventrally broken ammonoids is 2.7% with 95% binomial confidence interval ranging from 1.9% to 3.7%. Even excluding specimens whose apertural margin was partly lost during the extraction of the fossil-bearing slabs from the outcrop, the AF is 6.1%, still less than 10%. At the genus level, shell breakage is more frequent in hildoceratids than in dactylioceratids. *Cleviceras* is one of the common hildoceratid genera in the Nishinakayama Formation and 12 of the 286 *Cleviceras* specimens display shell breakage on the ventral side of the body chamber, whose LTF is 4.2%; the ratio is the largest among the specimens of four genera (*Dactylioceras*, *Cleviceras*, *Harpoceras*, and *Protogrammoceras*), whose sample sizes are larger than 200. On the other hand, only 3 of the 228 specimens of *Dactylioceras* suffered ventral breakage, showing a low LTF (1.3%). Ventral breakage was not observed in any lytoceratid and phylloceratid ammonoids recovered from the Nishinakayama Formation.

The Strauss Index (Table 1) is the highest for *Cleviceras* (0.124). *Fontanelliceras* and *Paltarpites* also possess positive values (0.025 and 0.050, respectively), although the numbers of the specimens examined are small. *Harpoceras* and *Fuciniceras* show values close to zero. On the other hand, specimens of *Dactylioceras* and *Protogrammoceras* both have negative values, -0.089 and -0.067, respectively.

Description of ventral shell breakage.—The ventral shell breakage observed in the 35 ammonoid specimens is characterised by irregular shapes (Figs. 4, 5). In nine individuals, both cast and mould were preserved (Fig. 5). The ventral shell breakage usually extends from the ventral to the flank portion. The length of breakage is longer than the depth of breakage. No traces of repair of the breakage were observed.

The position of ventral breakage relative to the aperture in a total of 24 specimens of 7 genera is shown in Fig. 6. The positions of the beginning and end of breakage are at an angle of 84–246° (mean 146°) and 134–318° (mean 200°) towards the aperture, respectively. Considering the length of the body chamber of a living ammonoid based on the whorl expansion rate, ventral breakage occurs intensively in the posterior portion of the body chamber (Fig. 6). The position of the midpoint of the breakage varies between 109° and 282° with a mean value of 173°, which is located on the opposite side of the aperture (Table 2). The angular range of the breakage varies between 18° and 77° (mean 52°).

Shell size of ammonoids.—In the ammonoid specimens examined, the shell diameters of 575 specimens were measured. The shell diameters of the measured ammonoid specimens are 6–130 mm (mean 23.9 mm). The size frequency histogram shows an apparent right-skewed distribution (Fig. 7). The ammonoids with ventrolateral shell breakage have a shell diameter range of 11–54 mm (mean 23.4 mm; Table 2), with a right skew. There is no significant difference between the size distributions of ammonoids with and without ventrolateral breakage ($p = 0.4094$, Kolmogorov-Smirnov test) of the populations inferred from our samples. A positive relation is observed between the length and depth of the ventrolateral shell breakage and shell diameter (Fig. 8).

Table 1. List of early Toarcian ammonoid genera collected from the Nishinakayama Formation and breakage frequencies for the specimens of individual genera and total assemblage (AF). Nd, number of ventrally damaged specimens; Nt, number of total specimens; CI, confidence interval. Breakage frequency and Strauss Index for genera represented by more than 20 specimens are shown in bold.

Ammonoid genera	Nd (Nt)	Breakage frequency	95% CI	Strauss Index
Coeloceratidae				
Coeloceras	0 (1)	0.0%		-0.001
Dactylioceratidae				
Dactylioceras	**3 (228)**	**1.3%**	**(0.3–3.8)**	**-0.089**
Peronoceras	0 (1)	0.0%		-0.001
Hildoceratidae				
Arieticeras	0 (1)	0.0%		-0.001
Cleviceras	**12 (286)**	**4.2%**	**(2.2–7.2)**	**0.124**
Fontanelliceras	1 (5)	20.0%	(0.5–71.6)	0,025
Fuciniceras	**3 (98)**	**3.1%**	**(0.6–8.7)**	**0.011**
Lioceratoides	0 (14)	0.0%		-0.011
Harpoceras	**10 (374)**	**2.7%**	**(1.3–4.9)**	**-0.001**
Hildoceras	0 (14)	0.0%		-0.011
Paltarpites	2 (9)	22.2%	(2.8–60.0)	0.050
Protogrammoceras	**4 (237)**	**1.7%**	**(0.5–4.3)**	**-0.067**
Lytoceratidae				
Lytoceras	**0 (24)**	**0.0%**		**-0.018**
Phylloceratidae				
Calliphylloceras	0 (10)	0.0%		-0.008
Holcophylloceras	0 (1)	0.0%		-0.001
Phylloceras	0 (2)	0.0%		-0.002
Total (AF)	35 (1305)	2.7%	(1.9–3.7)	

Table 2. Characteristics of ventral breakage of the early Toarcian ammonoid specimens from the Nishinakayama Formation; SD, standard deviation.

	Shell diameter (mm)	Midpoint of breakage towards aperture (degree)	Breakage extent (degree)	Breakage length (mm)	Breakage depth (mm)
Mean	23.4	172.9	51.6	7.1	3.3
SD	11.6	34.9	16.0	3.8	1.7
Min.	11	109	18	2.4	1.2
Max.	54	282	77	19.6	7.5

Discussion

Biological nature of breakage.—The shell breakage observed in the ammonoids from the Lower Jurassic Nishinakayama Formation has been shown in previous papers (e.g., Hirano 1971: pl. 16: 3a, pl. 17: 9; Hirano 1973a: pl. 4: 2; Hirano 1973b: pl. 9: 6), however, it has not been described in detail. Our study reveals that the breakage is characterised

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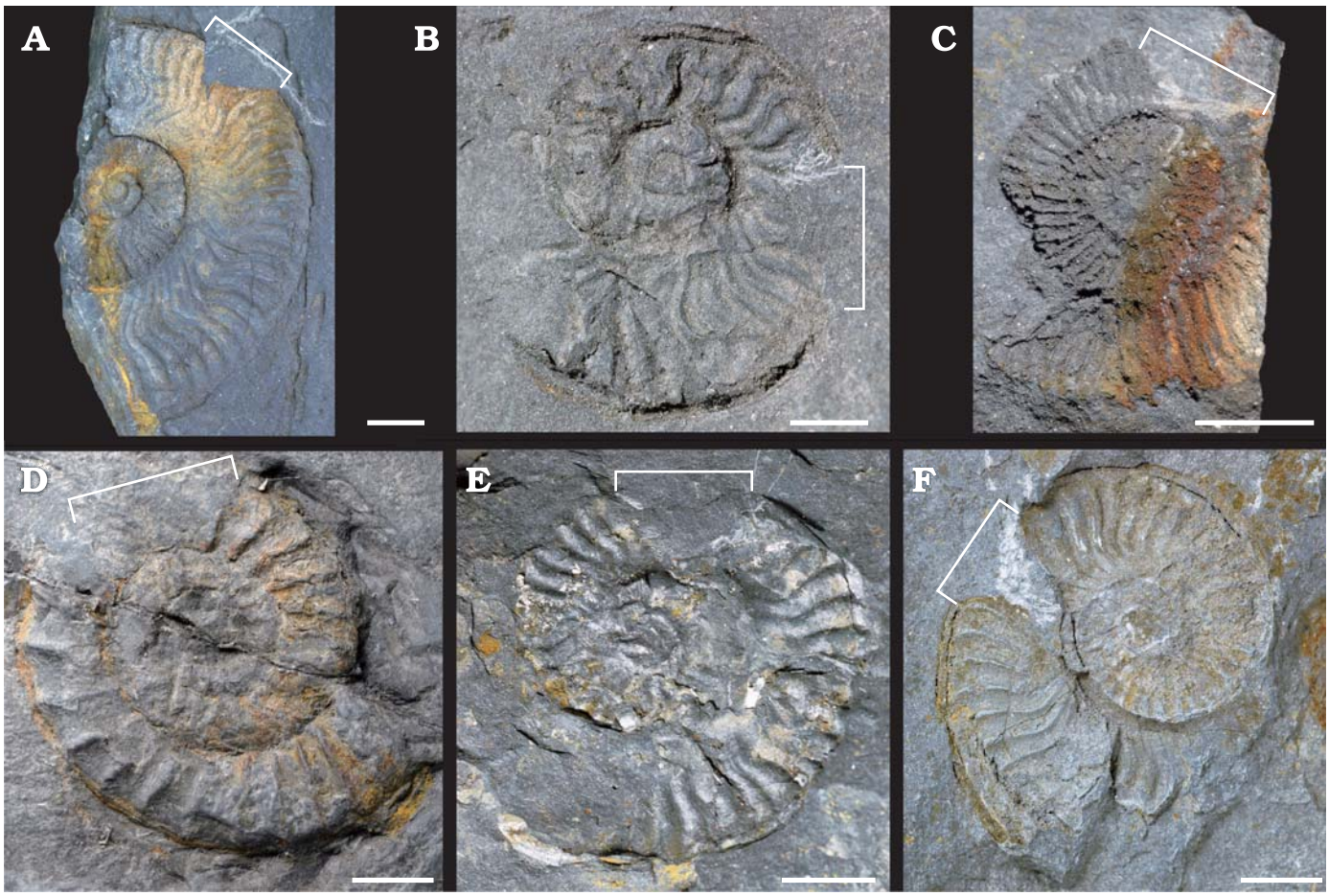


Fig. 4. Examples of early Toarcian ammonoids with ventral breakage, from the Toyora area, Japan (for detailed locality information see Fig. 2). **A**. *Cleviceras chrysanthemum* (Yokoyama, 1904), UMUT MM 31431, loc. 8. **B**. *Cleviceras* sp., UMUT MM 31432, loc. 5. **C**. *Dactylioceras helianthoides* (Yokoyama, 1904), UMUT MM 31433, loc. 10. **D**. *Fontanelliceras fontanellense* (Gemmellaro, 1885), UMUT MM 31434, loc. 10. **E**. *Fuciniceras nakayamense* (Matsumoto, 1947), UMUT MM 31435, loc. 3. **F**. *Protogrammoceras onoi* Hirano, 1971, UMUT MM 31436, loc. 10. The white brackets indicate the position and extent of the breakage. Scale bars 5 mm.

by a fixed position on the ammonoid shell, occurring on the ventrolateral side in the posterior part of the body chamber (Figs. 4–6).

Several patterns of shell breakage on planispiral ammonoid and modern *Nautilus* shells and their origins have been discussed based on field observations and laboratory experiments (e.g., Hamada 1965; Wani 2001, 2004; Mapes et al. 2010a, b). One of the most considerable processes that damage their shells is mechanical destruction during post-mortem drift. Such a process would cause breakage from the apertural margin, and leave behind the phragmocone and part of the body chamber of the ammonoids (Maeda and Seilacher 1996), as revealed by observation of breakage patterns of post-mortem drifted and beached *Nautilus* shells (Hamada 1965; Mapes et al. 2010a, b).

Another plausible form of physical destruction might occur during post-mortem transport after settling on the seafloor and perturbing of sunken shells by storm or turbidity currents. Based on the observation of geopetal structures and sediment infill within the camerae, Wani (2001) discussed the destruction pattern of ammonoid shells caused by reworking. Although we could not confirm whether or not geopetal structures were present in the examined specimens owing to their insufficient preservation, it is apparent that the destruction pattern we observe differs from that made by reworking. Moreover, there is no evidence of storms or turbidity currents in ammonoid-bearing lower Toarcian black shale based on the observation of sedimentary structures (Tanabe et al. 1982; Izumi et al. 2012). The middle part of the Nishinakayama Formation (Nb member) from which the examined ammonoid samples were collected is composed mainly of fine-laminated, bituminous black shale that might have been deposited under a low-energy bottom environment reflecting the early Toarcian global oceanic anoxic event (Izumi et al. 2012). These lines of evidence strongly suggest that the ventral shell breakage observed in our material did not occur during post-mortem transport. The fragmentation pattern of modern *Nautilus* shells initially buried in the sediment by post-mortem transport has been also examined experimentally (Wani 2004). The experiment with sediment fill in the body chamber revealed that the ventral parts of phragmocones of all the experimental shells

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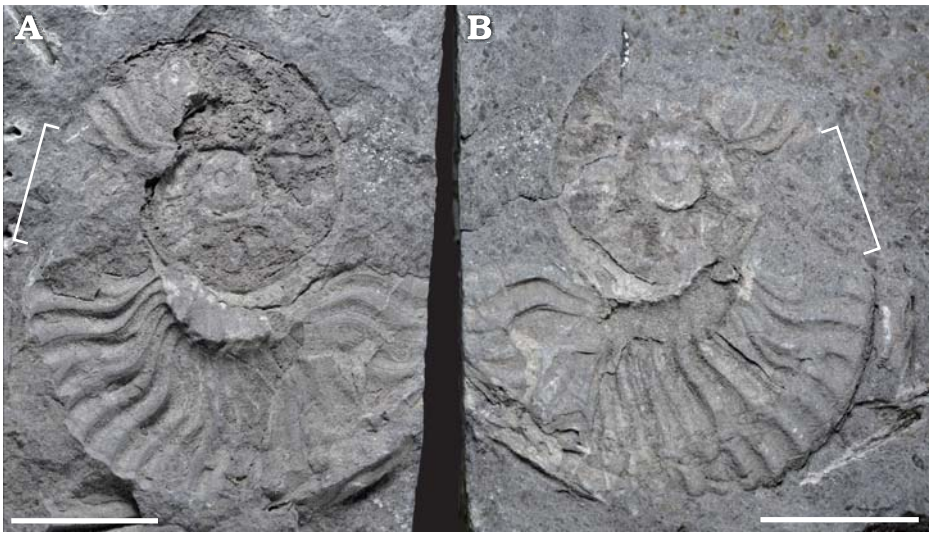


Fig. 5. Example of ventral breakage in the early Toarcian ammonoid from the Toyora area, preserved in the cast (**A**) and mould (**B**) of *Protogrammoceras onoi* Hirano, 1971, UMUT MM 31437, loc. 18 (for detailed locality information see Fig. 2). The white brackets indicate the position and extent of the breakage. Scale bars 10 mm.

were fragmented, in association with the ventral breakage of the body chamber in some shells (see Wani 2004: fig. 3). This kind of breakage on the phragmocone was not observed in our specimens.

Experimental analysis of post-depositional destruction of empty *Nautilus* shells revealed a characteristic shell fragmentation pattern of a shell edge that was straight and parallel to the growth lines (Wani 2004: fig. 4a, b). Such fragmentation diagnosis does not occur in our specimens that have ventral shell breakage.

These lines of evidence show that the ventrolateral shell breakage observed in the examined ammonoid specimens were not produced by a non-biological process, but were inflicted by a predator's attack. Since there is no shell regeneration in the breakage area, we suggest that the attack was lethal. The shell breakage observed in our material is similar in shape and fixed position, on the ventrolateral side of the body chamber, to that observed in various Mesozoic ammonoids (e.g., Taverne 2000; Klompmaker et al. 2009; Andrew et al. 2010; Ifrim 2013; Wright et al. 2014). Klompmaker et al. (2009) and Andrew et al. (2010) interpreted this type of ammonoid shell breakage as ventral bite marks made by durophagous predators rather than mechanical shell breakage caused by biostratinomic processes. Ventral "bite" marks have been reported in various Jurassic ammonoids from the European Tethys region (e.g., Taverne 2000; Schweigert 1997; Schweigert and Dietl 1999; Klompmaker et al. 2009; Andrew et al. 2010; Wright et al. 2014). Klompmaker et al. (2009) suggested that other Jurassic collections would show similar bite patterns and our study confirms their suggestion. This report is the first documentation of ventrolateral predatory bite marks on ammonoids from the lower Toarcian shallow marine deposits in the northwestern Panthalassa.

Potential predators.—Ventrolateral breakage observed on the early Toarcian ammonoid shells examined is thought to be lethal bite marks from durophagous (shell-crushing) predators because we did not observe any traces of healing. Since the breakage characteristically occurs on the posterior portion of the body chamber, the predators may have had the ability to break a living ammonoid shell to withdraw the ammonoid soft body. Because of the lack of benthic fossils in the anoxic bottom environment, the ammonoids examined in this study are considered to be pelagic. Therefore, the predators could attack a living ammonoid shell in the water column. Several types of nektonic animals are considered to be predators that could have produced the ventral shell breakage in the ammonoids examined.

Crustaceans are known to be common durophagous predators through the Phanerozoic (e.g., Walker and Brett 2002; Schweitzer and Feldmann 2010). However, it is questionable whether they could manipulate ammonoid shells, and attack the exact posteroventral portion of the body chamber in midwater. Moreover, an attack by benthic crustaceans would produce punctured breakage on one side or within the lower ventral part of the ammonoid shells (Keupp 2006; Klompmaker et al. 2009). Peeling is one of the characteristic predatory activities of crustaceans, but it mostly occurs at the apertural edge of shells. Kröger (2000) observed healed injuries on the apertural part of some ammonoid shells and suggested that their origin were sublethal decapod predation. The characteristics of these injuries they observed are different from those in our material, thus crustaceans can be precluded as the producer of the ventral lethal bite marks observed in our material.

Modern teleosts and sharks occasionally attack *Nautilus* and *Allonautilus* (Saunders et al. 1987; Tanabe 1988). This evidence suggests that fish could have been one of the predators of ammonoids. Indeed, Vullo (2011) reported direct evidence of hybodont shark predation on a specimen of the Late Jurassic ammonoid *Orthaspidoceras* which preserves the shark's tooth and possible tooth puncture marks on the lateral portion of the shell. Fish scales are relatively common in the Early Jurassic Nishinakayama Formation (Tanabe 1991) and a specimen of osteichthyan (bony fish) Leptolepiformes indet. was reported from the formation by Yabumoto and Uyeno

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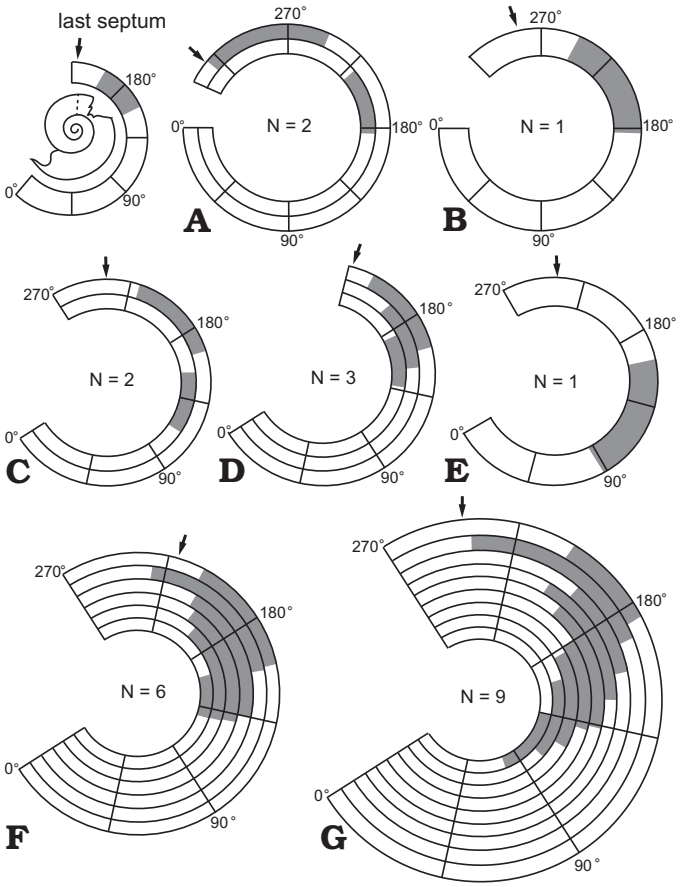


Fig. 6. Position of ventral breakage in the shells of seven early Toarcian ammonoid genera. Specimens whose position of the aperture is uncertain are excluded. Arrows indicate the average of the estimated position of last septum. The living orientation of the shells is based on Westermann (1996). **A**. *Dactylioceras*. **B**. *Fontanelliceras*. **C**. *Fuciniceras*. **D**. *Protogrammoceras*. **E**. *Paltarpites*. **F**. *Harpoceras*. **G**. *Cleviceras*.

(1992). Chondrichthyes had a worldwide distribution, including Japan, during the early Mesozoic (Schaeffer and Patterson 1984; Goto 1994), although their fossil representatives have not been found in the Nishinakayama Formation. Modern nautiluses attacked by large bony fish (grouper and triggerfish) exhibit a series of slashing bite marks on the shell aperture and soft parts, leaving chunks of broken shell (Saunders et al. 1987: figs. 6, 7). Predatory bite marks possibly made by jawed fishes have been reported in fossil cephalopods, represented by circular perforations on fragmented Pennsylvanian nautiloid shells (e.g., Mapes and Hansen 1984; Mapes et al. 1995; Mapes and Chaffin 2003) and semi-circular incisions on the aperture of the ammonoid *Kosmoceras* from the Callovian (Lower Jurassic) lower Oxford Clay Formation of England (Martill 1990) and on the phragmocones of the *Oxycerites* specimens from the Bajocian (Middle Jurassic) of southern Germany (Richter 2009). Irregularly shaped ventral bite marks observed in our early Toarcian ammonoid material are distinct from previously known fish bite marks by their overall shape and restricted occurrence in the rear part of the body chamber, suggesting that fish may be excluded as a possible producer of the bite marks.

Marine reptiles are also possible for the predators of ammonoids. A juvenile turtle fossil was collected from the Nishinakayama Formation (Hasegawa et al. 1998). Additionally, a marine crocodile assigned to the Atopsaulidae has been reported from the Nishinakayama Formation (Manabe and Hasegawa 1998), but other large reptiles such as plesiosaurs and ichthyosaurs, which occur abundantly in the lower Toarcian shales in the Tethys Realm (e.g., Hauff 1953), are unknown from the Nishinakayama Formation. We, however, regard that the lack of marine reptiles from the Nishinakayama Formation might be a bias resulting from the narrow outcropping area.

Ward and Hollingworth (1990) reported an uncrushed specimen of *Kosmoceras* possessing a number of circular and elliptical punctures on the phragmocone and body chamber from the Callovian (Middle Jurassic) middle Oxford Clay Formation of England, and interpreted them as bite marks by an unknown marine reptile. Ammonoid conch and jaw remains have been reported in the stomach contents of Cretaceous plesiosaurs and mosasaurs (Brown 1904; Sato and Tanabe 1998; Konishi et al. 2014), but such direct evidence of predation on ammonoids have not been found in Jurassic marine reptiles (Cicimurri and Everhart 1991). It is noteworthy that the cephalopod arm hooklets preserved in the gut contents of Jurassic ichthyosaurs, plesiosaurs, and pliosaurs have been attributed to belemnoids, and not to ammonoids (e.g., Tarlo 1959; Pollard 1968; Martill 1992; Taylor 1993).

Cephalopods, especially teuthoid coleoids, have been regarded as the most plausible predators to produce ventral bite marks on ammonoid shells (Kröger 2002; Klug 2007; Klompmaker et al. 2009; Andrew et al. 2010). Klompmaker et al. (2009) suggest that teuthoid coleoids would have the ability to grab ammonoids and aim for a specific part of their shells by means of tentacles, in view of the fixed position of the predatory breakage. Their hypothesis is plausible, but no reliable fossil record of teuthoid coleoids is known from the Jurassic, because most "teuthid" fossils reported from the Konservat-Lagerstätten of Jurassic and Cretaceous ages are eight-armed and are reinterpreted as Vampyropoda (Fuchs 2006; Kröger et al. 2012). Vampyropod and belemnoid coleoids possessed a jaw apparatus that was entirely made of a chitinous material, without a calcified tip (Tanabe et al. 2006, 2008b; Klug et al. 2010; Tanabe 2012). Rostral remains of belemnoids have been found in the Nishinakayama Formation (Tanabe 1991); accordingly, the ventral bite marks observed in our ammonoid material could be attributed to Belemnitida.

Ammonoids are another plausible candidate as producers of the lethal ventral bite marks observed in the Early Jurassic ammonoid material examined. This interpretation is supported by the indirect evidence that fragmented calcified lower jaws (aptychi) and chitinous upper jaws of small ammonoids were found in the stomach/crop remains of Jurassic ammonoids such as *Hildoceras*, *Oppelia*, and *Physodoceras* (Lehmann and Weitschat 1973; Riegraf et al. 1984; Jäger

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and Fraaye 1997; Keupp 2000, 2012; Ritterbush et al. 2014). Similarly to modern cephalopods, ammonoids are known to have possessed a jaw apparatus as a primary feeding organ. Five jaw morphotypes have been described in the Mesozoic Ammonoidea: normal, anaptychus, aptychus, intermediate and rhynchaptychus types (e.g., Tanabe et al. 2015). Among them, the rhynchaptychus-type jaw apparatuses are known from the Jurassic and Cretaceous Phylloceratina and Lytoceratina, and are characterised by the development of a thick and sharply pointed calcified tip on both the upper and lower jaws, whose morphology resembles the jaws of modern and fossil nautilids (Lehmann et al. 1980; Tanabe et al. 2013). Based on these characteristics, rhynchaptychus-type jaw apparatuses were interpreted to have been developed in the Phylloceratina and Lytoceratina for biting and cutting up prey, as an adaptation for the predatory scavenging modes of feeding, as in the jaws of modern nautilids (Tanabe et al. 1980, 2013). Since modern nautilus makes bite marks characterised by V-shaped serrated cutting edges near the apertural ventral shell margin of other nautiluses (Haven 1972; Tanabe et al. 1988), both lytoceratid and phylloceratid ammonoids could produce roughly V-shaped bite marks by means of calcified rostral tips of the jaws on the ventrolateral side of other ammonoids. It is noteworthy that none of the lytoceratid and phylloceratid specimens in our material possesses ventral bite marks, inferring that they were predators of other ammonoids rather than prey. Meanwhile, the jaw apparatuses of the dactylioceratids are of the anaptychus-type, consisting wholly of a chitinous material, while those of the hildoceratids are of the aptychus-type, characterised by the development of a thin bivalved calcitic plate on the outer surface of the chitinous lower jaw (Lehmann 1976; Tanabe and Fukuda 1999; Parent et al. 2014). The upper and lower jaws of both families lack a sharply pointed calcified tip (Tanabe and Fukuda 1999). These jaw features can be interpreted as having been adapted for microphagous mode of feeding (Parent et al. 2014), but not for durophagous feeding habits (Tanabe et al. 2015). Following this interpretation, jaw remains of ammonoids found by Lehmann and Weitschat (1973) and Riegraf et al. (1984) in the oesophagus/crop remains of hildoceratid ammonoids were presumably undigested food remains eaten by these ammonoids without durophagous predation. Besides the ammonoids with rhynchaptychus-type jaw apparatus, nautilids with a calcified rostral tip in their jaw apparatus could be durophagous predators on Jurassic and Cretaceous ammonoids. Indeed, their fossils co-occur with ammonoids with ventral shell breakage in the Lower Jurassic strata of the Tethyan regions (e.g., Riegraf et al. 1984), but have not been discovered in the Nishinakayama Formation.

To summarize the discussion above, lytoceratid and phylloceratid ammonoids are considered to be the most probable predators to produce the lethal ventral bite marks on the ammonoids in the Nishinakayama Formation, but some ventral bite marks might also have been produced by nautilid and coleoid cephalopods, jawed fishes and marine reptiles.

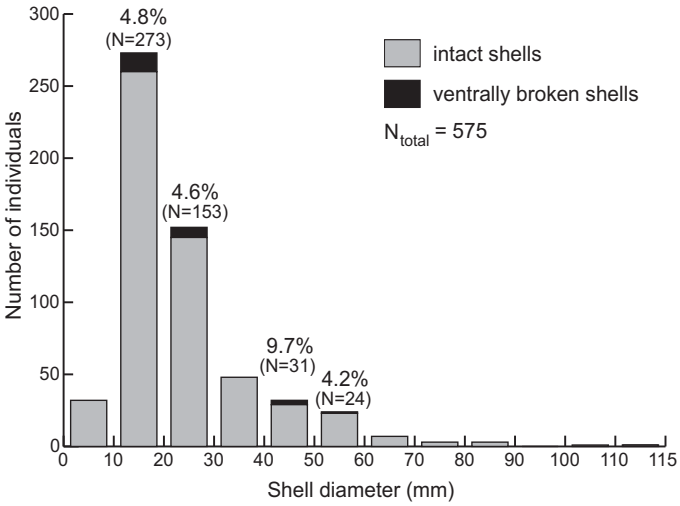


Fig. 7. Size distribution of ventrally intact and damaged early Toarcian ammonoid specimens from the Toyora area. Percentage represents the breakage frequency in each size class.

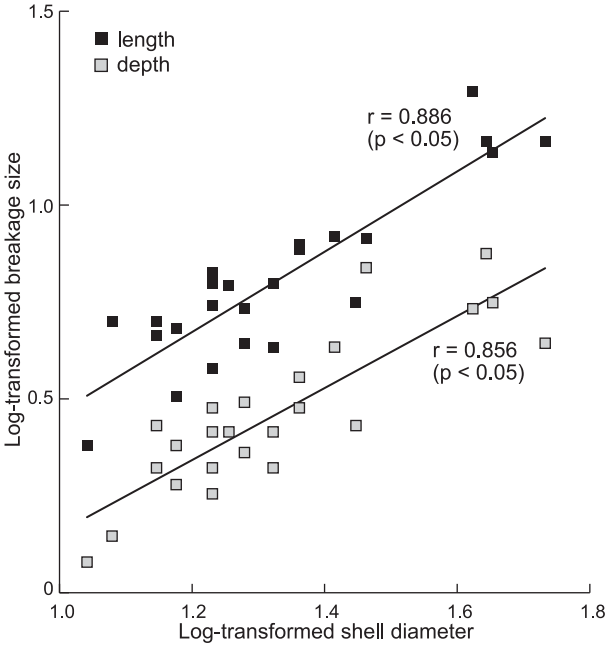


Fig. 8. Double logarithmic plots of breakage length and depth versus shell diameter. Regression lines with reduced major axis method. All seven genera were included.

Characteristics of predatory behaviour.—The orientation of the aperture of a planispirally coiled cephalopod shell when alive is mostly constrained by the body chamber length (Trueman 1941; Jacobs and Chamberlain 1996; Okamoto 1996). Since the ammonoids from the Nishinakayama Formation mostly belong to brevidome or mesodome groups based on the body chamber length (Westermann 1996), when their living posture is reconstructed, the ventral breakage in the specimens examined is mostly placed on the upper opposite side towards the aperture (Fig. 6). This means that the ammonoids were attacked from the opposite side of the aperture, as in the case of ammonoids reported by previous researchers (Taverne 2000; Klompmaker et al. 2009; Andrew

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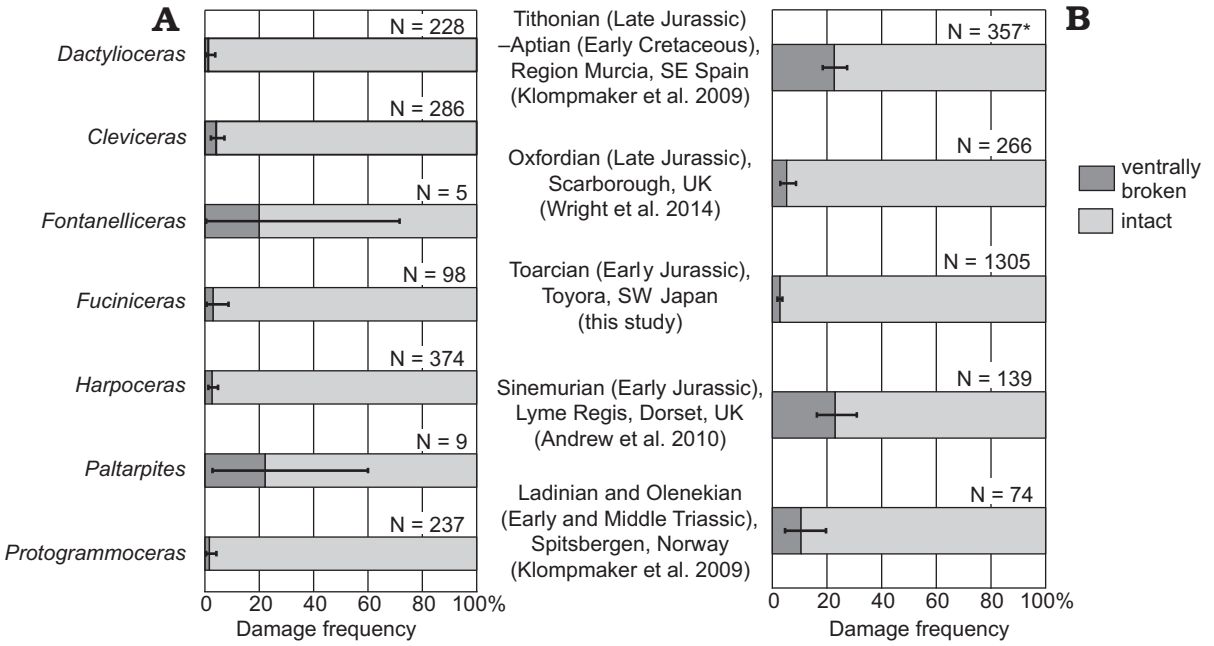


Fig. 9. Frequency of occurrence of lethal ventral damage on ammonoid shells. Error bars represent 95% binomial confidence intervals. **A**. Lower Taxon Frequency for the specimens of 7 genera from the Toyora area (see also Table 1). **B**. Assemblage Frequency for the selected Mesozoic ammonoid samples from different ages and/or regions. * The number is based on near-complete shells.

et al. 2010). For predators, there are several advantages to attacking from this direction. Not only would it be a surprise attack, but it would also be a way for the predator to avoid the prey's jaw apparatus. These anatomical features suggest that attacking a living ammonoid from the frontal side would not be effective for predators, compared to attacking from the posterior side. Observations of muscle and body attachment scars on ammonoid shells indicate the existence of organs in the posteroventral portion of the body chamber (e.g., Jones 1961; Jordan 1968; Doguzhaeva and Mutvei 1991, 1996; Landman et al. 1999). By damaging these areas, the predators could easily and effectively withdraw the ammonoid's soft parts from the body chamber.

Our analysis also revealed taxon-selective predation on ammonoids in the Early Jurassic northwestern Panthalassa shelf basin. Despite the relatively abundant occurrence of the dactylioceratid *Dactylioceras* and the hildoceratid *Protogrammoceras*, their LTFs are low, less than 2% (Table 1, Fig. 9), suggesting that they could avoid predatory attacks from the ventral side of their shells. The Strauss Index values of these two genera are negative among the seven genera with ventral bite marks. In addition, Taverne (2000) analysed ammonoids from the lower Toarcian *Posidonia* Shale in southern Germany, and obtained the similar result that the LTF of *Dactylioceras* was lower than those of the hildoceratid genera *Harpoceras* and *Hildoceras*, both with a flattened, moderately involute shell with a sharp ventral keel. These results indicate that *Dactylioceras* may have had some anti-predatory traits, for example, the unique shell structure, with double shells and flat-topped ribs on the inner shell (Howarth 1975). Kröger (2002) also suggested that the longidome body chamber (at around 365° in spiral length) of *Dactylioceras* might prevent efficient predation, because the muscle attachment portion near the base of the long body chamber was mostly covered by the outer body chamber; accordingly, predators could not attack the muscle attachment portion from the outside the shell. Interestingly, *Dactylioceras* was more commonly attacked by crustaceans than other ammonoid genera (Keupp 2006) and infested by parasites at other sites (Keupp 2012; De Baets et al. 2015), suggesting that differences in mode of life might also play a role on taxon-selective predation.

The ammonoid specimens examined in this study are relatively small (mean of 24 mm). However, in most of the examined specimens larger than 20 mm in shell diameter, the rostrum is preserved in the apertural margin, and the ribs tend to be closely spaced toward the aperture, indicating that they are mature shells. Size selectivity on predation is not obvious in our ammonoid samples from the Nishinakayama Formation. Generally, size-selective predation based on optimal foraging theory is observed in marine ecosystems (e.g., Harper et al. 2009; Kröger 2011). The bigger the prey, the more likely they are to be preyed on, because they are a better nutrient source for predators. On the other hand, bigger preys have a better defensive capability against predators (Hone and Benton 2005). As a result, considering these costs and benefits, once the prey has reached a certain functional size, the predation frequency would be very low. However, there is no statistical difference in the size frequency distribution between the intact ammonoids and bitten ammonoids (Fig. 7), which may be explained by the existence of predators of various body sizes.

There is a positive linear relationship between the breakage size and the shell diameter (≈ body size) of prey ammonoids in our material, indicating that larger ammonoids

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preserve larger predatory breakage (Fig. 8). Assuming that the size of predatory breakage is related to the body size of the predator (Klompmaker et al. 2009), it is suggested that the larger ammonoids were attacked by larger predators. A similar trend has been reported in ammonoids from the lower Toarcian *Posidonia* Shale (Klompmaker et al. 2009), suggesting that such predatory activity on ammonoids might occur globally in the Early Jurassic shallow marine setting.

Comparison of predation frequency with other localities and ages.—Our observation reveals that the frequency of predatory ventral bite marks on the early Toarcian ammonoids from the Nishinakayama Formation is very low (2.7% of AF). Klompmaker et al. (2009) calculated the LTF or AF of the ventrally damaged ammonoids in several unselectively collected large Mesozoic samples. They also documented that in the ammonoid shells collected from the lower Toarcian *Posidonia* Shale in southern Germany the frequency of ventral breakage was estimated to be up to 50%. Taverne (2000) also analysed the LTF of ammonoid genera from the *Posidonia* Shale, and reported LTF values of 27–43%. Andrew et al. (2010) estimated that up to 20% of ammonoids showed ventral damage in the Sinemurian ammonoid assemblage from the lower Lias of Dorset, England. Our study indicates that the predation frequency in the early Toarcian ammonoids from the northwestern Panthalassa shelf basin appears to be much lower than those of contemporaneous ammonoids from the Tethys shelf regions (Fig. 9). Moreover, the frequencies obviously vary between the *Posidonia* Shale (Taverne 2000; Klompmaker et al. 2009) and the Nishinakayama Formation, although both deposits consist mostly of bituminous black shale in which the early Toarcian oceanic anoxic event is recorded. There are some possibilities for this difference of predation frequency between the Early Jurassic Tethys and the Panthalassa shelf basins. Spatial and environmental variation (e.g., Hoffmeister and Kowalewski 2001) might be taken into consideration for such difference of predation frequency. For example, some environmental factors such as salinity or temperature may have played a role in the observed difference, but their effects on predator-prey relationship between animals in the water column are still unknown. Rather, the faunal difference between the Tethys and the northwestern Panthalassa (e.g., Page 1996, 2008; Westermann 2000) seems to be a more important factor. Lytoceratid and phylloceratid ammonoids, both of which are the plausible predators for the ventrally damaged ammonoids, were more abundant in the Early Jurassic low latitude Tethyan regions than in the Panthalassa (Page 2008). Jawed fishes, coleoid and nautilid cephalopods, and marine reptiles are also possible predators of ammonoids, although their fossils are scarce in the Nishinakayama Formation (Yabumoto and Uyeno 1992; Manabe and Hasegawa 1998; Hasegawa et al. 1998). The control of bioprovince on the abundance of such predators appears to have influenced the durophagous predation frequency on contemporaneous ammonoid faunas.

Conclusions

The lower Toarcian strata in the Toyora area, west Japan, yield abundant ammonoid fossils, some of which preserve a ventral shell breakage on the rear part of the body chamber. Since the traits of the breakage are different from those produced by physical taphonomic processes, and the ammonoid-bearing strata consist mostly of well-laminated, bituminous black shale deposited under anaerobic to oxygen-depleted, low energy bottom conditions, their origin is thought to be lethal predatory marks.

Based on the position of the breakage, the ammonoids were attacked from a specific aspect, the opposite side of the aperture. This would be an effective method of attack for predators not only in terms of safety, but also for detaching the soft parts of the prey ammonoids. It is suggested that the predators were able to capture the moving ammonoids shells. Considering the co-occurrence of the "bitten" ammonoids and the development of a sharp and thick calcified tip on the jaws, lytoceratid and phylloceratid ammonoids are suggested to be the most probable predators to have produced the lethal ventral bite marks on the ammonoids in the Nishinakayama Formation. However, some of the "bite" marks might also have been made by jawed fishes, coleoid and nautilid cephalopods, and marine reptiles.

This study also demonstrates that the frequency of predatory "bite" marks could have been much lower in the northwestern Panthalassa than in the Tethys region in the Early Jurassic. This fact suggests that the predatory activity on ammonoids by attacking from behind the aperture differs between the two bioprovinces.

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