

# Dimorphism in tetragonitid ammonoid *Tetragonites minimus* from the Upper Cretaceous in Hokkaido, Northern Japan

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Mature modifications, ontogeny, and dimorphism of the small-sized tetragonitid ammonoid *Tetragonites minimus* were investigated in 43 specimens from the Santonian, Upper Cretaceous of the northwestern area of Hokkaido, Japan. Four types of mature modifications were recognised in the shell diameters of 11–13 mm and 16–19 mm, and two differently sized adults were regarded as microconchs and macroconchs respectively. The conch forms of dimorphic pairs were similar in juvenile but differ in the later stage. The supplementary analysis showed that the remarkable adult size differences in antidimorphs continued at least in the Turonian–Santonian. The mature size and size difference between dimorphic pairs decreased chronologically. 36 specimens (84% of examined specimens) were mature, and immature shells were rare in the Santonian. Most of the shells were remarkably well preserved, indicating that *T. minimus* assemblage fossilised quickly near their original habitat without long-distance post-mortem transport. Hence the bias in the fossil occurrence of adult *T. minimus* is unlikely to be due to taphonomy such as the bias of fossilisation potential and floatability in the bottom currents. *Tetragonites minimus* might have been changing their habitats during their life cycle.

Key words: Ammonoidea, *Tetragonites*, dimorphism, taphonomy, Late Cretaceous, Yezo Group, Hokkaido.

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## Introduction

The genus *Tetragonites* Kossmat, 1895, belongs to the family Tetragonitidae, superfamily Lytceratoidea (Hoffman 2015). This genus is characterized by involute sub-rectangular whorl section and smooth shell surface (Murphy 1967a, b; Wiedmann 1973; Shigeta 1989; Wright et al. 1996; Hoffmann 2010, 2015). The genus ranges from Aptian to Maastrichtian strata worldwide (e.g., Hoffmann 2015). Five species of *Tetragonites* are known from the Yezo Group cropping out in Hokkaido, northern Japan and Sakhalin, Russian Far East (Jimbo 1894; Yabe 1903; Matsumoto 1942; Shigeta 1989; Matsumoto and Toshimitsu 1991; Maeda et al. 2005). One remarkable species among them, *Tetragonites minimus* Shigeta, 1989, having small-sized shell with adorally convex aperture on the venter was established by Shigeta (1989). This species occurs from Turonian to Campanian strata in the north-western Pacific realm, but is thought to be derived from *Tetragonites spathi* (Fabre,

1940), which inhabited southern regions in the Cenomanian (Shigeta 1989, 2001).

Mature modifications are morphological changes that appear only in the adult shell of fossil molluscs and are clues to recognising dimorphism. Numerous cases of dimorphism have been reported among ammonoids across geologic eras and taxa (e.g., Callomon 1955, 1963; Makowski 1962; Davis et al. 1969, 1996; Klug et al. 2015). In several cases, species that had been assigned to different taxa were identified as the dimorphic pairs by later authors. Therefore, the detection of dimorphism is important for ammonoid taxonomy. Recognising the mature modification and dimorphism is important not only from the point of view of taxonomy, but also from the palaeoecological viewpoint such as reproduction and mating, because the concept that dimorphic pairs correspond to sex is widely accepted (Makowski 1962; Davis et al. 1996; Klug et al. 2015).

Dimorphism is known in Cretaceous ammonoids (e.g., Cobban 1969; Tanabe 1977, 2022; Futakami 1990; Cobban

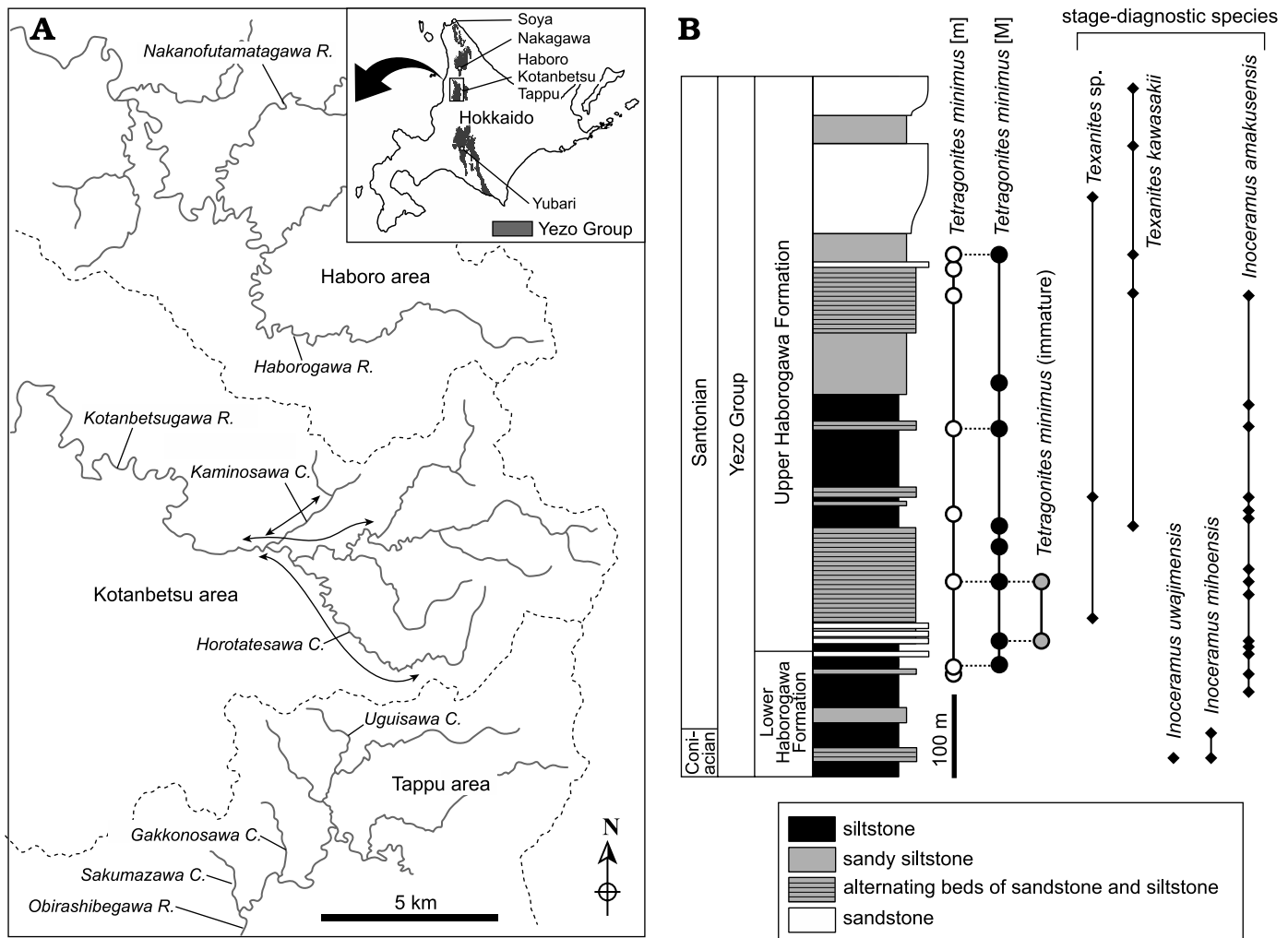


Fig. 1. A. Location map around studied areas in Hokkaido, Japan (inset showing location of Yezo Group deposits). B. Generalized columnar section of the Santonian, Yezo Group in the Kotanbetsu area showing stratigraphic occurrence of dimorphic pairs of *Tetragonites minimus* Shigeta, 1989, and the selected stage-diagnostic mega-fossils. Double head arrows indicate the areas where the columnar sections were constructed. See Aiba (2019) for details of stratigraphy. Abbreviations: C., Creek; R., River.

and Kennedy 1993; Landman and Waage 1993; Maeda 1993; Davis et al. 1996; Metzdorf and Sowiak 2003; Machalski 2005; Landman et al. 2012), but has not yet been reported in the genus *Tetragonites*. Davis et al. (1996) pointed out that the differences in adult sizes among some species of *Tetragonites* described by Wiedmann (1973), could indicate dimorphism. However, this hypothesis remained untested. In this paper, the mature modifications and dimorphism of *T. minimus* are described. In addition, the taphonomy and palaeoecology of this species is discussed.

**Institutional abbreviations.**—MCM, Mikasa City Museum, Hokkaido, Japan; UMUT, University Museum, University of Tokyo, Japan.

**Other abbreviations.**—B, whorl breadth; B/D, whorl breadth ratio to D; D, shell diameter;  $H_1/D$ , whorl height ratio to D;  $H_2/D$ , ventral whorl height ratio to D; [m], microconch; [M], macroconch; PD, phragmocone diameter; U/D, umbilical width ratio to D.

## Geological setting

The Cretaceous (Aptian–Maastrichtian) forearc basin deposits, the Yezo Group, is widely distributed in a north to south direction, from Sakhalin, Russian Far East to Hokkaido, northern Japan (Matsumoto 1954; Takashima et al. 2004; Shigeta and Maeda 2005). The Yezo Group is well exposed in the Haboro, Kotanbetsu, and Tappu areas of northwestern Hokkaido, and its stratigraphy has been studied in detail (e.g., Tanabe et al. 1977; Toshimitsu 1985, 1988; Wani and Hirano 2000; Okamoto et al. 2003; Oizumi et al. 2005; Honda and Hirano 2014; Fig. 1). The Haborogawa Formation, widely distributed in these areas is composed of mudstone, sandy mudstone, and sandstone; and by correlation is assigned to the Turonian–lower Campanian stages (Toshimitsu 1985, 1988; Wani and Hirano 2000; Okamoto et al. 2003; Takashima et al. 2004). The strata with north-south strike dip generally westward, and are successively exposed ascending from east to west (Toshimitsu 1985,

1988; Wani and Hirano 2000; Aiba 2019). The strata consist of several cycles of upward-coarsening sequences ranging from sandy siltstone to sandstone, and from the sedimentary structures, it is assumed that the depositional environments correspond to an outer shelf and storm-dominated inner shelf to shoreface (Toshimitsu 1985, 1988; Wani 2003; Tsujino and Maeda 2007).

## Material and methods

**Material.**—43 specimens of *Tetragonites minimus*, collected from the Santonian in the Kotanbetsu, Tappu, and Haboro areas, Hokkaido, Japan were studied (Figs. 1, 2; Table 1). These specimens are housed in the Mikasa City Museum (Hokkaido, Japan). The numbering of localities used in this paper corresponds to that used in the previous studies in Kotanbetsu (Aiba 2019) and Tappu (Oizumi et al. 2005). Some of the Tappu specimens are listed as “*Tetragonites glabrus*” or “*Tetragonites* sp.” in Oizumi et al. (2005). All the specimens were extracted from calcareous concretions encased in siltstone or sandy siltstone beds. Some of them were preserved in the same concretion or horizon. 33 specimens were collected from calcareous concretions in situ in the outcrops, and the other ten were collected from calcareous concretions as floats in the river. The

geological age of all specimens is Santonian, judging from the co-occurring stage-diagnostic ammonoids and inoceramid bivalves (Toshimitsu et al. 1995, 2007). In addition to the Santonian specimens of *T. minimus*, 30 specimens from the Turonian–Coniacian and the Campanian were examined (Table 2). The locality numbers are shown in the following publications: UMUT specimens, Shigeta (1989 and references therein); MCM specimens from Kotanbetsu area, Aiba (2019); and MCM specimens from Tappu area, Funaki and Hirano (2004).

**Methods.**—Each specimen was polished near the median plane, and investigated for the mature modifications on the outer and inner structures. For the specimens with mature modifications, the size distribution, ratio of numbers and stratigraphic occurrences of microconchs and macroconchs were examined.

The size distribution of the matured specimens was statistically tested by Silverman’s test. The “VISUAL-SILVERMAN”, programmed and provided by Kusuhashi and Okamoto (2015) was used for the test (<http://www.palaeo-soc-japan.jp/publications/fossil/vol97/>).

Twenty three specimens polished exactly along the median plane were measured for the conch dimensions (Fig. 3A). Parameter “B” was calculated by multiplying the original parameter “B/2” by 2. Each parameter was mea-

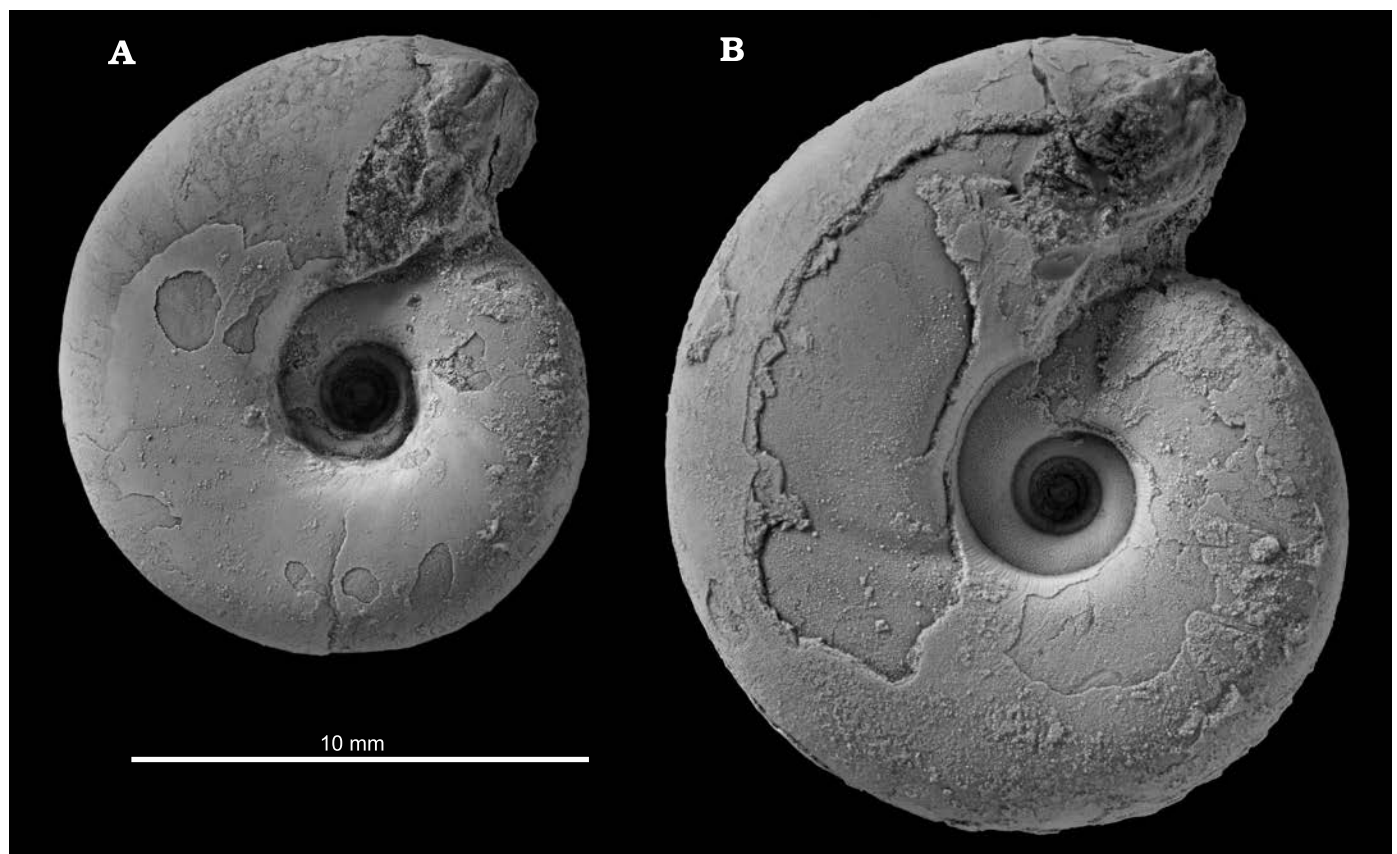


Fig. 2. Photographs of microconch and macroconch in lateral view of tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Santonian, Yezo Group, Horotatesawa Creek (A, outcrop HR001, and B, HR109) the Kotanbetsu area, Hokkaido, Japan. A. MCM-W1560 [m]. B. MCM-W1572 [M].

Table 1. List of Santonian specimens of tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Yezo Group in Hokkaido, Japan. Measurements in mm. Abbreviations: C., Creek; D, shell diameter; [m], microconch; [M], macroconch; PD, phragmocone diameter; R., River; + satisfied; – unsatisfied; ?, unmeasurable or undecidable. The preservation categories: A, complete or almost intact; B, incomplete.

Specimen number	Locality	Area	D	PD	Adult	Mature modifications				Antidimorphs	Preservation category
						(i)	(ii)	(iii)	(iv)		
MCM-W0239-1	Sakumazawa C. (OB33013y)	Tappu	15.0	10.3	+	+	?	?	?	[M]	A
MCM-W0249-1	Gakkonosawa C. (OB35017b)	Tappu	17.7	11.3	+	+	+	+	–	[M]	A
MCM-W0252-1	Gakkonosawa C. (OB35021a)	Tappu	16.5	10.4	+	+	+	–	–	[M]	A
MCM-W0256-1	Gakkonosawa C. (OB35041a)	Tappu	16.3	10.6	+	+	?	–	–	[M]	A
MCM-W0499-1	Uguisawa C. (OB40599a)	Tappu	19.3	11.3	+	+	?	+	–	[M]	A
MCM-W1549	Kotanbetsugawa R. (float)	Kotanbetsu	15.4	10.2	+	+	+	+	+	[M]	A
MCM-W1550	Kotanbetsugawa R. (KT045k)	Kotanbetsu	13.0	8.3	+	+	?	+	–	[m]	A
MCM-W1551	Kotanbetsugawa R. (KT093b)	Kotanbetsu	17.9	11.2	–	?	?	?	?	?	A
MCM-W1553	Kotanbetsugawa R. (KT093a)	Kotanbetsu	12.7	8.9	+	+	?	?	?	[m]	A
MCM-W1554	Kotanbetsugawa R. (KT093g)	Kotanbetsu	11.6	7.5	+	+	+	?	–	[m]	A
MCM-W1555	Kotanbetsugawa R. (KT093y)	Kotanbetsu	?	7.9	+	+	?	+	+	[m]	B
MCM-W1556	Kotanbetsugawa R. (KT093d)	Kotanbetsu	18.2	10.9	+	+	?	?	?	[M]	A
MCM-W1557	Kotanbetsugawa R. (KT113b)	Kotanbetsu	?	11.9	+	?	?	+	+	[M]	B
MCM-W1558	Kotanbetsugawa R. (KT121a)	Kotanbetsu	13.1	8.6	+	+	?	–	?	[m]	A
MCM-W1559	Kotanbetsugawa R. (KT121a)	Kotanbetsu	12.3	8.3	+	+	?	+	?	[m]	A
MCM-W1560	Horotatesawa C. (HR001y)	Kotanbetsu	13.0	8.5	+	+	+	+	–	[m]	A
MCM-W1561	Horotatesawa C. (HR001y)	Kotanbetsu	18.1	11.2	+	+	?	+	–	[M]	A
MCM-W1562	Horotatesawa C. (HR003a)	Kotanbetsu	13.1	8.4	+	+	?	+	+	[m]	A
MCM-W1563	Horotatesawa C. (HR015c)	Kotanbetsu	17.1	11.5	+	+	?	?	?	[M]	A
MCM-W1564	Horotatesawa C. (HR023e)	Kotanbetsu	12.1	8.0	+	?	?	+	+	[m]	A
MCM-W1565	Horotatesawa C. (HR023c)	Kotanbetsu	?	11.7	+	?	?	+	–	[M]	A
MCM-W1567	Horotatesawa C. (HR057y)	Kotanbetsu	12.2	8.3	+	+	?	–	–	[m]	A
MCM-W1568	Horotatesawa C. (HR109a)	Kotanbetsu	18.1	11.4	+	+	+	+	–	[M]	A
MCM-W1569	Horotatesawa C. (HR109a)	Kotanbetsu	?	11.1	–	?	?	?	?	?	B
MCM-W1570	Horotatesawa C. (HR109a)	Kotanbetsu	17.4	11.5	+	+	?	+	+	[M]	A
MCM-W1571	Horotatesawa C. (HR109b)	Kotanbetsu	?	11.4	–	?	?	?	?	?	B
MCM-W1572	Horotatesawa C. (HR109c)	Kotanbetsu	16.6	10.6	+	+	–	+	–	[M]	A
MCM-W1573	Horotatesawa C. (HR109c)	Kotanbetsu	11.3	7.6	+	+	?	+	+	[m]	A
MCM-W1574	Horotatesawa C. (HR109c)	Kotanbetsu	?	7.4	+	?	?	+	–	[m]	A
MCM-W1575	Horotatesawa C. (HR119b)	Kotanbetsu	?	10.0	+	?	?	+	?	[M]	A
MCM-W1576	Horotatesawa C. (HR119b)	Kotanbetsu	?	11.0	+	+	?	?	?	[M]	A
MCM-W1577	Horotatesawa C. (HR119b)	Kotanbetsu	?	11.0	+	+	?	+	?	[M]	B
MCM-W1578	Kotanbetsugawa R. (float)	Kotanbetsu	?	10.6	+	?	?	–	?	[M]	A
MCM-W1579	Kotanbetsugawa R. (float)	Kotanbetsu	15.9	9.9	+	+	+	+	?	[M]	A
MCM-W1580	Kaminosawa C. (float)	Kotanbetsu	14.5	8.9	–	–	–	–	–	?	A
MCM-W1581	Kotanbetsugawa R. (float)	Kotanbetsu	13.2	8.7	+	+	–	?	?	[m]	A
MCM-W1582	Kotanbetsugawa R. (float)	Kotanbetsu	?	11.3	–	?	?	–	–	?	A
MCM-W1588	Nakanofutamagawa R. (float)	Haboro	14.1	9.0	–	–	–	?	?	?	A
MCM-W1591	Kotanbetsugawa R. (KT093)	Kotanbetsu	17.2	11.3	+	+	?	–	+	[M]	A
MCM-W1593	Nakanofutamagawa R. (float)	Haboro	17.5	12.0	+	+	?	+	–	[M]	A
MCM-W1594	Kotanbetsugawa R. (float)	Kotanbetsu	16.1	10.7	+	+	?	+	–	[M]	A
MCM-W1595	Kotanbetsugawa R. (float)	Kotanbetsu	?	9.5	–	?	?	–	–	?	B
MCM-W1596	Horotatesawa C. (HR023f)	Kotanbetsu	?	11.4	+	+	?	+	+	[M]	A

sured at maximum of two points (near the aperture and last septum) on the preserved last whorl. These parameter measurements were not carried out on the points with significant deformation. Furthermore, two medially sectioned specimens (identified as macroconch and microconch, respectively) were polished along the perpendicular plane

on the top of the caecum, and examined for ontogenetic changes of the conch geometries (Fig. 3B). In addition to the measurements in the perpendicular section, each parameter was measured near the aperture in the two specimens. The purpose was to record the ontogenetic changes until the end of the growth, as far as possible.



Table 2. List of Turonian, Coniacian, and Campanian specimens of tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Yezo Group in Hokkaido, Japan. Measurements in mm. Abbreviations: C., Creek; D, shell diameter; [m], microconch; [M], macroconch; PD, phragmocone diameter; R., River; + satisfied; – unsatisfied; ?, unmeasurable or undecidable.

Specimen number	Locality	Area	D	PD	Adult	Antidimorphs
Turonian specimens						
MCM-TS0023	Pankemoshuparogawa R. (float)	Yubari	35.0	?	+	[M]
MCM-TS0029	Pankemoshuparogawa R. (float)	Yubari	19.0	?	+	[m]
MCM-W0414-1	Okufutamatazawa C. (OB40103a)	Tappu	18.3	12.3	+	[m]
MCM-W1583	Horotatesawa C. (HR171)	Kotanbetsu	20.6	?	+	[m]
MCM-W1584	Horotatesawa C. (HR185)	Kotanbetsu	20.3	14.9	+	[m]
MCM-W1587	Horotatesawa C. (HR199)	Kotanbetsu	14.2	9.0	–	?
MCM-W1597	Horotatesawa C. (HR185)	Kotanbetsu	10.3	?	–	?
MCM-W1598	Horotatesawa C. (HR185)	Kotanbetsu	26.8	16.7	–	[M]?
MCM-W1599	Horotatesawa C. (HR185)	Kotanbetsu	29.4	16.6	–	[M]?
UMUT-MM18671-1 (paratype)	Obirashibegawa R. (R4018)	Tappu	?	18.4+	–	[M]?
UMUT-MM18671-2 (paratype)	Obirashibegawa R. (R4018)	Tappu	18.4	?	+	[m]
UMUT-MM18678-2 (paratype)	Obirashibegawa R. (R2110)	Tappu	21.3	15.4	+	[m]
UMUT-MM18678-3 (paratype)	Obirashibegawa R. (R2110)	Tappu	18.0	11.2	+	[m]
UMUT-MM18678-4 (paratype)	Obirashibegawa R. (R2110)	Tappu	?	14.5	+	[m]
UMUT-MM18681-1 (paratype)	Higashiura	Soya	22.6	?	+	[m]
UMUT-MM18682-3 (paratype)	Nakakinenbetsugawa R. (R6394)	Tappu	17.9	?	+	[m]
Coniacian specimens						
MCM-W0115-1	Obirashibegawa R. (OB11189b)	Tappu	15.8	?	+	[m]
MCM-W0115-2	Obirashibegawa R. (OB11189b)	Tappu	15.5	?	+	[m]
MCM-W0118-1	Obirashibegawa R. (OB11193c)	Tappu	14.6	?	+	[m]
MCM-W1592	Obirashibegawa R. (OB11181)	Tappu	21.2	?	–	[M]?
UMUT-MM18667 (holotype)	Obirashibegawa R. (T1220 (= OB11189))	Tappu	28.1	?	+	[M]
Campanian specimens						
UMUT-MM18642-2 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	13.6	?	+	?
UMUT-MM18642-3 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	12.9	8.6	–	?
UMUT-MM18642-4 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	13.0	8.8	+	?
UMUT-MM18642-5 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	?	8.9	+	?
UMUT-MM18642-6 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	13.5	9.0	+	?
UMUT-MM18642-7 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	8.5	5.8	–	?
UMUT-MM18642-8 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	10.7	7.5	–	?
UMUT-MM18642-9 (paratype)	Wakkaenbetsugawa R. (T313)	Nakagawa	?	9.6	+	?
UMUT-MM18644 (paratype)	Osoushinaisawa C. (T205)	Nakagawa	?	8.5	+	?

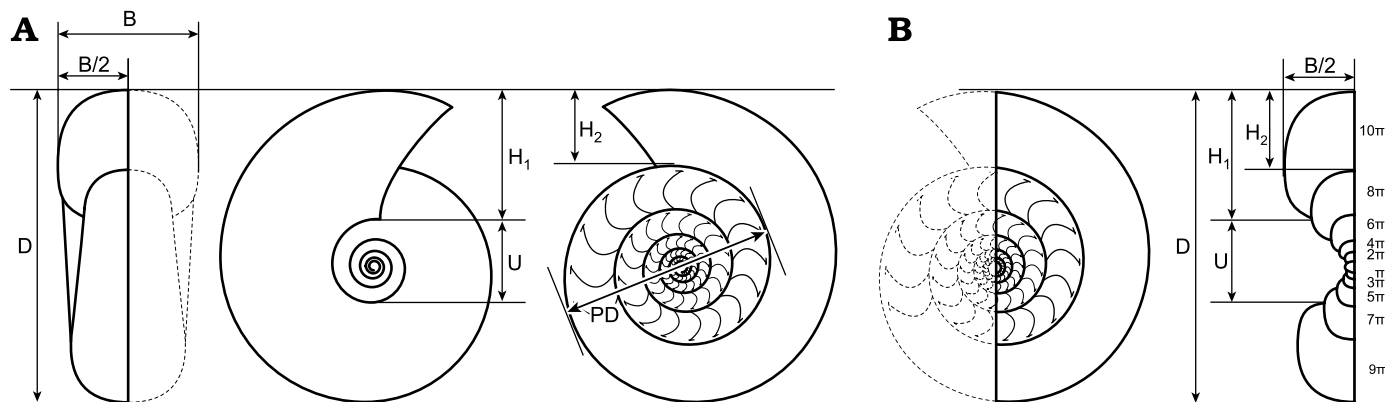


Fig. 3. Measurements of the conch geometries of tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Yezo Group in Hokkaido, Japan. **A.** Measured parameters on the specimens polished along the median plane. **B.** Measured ontogenetic changes of parameters on the specimens polished along the perpendicular plane. Abbreviations: B, whorl breadth; D, shell diameter;  $H_1$ , whorl height;  $H_2$ , ventral whorl height; PD, phragmocone diameter; U, umbilical width.

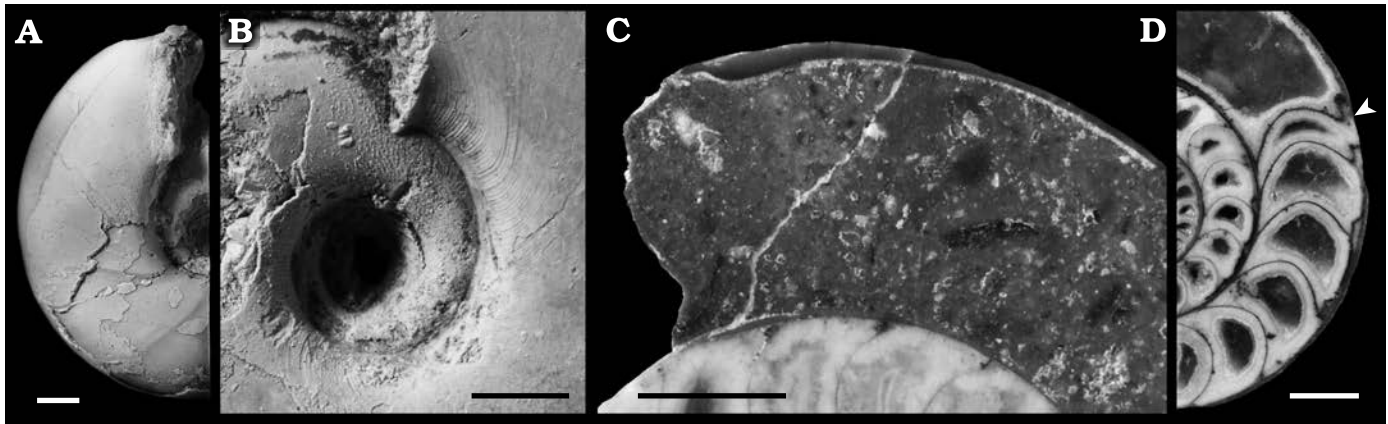


Fig. 4. Mature modifications recognised in tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Yezo Group in the Haboro, Kotanbetsu, Tappu, Nakagawa, Soya, and Yubari areas, Hokkaido, Japan. **A, B.** Changes in the shape of the body chamber: modification appeared at venter (**A**, MCM-W1591) and umbilicus (**B**, MCM-W1556). **C.** Shell thickening in the aperture, MCM-W1560. **D.** Septal crowding and increase in septal thickness, MCM-W1565; arrowhead indicates the last septum. Scale bars 2 mm.

To investigate their earlier taphonomic histories (post-mortem to final burial) and palaeoecology, the damage to the body chamber was examined. In addition, the conditions of the air chamber and sediment infill in the body chamber were also observed.

The above methods were carried out on the 43 Santonian specimens. Turonian, Coniacian, and Campanian-aged specimens of *T. minimus* were morphologically investigated to verify the chronological continuity of the dimorphism. Therefore, unless otherwise noted, the following results and discussion of the analyses are based on the Santonian specimens only.

## Results

*Mature modifications.*—Four types of mature modifications were recognised in *Tetragonites minimus*; (i) changes in the shape of the body chamber, (ii) shell thickening in the aperture, (iii) septal crowding, and (vi) increase in septal thickness (Fig. 4). In some specimens, more than one of the four types were combined simultaneously (Fig. 4D).

(i) Changes in the shape of the body chamber (Figs. 2, 4A, B). The whorl rapidly deviated inward and constricted in the venter (Figs. 2, 4A) and the umbilicus became slightly wider (Figs. 2, 4B). In some specimens, the whorl reduced the expansion rate, which is deviated from the previous logarithmic spiral before forming of a rapid constriction. These changes were also shown in the ontogenetic changes of the parameters  $H_1/D$  and  $U/D$ , as discussed later in the text. The apertural edge is turned slightly up on the umbilical seam (Fig. 4B). These terminal apertural modifications were significantly more obvious than the constrictions appearing sometimes in the immature conchs. Type (i) changes in the shape of the body chamber were observed in 30 specimens (69.8%).

(ii) Shell thickening in the aperture was characteristic (Fig. 4C); the shell thickness rather gradually increases and

suddenly decreases toward the apertural edge. On the specimens with peeled shell, the terminal shell thickening appeared like a constriction in the internal mold. It was also obvious than the constrictions sometimes appearing on the immature conch. This was recognised in seven specimens (16.3%). Regardless of the change in shell thickness and the subsequent constriction, the deviation of the aperture inward appeared at the venter. Thus, types (i) changes in the shape of the body chamber and (ii) shell thickening in the aperture are independent phenomena.

(iii) Septal crowding is a reduction in the angle between the last two septa (Fig. 4D). Compared to the spacing in previous growth, the angle narrowed up to about half. It was also observed on the suture lines in some specimens. This was observed in 23 specimens (53.5%).

(iv) Septal thickness increased in last septa (Fig. 4D). In the most prominent case, thickness of the last septum was about twice the thickness of the previous septa. This was especially visible on the dorsal side of the septa. This was noted in nine specimens (20.9%).

Types (iii) septal crowding and (vi) increase in septal thickness of *T. minimus* were reported and figured by Shigeta (1989, 2001). All types have previously been found in other ammonoids (Klug et al. 2015), but type (iii) might also appear in the middle of growth in some cases and is a weaker criterion for maturity (e.g., Bucher et al. 1996; Klug et al. 2015), while change in the shape of the body chamber (type (i)) is a more robust criterion for maturity (e.g., Parent 2021). The types (i), (iii), and (iv) have also been observed in the recent *Nautilus* (Collins and Ward 1987; Ward 1987; Klug 2004; Klug et al. 2015).

*Size distribution, ratio of numbers and stratigraphic occurrence of dimorphic pair.*—Among the specimens examined, 36 specimens (84%) had any type of mature modification (Fig. 5A, Table 1). The compilation histogram of all mature size (specimens with mature modifications) demonstrated two peak distributions (Fig. 5B). Note that this histogram

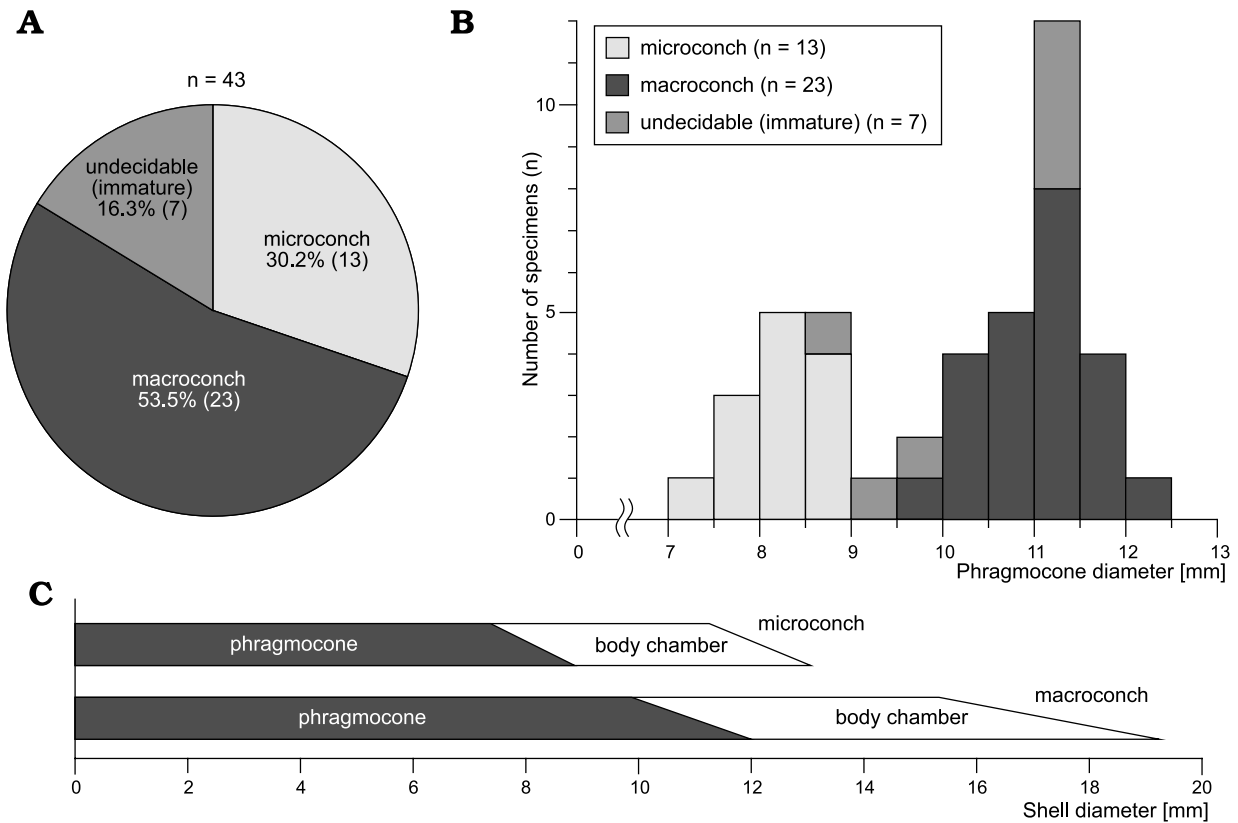


Fig. 5. Characteristics of ratio of numbers and size of dimorphism in tetragonitid ammonoid *Tetragonites minimus* Shigeta, 1989, from the Yezo Group in Hokkaido, Japan. The specimens treated here were collected from various stratigraphic levels in the Santonian in the Kotanbetsu, Tappu, and Haboro areas. **A.** The ratio of numbers of dimorphic pairs. **B.** Compilation of the size distribution in phragmocone diameter (PD). **C.** Comparative representation of the size of dimorphic pairs with indication of the phragmocone and body chamber.

is displayed by the diameter at the last septum (Fig. 3A) because the body chambers of some specimens were lacking or deformed. The results of the Silverman’s test for the adult size distribution showed that the null hypothesis of unimodal distribution was rejected (p-value: 0.0441; 95% CI: 0.0402~0.0483), and the null hypothesis of bimodal distribution was not rejected (p-value: 0.8425; 95% CI: 0.8352~0.8495). The size distribution was also examined in the specimens yielded by a single horizon, outcrop HR109 in the Horotatesawa Creek of the Kotanbetsu area. These specimens are considered to constitute a population sample.

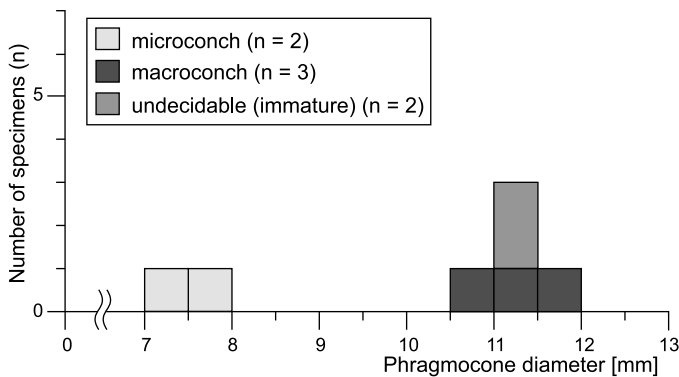


Fig. 6. The size distribution in a single horizon: outcrop HR109 (Santonian) in the Horotatesawa Creek of the Kotanbetsu area, Hokkaido, Japan.

The histogram also showed a two-peak trend in spite of the small sample size (Fig. 6). Small mature shells can be regarded as microconchs and large mature shells as macroconchs (Callomon 1955, 1963; Fig. 2).

Each mature shell size (body chamber diameter) did not overlap; 11–13 mm for microconchs and 16–19 mm for macroconchs (Figs. 3, 5C). Macroconchs are approximately 1.4 times larger than microconchs. The number of dimorphic pairs was 13 [m] and 23 [M] respectively (Fig. 5A). In the Santonian strata in the Kotanbetsu area, there were no significant differences in the stratigraphic occurrences of dimorphic pairs (Fig. 1B). In four of the 12 horizons, dimorphic pairs occur.

*Morphological analysis.*—Comparisons of the conch forms between microconchs and macroconchs in the four parameters are shown in Fig. 7. Each comparison demonstrates that the conch forms are similar in juvenile (approximately less than 10 mm in D) but clearly differ in the later part (approximately more than 10 mm in D). Especially in the parameters  $H_1/D$  and  $U/D$ , the ontogenetic changes of the later stage in microconchs (the whorl height becomes smaller; the umbilicus becomes wider) precede those in macroconchs (Fig. 7A, C). Ontogenetic changes on these parameters could also be observed in actual specimens as changes in the shape of the body chamber (Fig. 2, 4A, B).

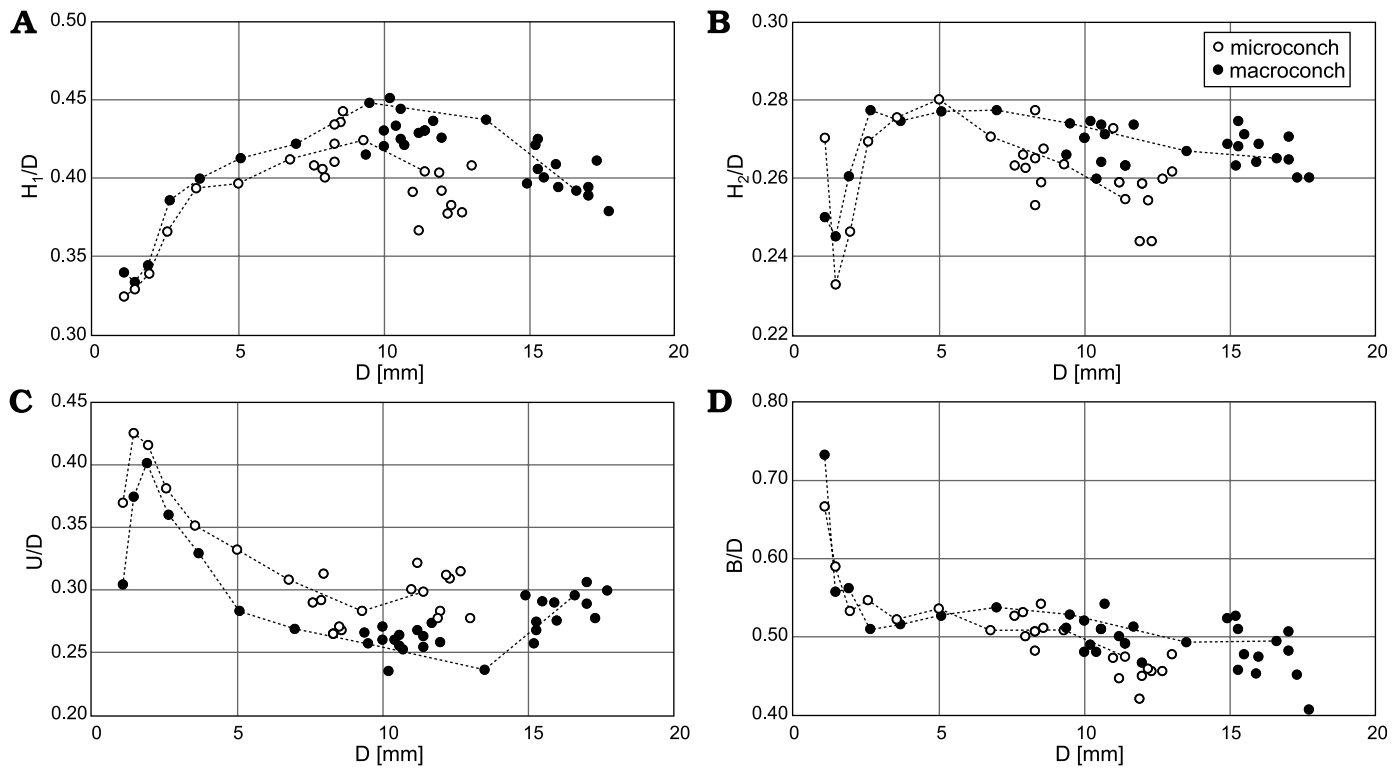


Fig. 7. Scatter diagrams of four parameters versus shell diameter (D) of tetragonitid ammonoid *Tetragnostes minimus* Shigeta, 1989, from the Santonian, Yezo Group in Hokkaido, Japan. **A.**  $H_1/D$  (whorl height ratio). **B.**  $H_2/D$  (ventral whorl height ratio). **C.**  $U/D$  (umbilical width ratio). **D.**  $B/D$  (whorl breadth ratio). Abbreviations:  $H_1$ , whorl height;  $H_2$ , ventral whorl height; U, umbilical width; B, whorl breadth.

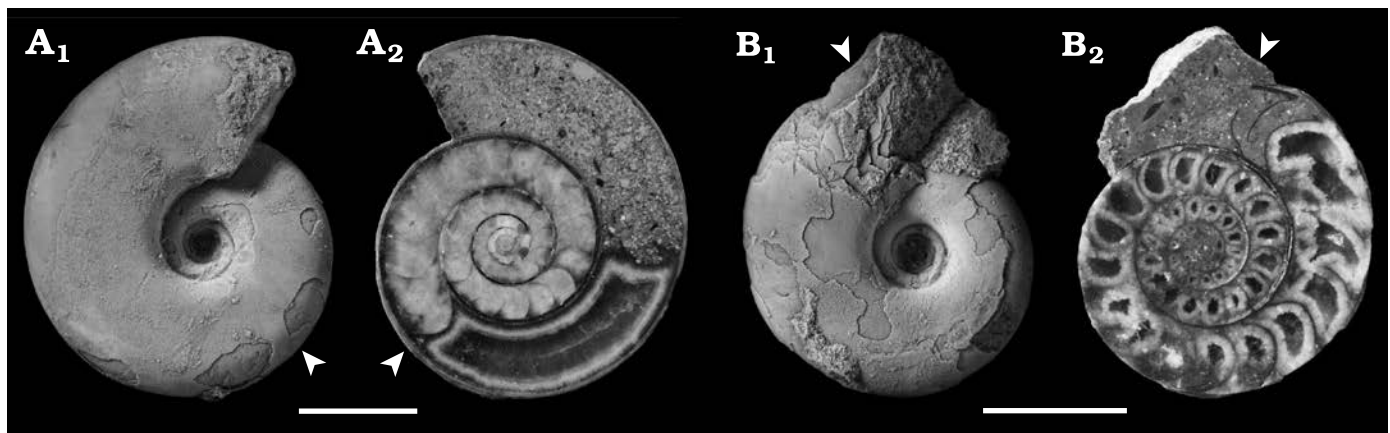


Fig. 8. Two categories of the preservation pattern of the body chamber of tetragonitid ammonoid *Tetragnostes minimus* Shigeta, 1989, from the Santonian, Yezo Group in the Haboro, Kotanbetsu, and Tappu areas, Hokkaido, Japan. **A.** MCM-W1549, complete or almost intact specimen, note the interiors of the body chamber filled with sparry calcite. **B.** MCM-W1555, incomplete specimen. In lateral ( $A_1$ ,  $B_1$ ) and median section ( $A_2$ ,  $B_2$ ) views. Arrowheads indicate the last septum. Scale bars 5 mm.

*Dimorphism in Turonian, Coniacian, and Campanian specimens.*—Mature modifications were also identified in Turonian, Coniacian, and Campanian-aged specimens (Table 2). Turonian and Coniacian specimens were matured at the shell diameters of approximately 20 and 35 mm (macroconch), and approximately 16 and 28 mm (microconch), respectively. These seem to be discontinuous and likely dimorphic pairs. On the other hand, mature size differences are obscure in the Campanian specimens.

*Taphonomic analysis.*—The damage of the body chamber

was classified into two categories: A, completely or almost intact; B, incomplete (Fig. 8). The numbers and ratios of each category are following: category A,  $n = 37$ , 86%; category B,  $n = 6$ , 14%. The interior of the body chamber was filled with sparry calcite in 16 specimens (37%) (Fig. 8A). The air chambers showed occasional intrusion of sediments, but most were intact or internally fractured with no punctures. The epifauna were not attached to any of the specimens. Jaw apparatuses were not observed in any specimens.



## Discussion

**Characteristics of dimorphism of *Tetragonites minimus*.**—The results show it is reasonable to regard the two different adult-size groups in *T. minimus* as dimorphs, since many of the characteristics identified as the criteria for dimorphism of ammonoids are met (Klug et al. 2015). The idea of dimorphism of ammonoids as sexual is widely accepted. However, as in many other cases, no clues have been obtained to determine whether microconchs or macroconchs are female or male for *T. minimus*.

Size differences between other known dimorphic pairs varied among taxa. In some Jurassic and Cretaceous cases, macroconchs were much larger than microconchs (Makowski 1962; Cobban and Kennedy 1993). On the other hand, in other cases there is only a slight difference and in other cases the sizes overlap (Landman and Waage 1993). Among the modern cephalopods, the size difference between the sexes might be extremely large like in species of *Argonauta* (Roper et al. 1984; Nesis 1987), or slight like in species of *Nautilus* (Willey 1902; Saunders and Spinosa 1978; Saunders and Ward 1987; Hayasaka et al. 1987; Dunstan et al. 2011a). The difference in the conch size of dimorphic pairs of *T. minimus* of the Santonian was approximately 1.4 times, which could be considered relatively small. The size differences of antidimorphs in the Turonian and Coniacian are larger than that of the Santonian, at approximately 1.8 times. Same cases in which the dimorphic size difference has changed in the lineage, have been reported (Dzik 1994; Parent 1998; Schweigert and Dietze 1998). On the other hand, no remarkably discontinuous maturity size difference was observed in Campanian specimens. Considering the trend of decreasing mature conch size and size difference between dimorphic pairs from the Turonian–Coniacian to the Santonian, the trend might have continued to the Campanian and the size overlap might occur at that time. This should be verified with sufficient numbers of specimens by the statistical testing in the future work.

It is common for the ratio of the number of ammonoid dimorphic pairs to not be equal (Makowski 1962; Cobban 1969; Kennedy 1988; Cobban and Kennedy 1993; Landman and Waage 1993; Davis et al. 1996; Machalski 2005). Even in the Recent *Nautilus pompilius*, population differences can be noted depending on the season and region (Hayasaka et al. 1987). Therefore, approximately 1 [m]: 2 [M] of *T. minimus* is a possible ratio.

The similarity at the juvenile stage, but different at the adult stage of the conch form has been confirmed in many cases of dimorphism of ammonoids (e.g., Palframan 1966, 1967; Tanabe 1977, 2022; Parent 1997; Zatoń 2008; Parent and Zatoń 2016). The ontogenetic pattern of dimorphs in shell morphology of *T. minimus* is similar to these cases (Fig. 7).

**Taphonomic history.**—Understanding the taphonomic processes of fossils is essential for reconstructing their palaeoecology (Maeda and Seilacher 1996; Wani and Gupta 2015).

The present analyses showed a somewhat peculiar trend in which the mature or nearly mature conchs were predominant. In this section, the mode of occurrence is discussed from the aspect of taphonomy.

The shells of dead ammonoids followed variable paths before become finally buried in the sea floor. Sometimes, the dead shells surfaced and drifted away on the sea surface, thereby losing the chance of being fossilised (Maeda and Seilacher 1996; Maeda 1999). First, the body chamber might be damaged or lost during post-mortem transport on both the sea surface and the sea floor (Maeda 1991, 1999; Maeda and Seilacher 1996; Wani 2004; Maeda et al. 2010). There is an example of an ammonoid assemblage consisting of more than 600 specimens that transported on the sea surface and beached, with none preserving body chamber (Maeda et al. 2003). Therefore, based on the preservation of the body chamber, it is possible to estimate the degree of post-mortem transport of the shell. The results of this study showed that preservation of the body chamber of *T. minimus* from the Yezo Group, Hokkaido, was remarkably good. In particular, specimens with almost complete body chambers belonging to the category A are unlikely to have experienced long-distance post-mortem transport (Maeda and Seilacher 1996; Maeda 1999; Wani 2001). The results showed that the part of the body chamber was partially filled with sparry calcite in 37% of the specimens. It has been suggested that the body chamber might have contained un-decayed soft parts, suggesting that they were buried quickly after death (Tanabe and Fukuda 1987; Landman et al. 2015; Cherns et al. 2021). Additionally, a previous field experiment revealed that the smaller conchs of ectocochleate cephalopods (e.g., those of Recent *Nautilus*) tend to sink sooner than the large conchs of the same species (Wani et al. 2005). As discussed above, it is highly likely that *T. minimus* assemblage examined here have fossilised quickly near their original habitat without long-distance post-mortem transport. However, if so, the jaw apparatus preserved in the body chamber would be expected to be found (Maeda and Seilacher 1996; Tanabe and Landman 2002; Klug and Jerjen 2012; see also Wani 2007 for an alternative opinion), but were not identified in this study. In the future studies, a more detailed examination should be performed utilizing CT (computed tomography) or other techniques for the present specimens (such as the analysis performed in Kruta et al. 2011).

On the other hand, it is necessary to understand why juvenile conchs are rare. One possible cause is the taphonomic due to different fossilisation potential of small juvenile conchs. It is possible that the small-sized shells are less likely to be fossilized than large shells because of the dissolution and other factors (Maeda 1991). This is supported by the selective dissolution of the early growth stages of large ammonoid shells during post-mortem exposition to seawater (Maeda 1987; Maeda and Seilacher 1996; Maeda et al. 2010). However, the other coiled ammonoids which are smaller than *T. minimus* (<10 mm), are common in the Yezo Group, and are particularly abundant in the Santonian

(DA unpublished data). Therefore, there is no convincing explanation for the nearly absent small-sized *T. minimus*, unless they were selectively dissolved. Another possibility is that the difference in the floatability in bottom currents of differently-sized shells causes a bias in occurrence (Wani and Ikeda 2006). Smaller shells might have been more easily carried away by the bottom currents, and assuming this case, the scenario is that the small juvenile *T. minimus* were selectively carried, even though they were inhabiting the study area during the Late Cretaceous. However, this scenario is also implausible. If floatability by size is considered, then the equal-sized conchs of microconchs and “juvenile” macroconchs should show the same behaviour to currents, and both are expected to occur. However, even though 11–13 mm in diameter microconchs were found, juvenile macroconchs of almost the same size were not obtained. In addition, if small-sized ( $D < 10$  mm) *T. minimus* were to be carried away in the bottom currents, then the same-sized shells of the other coiled ammonoids should have also been carried away. However, small-sized ( $D < 10$  mm) conchs of the other coiled ammonoids are common in the study area. Thus, the absence of the small-sized *T. minimus* cannot be explained by the difference in floatability for conch sizes. It is reasonable to interpret that the absence of juvenile shells was not caused by the taphonomic factors but instead by primary reasons, i.e., they did not originally inhabit the area.

**Predominance of adult conchs and speculative palaeoecology.**—The reason for absence of juvenile conch of *T. minimus* in the study area is possibly connected to the palaeoecology of the species. If individuals of *T. minimus* changed their habitat during their life cycle and became fossilised in their respective habitats, this would result in bias in the proportion of variously aged specimens. Ontogenetic active migration is assumed among some Mesozoic ammonoids and well known in many modern cephalopods (ammonoids; Morton 1988; Lukeneder et al. 2010; Ikeda and Wani 2012; Brayard and Escarguel 2013; Lukeneder 2015; Moriya 2015; modern cephalopods: Clarke 1970; Crick 1988; Landman 1988; Oba et al. 1992; Westermann 1996; Rexfort and Mutterlose 2006; Lukeneder et al. 2008; Price et al. 2009; Warnke et al. 2010; Dunstan et al. 2011b; Ritterbush et al. 2014).

Here, two working hypotheses are proposed to explain the predominance of adult *T. minimus* in the Santonian of the Yezo Group. Working hypothesis A: *T. minimus* inhabits the sea outside the Yezo sedimentary basin at juvenile stage, migrates geographically during growth, and inhabits the Yezo sedimentary basin at adult stage. Working hypothesis B: *T. minimus* inhabits the shallow-water column at juvenile stage, migrates vertically to deeper parts of the water column during growth, and inhabits bottom waters at the adult stage. In the working hypothesis B, the bias in the occurrence of adult and juvenile specimens is attempted to explain by the difference in fossilisation potentials depending

on the concept of the limit depth on post-mortem surfacing (Maeda and Seilacher 1996).

However, at this time it is not possible to determine which working hypothesis is more plausible. Stable isotope analysis is effective in clarifying detailed habitat changes during the life cycle (Lukeneder 2015; Moriya 2015), and the hybrid analyses of the actual fossil occurrence and the stable isotope analysis might provide new insights into the ammonoid's palaeoecology and taphonomy (Landman et al. 2015).

## Conclusions

Mature modifications, ontogeny, and dimorphism of *Tetragonites minimus* from the Santonian, the Upper Cretaceous in the northwestern area of Hokkaido, were examined. The conch form of the dimorphs is similar at the juvenile stage, but differs at the adult stage in microconch and macroconch. The mature shell size of microconchs and macroconchs did not overlap; 11–13 mm for microconchs and 16–19 mm for macroconchs. The approximate ratio of dimorphic pairs was 1 [m]: 2 [M]. Dimorphism was recognised by shell size differences of the dimorphs at least in the Turonian–Santonian in the supplementary analysis. The mature conch size and size difference between dimorphic pairs decreased chronologically.

More than 80% of the examined specimens were adults. Taphonomic analysis focused on shell preservation showed that the *T. minimus* assemblages fossilised quickly near their original habitat. Hence, the bias in the fossil occurrence of *T. minimus* was not caused by the taphonomic factors such as the bias of fossilisation potential and floatability in the bottom currents, and was interpreted by the ontogenetic active migration. Two working hypotheses of migration (geographical migration and vertical migration) were proposed to explain the predominance of adults, but it was not possible to determine which working hypothesis was more plausible.

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