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892. SYSTEMATICS OF THE AMMONITE GENUS *TETRAGONITES* FROM THE UPPER CRETACEOUS OF HOKKAIDO*

YASUNARI SHIGETA

Geological Institute, University of Tokyo,
Tokyo 113, Japan

Abstract. The ammonite genus *Tetragonites* (Lytoceratina, Lytocerataceae) from the Upper Cretaceous (Turonian to Maastrichtian) of Hokkaido includes three species: *T. glabrus* (Jimbo), *T. minimus*, n. sp. and *T. terminus*, n. sp., based on the shell size, apertural shape and early internal shell structure. Although the three species are similar in external shell shape, they are clearly distinguishable from one another on the basis of the above characters without any intermediate form.

T. glabrus, occurring in the Middle Turonian to the Upper Campanian, exhibits remarkable variation in shell form, and the previously described species *T. sphaeronotus* (Jimbo), *T. crassus* (Jimbo), *T. popetensis* Yabe and *T. glabrus problematicus* Matsumoto should all be regarded as synonyms of this species. The specimens illustrated as *T. superstes* Van Hoepen and *T. epigonus* Kossmat from Hokkaido are also identified with this species. *T. glabrus* shows a chronocline in which the sizes of initial chamber and ammonitella decrease with time. *T. minimus*, n. sp., occurring from the Lower Turonian to the Upper Campanian, is much smaller in adult shell size (less than 30 mm in diameter) than *T. glabrus*, and shows also a chronocline of miniaturization in adult shell size and of narrower umbilicus toward later forms. *T. terminus*, n. sp., restricted to the Lower Maastrichtian, has an unusually large embryonic shell and a peculiar early internal shell structure.

Key words. *Tetragonites*, Upper Cretaceous, Hokkaido, variation, aperture, internal shell structure.

Introduction

The genus *Tetragonites*, established by Kossmat in 1895, is considered to be one of the derivatives from the lytoceratid main stock (Murphy, 1967b). It was defined by the suture formula $ELU_2U_3(=S)U_1Is$, irregularly bifid or trifid termination for the first lateral saddle (E/L), and nearly symmetrical lobe (L) (Drushchits and Mikhailova, 1976; Krivoshapkina, 1978). *Tetragonites* ranges from the Late Aptian to the Early Maastrichtian, having an almost world-wide distribution (Collignon, 1956). Specimens of this genus occur in the Albian to the Lower Maastrichtian sequences of the Yezo Group or Yezo Supergroup (Okada, 1979, 1983) in Hokkaido, and are relatively common in the Turonian to the Campanian horizons (*e.g.* Matsumoto, 1942a, 1943; Tanabe *et al.*, 1977).

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In spite of the seemingly conservative shell characters, this genus includes many "species" based on the external shell characters (*i.e.* whorl shape and ornamentation). However, taxonomic validity of these characters has not been confirmed by studies of large samples. Furthermore, more critical characters such as early internal shell features have little been investigated in *Tetragonites*.

In this paper, I evaluate the taxonomic validity of various morphological characters in specimens of *Tetragonites* from horizons in the Upper Cretaceous of Hokkaido, and discuss the systematics of *Tetragonites*.

Previous studies

Japanese species of *Tetragonites* were first described by Jimbo (1894) from the Upper Cretaceous Yezo Group of Hokkaido. He distinguished three species based on umbilical shape and ornamentation: *Lytoceras glabrum*, *L. sphaeronotum* and *L. crassum*. One of the two syntypes of *L. sphaeronotum* was later regarded by Matsumoto (1942b) as a variety of *Epigoniceras glabrum* (Jimbo). *Tetragonites epigonus* Kossmat was proposed by Spath (1925) as the type species for the genus *Epigoniceras*, but Howarth (1958) pointed out that this genus is a synonym of *Tetragonites*. The other syntype of *L. sphaeronotum* is a deformed specimen of *Desmophyllites* cf. *diphylloides* (Forbes) (Matsumoto, 1942b, 1963).

Yabe (1903) pointed out that the holotype of *L. crassum* could be an immature example of *T. glabrus* (Jimbo). Later, this specimen was regarded by Matsumoto (1942b) as a variety of *E. glabrum* (Jimbo). Matsumoto (1942b) also described a varietal form of this species from Sakhalin as *E. glabrum* var. *problematica*, but later he regarded it as a subspecies, *T. glabrus problematicus* (Matsumoto, 1959). The fourth species was described by Yabe (1903) as *T. popetensis*. Afterwards, Matsumoto (1942b) reported a varietal form of this species as *E. popetense* var. *frequence*, but detailed description and illustration of the shell were not presented. Several specimens of *Tetragonites* from the Yezo Group were hitherto referred to the following species that were originally described from abroad: *T. epigonus* Kossmat reported by Yabe (1903) and *T. superstes* Van Hoepen by Matsumoto and Miyauchi (1984).

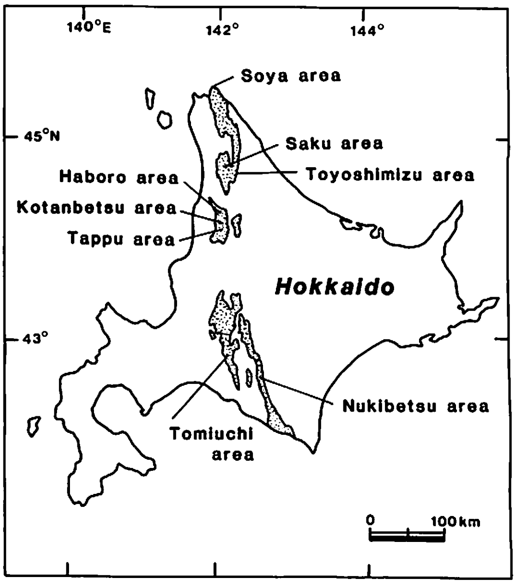


Figure 1. Map showing the distribution of Cretaceous deposits in the central zone of Hokkaido (dotted) and sampling areas of the specimens examined.

Material and methods

Material: A total 320 specimens belonging to 48 samples of *Tetragonites* were examined in this study (Table 1). These specimens were collected from the Upper Cretaceous (Turonian to Maastrichtian) deposits of Soya, Saku, Toyoshimizu, Haboro, Kotanbetsu, Tappu, Tomiuchi and Nukibetsu areas from north to south of Hokkaido (Figure 1).

Specimens in each sample were extracted from several calcareous nodules at the same horizon in an outcrop (AW1001A, AW1003, SM1048 and SF1104) or from a single nodule (remaining samples). The localities and biostratigraphic ages of the samples examined are summarized in Table 1. All specimens are kept at the University Museum, University of Tokyo (UMUT).

Analysis of external shell morphology: A total 229 specimens (Table 1) were used for the biometric analysis of the shell

Table 1. List of material. Specimens used in SEM observation are shown in parentheses. For details of sampling localities with the following prefixes see the following papers; H and T (except for T1220): Matsumoto (1942a), W: Matsumoto and Miyauchi (1984), Nk: Kanie *et al.* (1981), RH, RK and RO: Toshimitsu (1988), R: Tanabe *et al.* (1977), and T1220: Sekine *et al.* (1985).

Sample	N	Registered number	Locality	Horizon
SM1048	8	UMUT MM18635 [1-6,(7,8)]	Tomiuchi,H12d	L. Maast.
SM1041	3	UMUT MM18636 [(1-3)]	Tomiuchi,H12a	L. Maast.
SF1104	6	UMUT MM18637 [1-3,(4-6)]	Tomiuchi,Tonaizawa.R.	L. Maast.
AW1001A	110	UMUT MM18638 [1-90,(91-110)]	Soya,W7A	Up. Camp.
AW1001B	3	UMUT MM18639 [1-3]	Soya,W7A	Up. Camp.
AW1003	18	UMUT MM18640 [1-15,(16-18)]	Soya,W7C	L. Camp.
AS2038A	7	UMUT MM18641 [1-6,(7)]	Saku,T313	L. Camp.
AS2038B	9	UMUT MM18642 [1-5,(6-9)]	Saku,T313	L. Camp.
AS3027A	3	UMUT MM18643 [1-3]	Saku,T205	L. Camp.
AS3027B	1	UMUT MM18644 [1]	Saku,T205	L. Camp.
AS3014P	1	UMUT MM18645 [1]	Saku,T208	L. Camp.
AS-TY1	3	UMUT MM18646 [(1-3)]	Toyoshimizu,Teshio R.	L. Camp.
SN1001	2	UMUT MM18647 [1,2]	Nukibetsu,Nk11	L. Camp.
SN2001	1	UMUT MM18648 [1]	Nukibetsu,Soushibetsu R.	L. Camp.
TP422	2	UMUT MM18649 [1,2]	Tappu,Akanosawa R.	Up. Sant.
AH3064	7	UMUT MM18650 [1,(2-7)]	Haboro,RH1262	L. Sant.
AH4032	3	UMUT MM18651 [1,(2,3)]	Haboro,RH4032	L. Sant.
AH1018	2	UMUT MM18652 [1,2]	Haboro,RH5036	L. Sant.
AH6033P	1	UMUT MM18653 [1]	Haboro,RH5107	L. Sant.
AK1029A	1	UMUT MM18654 [1]	Kotanbetsu,RK0043	L. Sant.
AK1029B	4	UMUT MM18655 [1-3,(4)]	Kotanbetsu,RK0043	L. Sant.
AK1033	3	UMUT MM18656 [1-3]	Kotanbetsu,RK0046	L. Sant.
AK1018	2	UMUT MM18657 [1,2]	Kotanbetsu,RK0030	L. Sant.
AT-AR1A	1	UMUT MM18658 [1]	Tappu,Arakizawa R.	L. Sant.
AT-AR1B	2	UMUT MM18659 [1,(2)]	Tappu,Arakizawa R.	L. Sant.
AT8025	14	UMUT MM18660 [1-13,(14)]	Tappu,R2663	L. Sant.
AT8026	1	UMUT MM18661 [1]	Tappu,R2665	L. Sant.
AT1514	10	UMUT MM18662 [1-10]	Tappu,Kawakami	L. Sant.
AT8023	1	UMUT MM18663 [1]	Tappu,R2662	L. Sant.
AT7067	1	UMUT MM18664 [1]	Tappu,R2185	L. Sant.
AH4087	2	UMUT MM18665 [(1,2)]	Haboro,RH2131	Con.
AT6003	2	UMUT MM18666 [(1,2)]	Tappu,R2144	Con.
AT1551	1	UMUT MM18667 [1]	Tappu,T1220	Con.
AS1000	6	UMUT MM18668 [1-5,(6)]	Saku,T679	Up. Tur.
AT1206	3	UMUT MM18669 [1,(2,3)]	Tappu,R4016	Mid. Tur.
AT1201A	15	UMUT MM18670 [1-4,(5-15)]	Tappu,R4018	Mid. Tur.
AT1201B	3	UMUT MM18671 [1-3]	Tappu,R4018	Mid. Tur.
AT1207	6	UMUT MM18672 [1,2,(3-6)]	Tappu,R4019	Mid. Tur.
AT1208	11	UMUT MM18673 [1-5,(6-11)]	Tappu,R4020	Mid. Tur.
AT1214	2	UMUT MM18674 [(1,2)]	Tappu,R7001	Mid. Tur.
AT1202	5	UMUT MM18675 [1-5]	Tappu,R4017	Mid. Tur.
AT1103	13	UMUT MM18676 [1-10,(11-13)]	Tappu,R4001	Mid. Tur.
AT1575	5	UMUT MM18677 [(1-5)]	Tappu,R2115	Mid. Tur.
AT1578	7	UMUT MM18678 [1-4,(5-7)]	Tappu,R2110	Mid. Tur.
AT1577	1	UMUT MM18679 [1]	Tappu,R2113	Mid. Tur.
AT1562	2	UMUT MM18680 [1,2]	Tappu,R2129	Mid. Tur.
AW2001P	2	UMUT MM18681 [1,2]	Soya,Higashiura	L. Tur.
AT2100	4	UMUT MM18682 [1-4]	Tappu,R6394	L. Tur.

form. Shell diameter (D), umbilical diameter (U), whorl height (H) and whorl breadth (B) were measured with the aid of a slide caliper (accuracy, ± 0.05 mm) and two geometric parameters: relative umbilical size (U/D) and relative whorl thickness (B/H), were calculated for each specimen (abbreviations used in the text are shown in parentheses) (Figure 2).

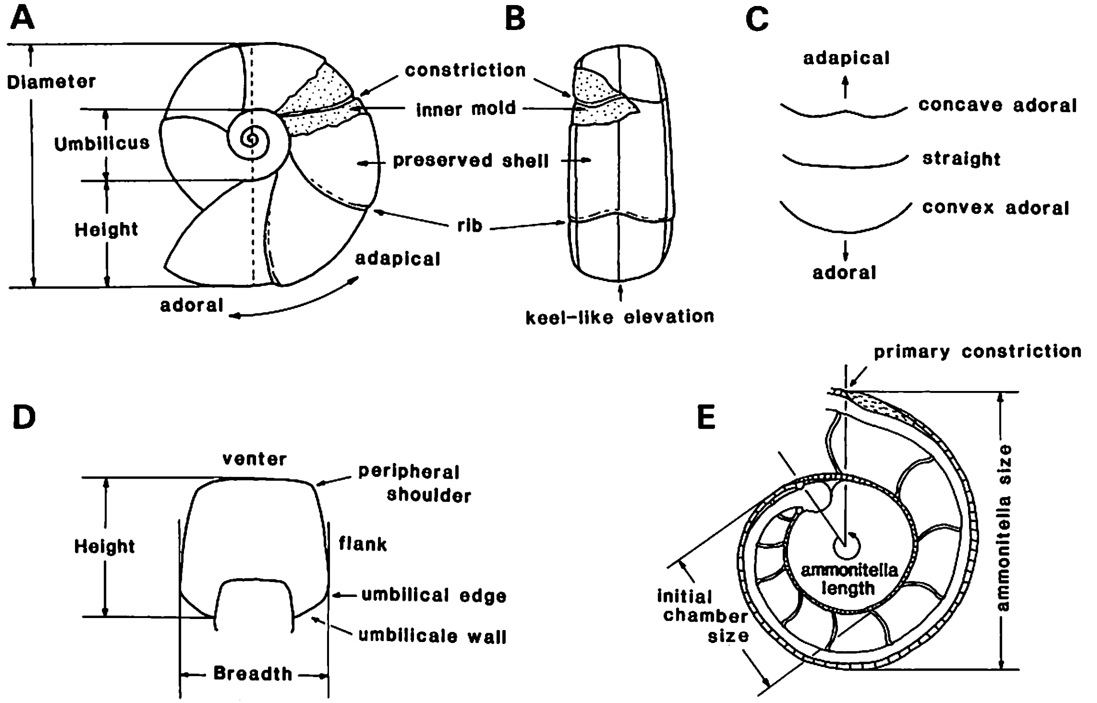
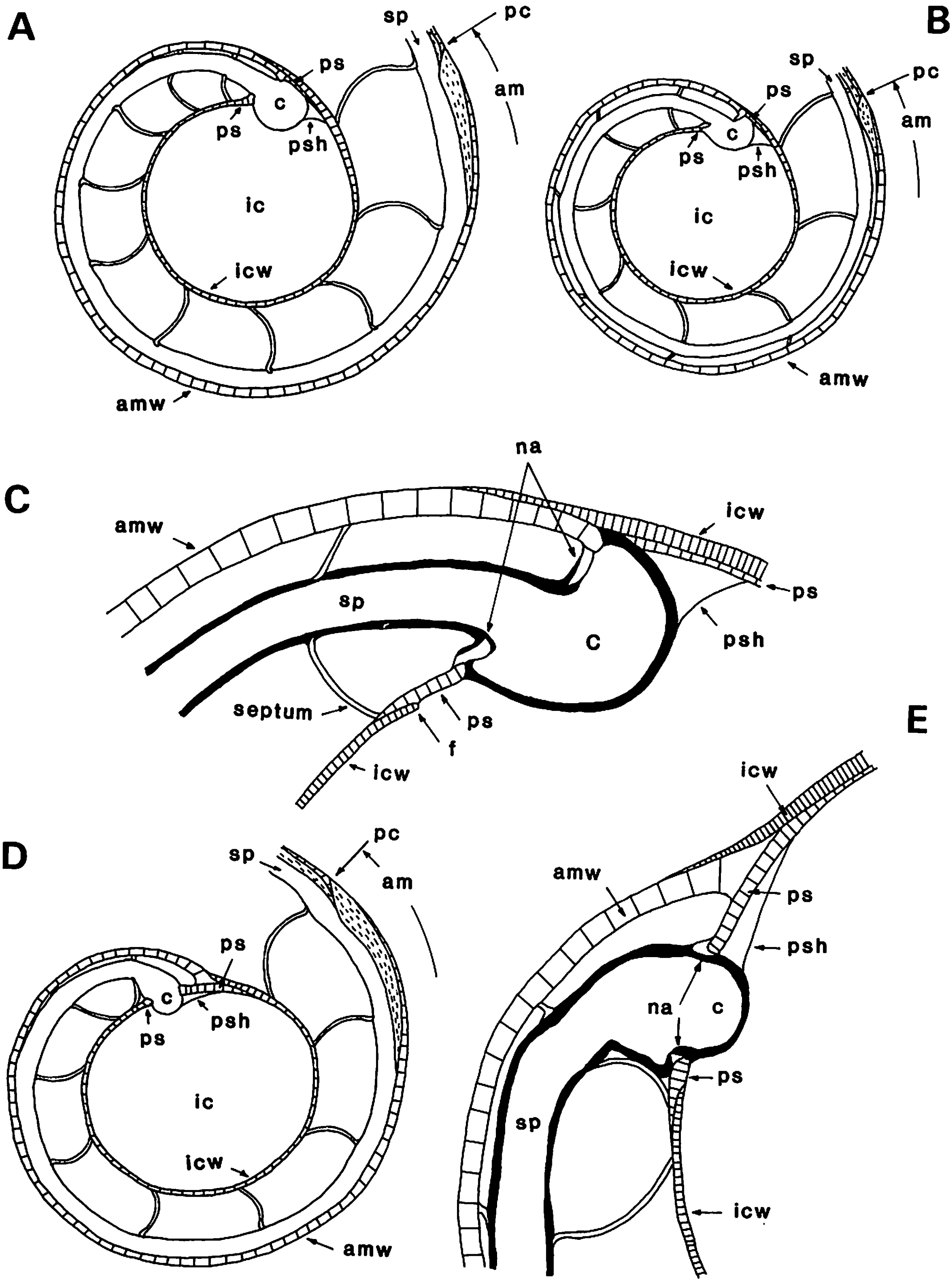


Figure 2. Morphology and measurements of *Tetragonites*. A. Lateral view. B. Ventral view. C. Apertural margin on the venter. D. Whorl cross section. E. Early whorls in median section.

Additionally, 7 specimens (UMUT MM 18638-1~4, MM 18642-5, MM 18678-4, MM 18637-3) were selected and prepared in the following manner for ontogenetic study of the shell form. Every specimen was cut and polished along the median plane, and subsequently the "median-sectioned" specimen was also cut along a plane perpendicular to the polished surface at the base of the caecum. The cross-sectioned surface was etched with 10% acetic acid for two to three minutes, and then an acetate peel was prepared by pressing a sheet of triacetylcellulose film (25 μm in thickness) onto the etched surface while it is flooded with acetone. The four portions (D, U, H, B/2) were measured at intervals of a half volution (90°) on the peeled cross section using a digital micrometer (accuracy ± 1 μm) attached to a profile projector (Nikon Model V-16D).

Analysis of early internal shell morphology: A total 236 specimens (Table 1) were used for observations of early internal shell morphology. For this purpose every specimen was cut and polished along the median plane, and the internal features of early whorls in median section were observed under a binocular microscope with magnification of 20 times. Moreover, 91 specimens among them were prepared in the following manner for scanning electron microscopy. The polished median plane of each specimen was etched with 5% acetic acid for one to two

→ **Figure 3.** Diagrams of early internal shell structural types of *Tetragonites* in median section. A ; IA type. B and C ; IB type. D and E ; IC type. Terminologies from Branco (1879-80), Grandjean (1910), Drushchits and Khiami (1970). am : ammonitella, amw : ammonitella wall, c : caecum, f : flange, ic : initial chamber, icw : initial chamber wall, na : neck-like attachment, pc : primary constriction, ps : proseptum, psh : prosiphon, sp : siphunclar tube.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minutes, and the etched surface was then coated with platinum using an ioncoater (Eiko Engineering Model IB-5). The early internal features of each specimen were then observed by means of a scanning electron microscope (SEM) (Hitachi Model S-430). The following three characters were measured on the enlarged SEM photograph (×100-×500): maximum initial chamber size, ammonitella size and ammonitella length (Figure 2).

Shell morphology of *Tetragonites*

External shell morphology: As shown diagrammatically in Figure 2, most of the specimens examined possess a round to subrectangular whorl section and a fairly narrow (U/D=0.20) to wide (U/D=0.37) umbilicus in the middle to late growth stage. The umbilicus is surrounded by a nearly vertical to subvertical wall, and has a subangular to abruptly rounded shoulder. The outer shell surface is nearly smooth throughout the post-ammonitella stage, and is marked only with fine and dense growth lines and rib-like weak elevations. Some specimens have a keel-like elevation on the venter in the middle to late growth stage. In many specimens the apertural margin is strongly prorsiradiate on the flank and possesses an adorally concave sinus on the venter. Some specimens, however, have an adorally convex aperture on the venter. These two apertural types are distinct, with any intermediate form between them.

Internal shell structure: The early whorls of *Tetragonites* consist of initial chamber (="protoconch"), proseptum, caecum, prosiphon, flange, septa, siphuncular tube and outer shell wall (Figure 3, for details of these structures, see Ohtsuka, 1986), as in other Mesozoic Ammonoidea. The early internal features of the specimens can be divided into three types; here named **IA, IB** and **IC types** (Figure 3).

IA type (Figures 3A and 11A-B) — The initial chamber is nearly circular in median section. Caecum is subellipsoid with a weakly constricted base at the connected portion with proseptum. One to three short, adorally concave prosiphons extend from the adapical portion of caecum to the inner side of initial chamber. Initial chamber wall connects with proseptum at the dorsal side of caecum, forming an indistinct short flange. Siphuncle occupies a central position in the earliest portion of the first whorl near the proseptum, but rapidly shifts toward the ventral side near the second or third septum. Thereafter, it retains a ventral position.

IB type (Figures 3B-C and 11C-D) — The initial chamber is nearly circular in median section. Caecum is hemispherical with a strongly constricted base; hence the shape of the earliest portion of the caecum-siphuncle system is like a mushroom. It is linked with the inner surface of the initial chamber wall by one to three short, adorally concave prosiphons. Flange is short as in IA type, and is sometimes obscure in some specimens. Siphuncle is initially located at a central position in the early portion of the first whorl, and subsequently shifts its position gradually toward the venter. The marginal approximation of siphuncle is completed at the end of the first to second whorls.

IC type (Figures 3D-E and 11E-F) — The initial chamber is nearly circular in median section. The caecum is elongate and subelliptical, without a conspicuous constricted base. It is connected with the inner surface of initial chamber by a relatively long and nearly straight prosiphon. Proseptum resting on the ventral side of initial chamber wall is long, and acutely projects toward the caecum. Early portion of the first whorl swells markedly as a result of discordant underlay of the ammonitella wall with the initial chamber wall. Siphuncle is initially located at dorsal side. At the middle part of the first camera it makes an abrupt turn inward, and thereafter it immediately approximates to the ventral side within the second-third camerae. The first septum is adorally concave, but subsequent septa are adorally convex.

The above characteristic features of the early internal shell structure are consistent in all the examined specimens of each type, and no intermediate forms have been found.

Grouping of specimens

The 236 specimens studied in median section can be classified into three groups, **A**, **B**, and **C**, based on the characteristic features in the early internal shell structure and apertural shape (Table 2). The 84 specimens used for observations of external morphology can also be classified into the above three groups by using the differences in adult shell size and apertural shape, because the specimens with the same early internal shell structural type share the same apertural shape. Diagnostic features of each group other than the early shell structure are summarized below.

Group A : Specimens of this group possess the early internal morphology of IA type and adorally concave sinus of aperture on the venter. They exhibit wide but continuous variation in overall shell shape ; a round to subrectangular whorl section and a fairly narrow to wide umbilicus. Specimens of this group were collected from the Middle Turonian to the Upper Campanian of many areas of Hokkaido. Morphologic variation in the specimens from various horizons is summarized as follows.

Variation in juvenile stage — Specimens of this group show wide variation in the sizes of initial chamber and ammonitella in median section, ranging from 475 to 875 μm and from 900 to 1,700 μm in diameter, respectively

Table 2. Classification of 236 specimens of *Tetragonites* based on the early internal shell morphology and apertural shape. CC : adorally concave, CV : adorally convex.

Sample	No.	N	Internal morphology			Aperture		Group
			IA	IB	IC	CC	CV	
AW1001	MM18638 (1-110)	110	X			X		
AW1003	MM18640 (9-18)	10	X			X		Group A
AS2038A	MM18641 (1-7)	7	X			X		
AS3027A	MM18643 (1-3)	3	X			X		
AS-TY1	MM18646 (1-3)	3	X			X		
AH3064	MM18650 (2-7)	6	X			X		
AH4032	MM18651 (2,3)	2	X			X		
AT8025	MM18660 (5-14)	10	X			X		
AH4087	MM18665 (1,2)	2	X			X		
AT6003	MM18666 (1,2)	2	X			X		
AS1000	MM18668 (1-6)	6	X			X		
AT1206	MM18669 (2,3)	2	X			X		
AT1201A	MM18670 (5-15)	11	X			X		
AT1207	MM18672 (3-6)	4	X			X		
AT1208	MM18673 (4-11)	8	X			X		
AT1214	MM18674 (1,2)	2	X			X		
AT1202	MM18675 (1-5)	5	X			X		
AT1103	MM18676 (1-13)	13	X			X		
AT1575	MM18677 (1-5)	5	X			X		
AS2038B	MM18642 (3-9)	7		X			X	
AS3027B	MM18644 (1)	1		X			X	
AT-AR1B	MM18659 (1,2)	2		X			X	Group B
AK1029B	MM18655 (4)	1		X			X	
AT1578	MM18678 (2-7)	6		X			X	
SM1048	MM18635 (7,8)	2			X	X		
SM1041	MM18636 (1-3)	3			X	X		Group C
SF1104	MM18637 (4-6)	3			X	X		

(Figure 8). The extent of variation of the two measurements is, however, reduced in specimens selected from a stratigraphic interval, and furthermore both sizes tend to decrease upwards in stratigraphic succession (Figure 8).

The spiral length of the ammonitella is, in contrast, less variable than the ammonitella size. The sample mean of the Turonian specimens is larger by 10° than that of the Campanian specimens, but the difference is not significant statistically (Figure 9).

Variation in the middle to late growth stage — Wide variation in the shell shape is

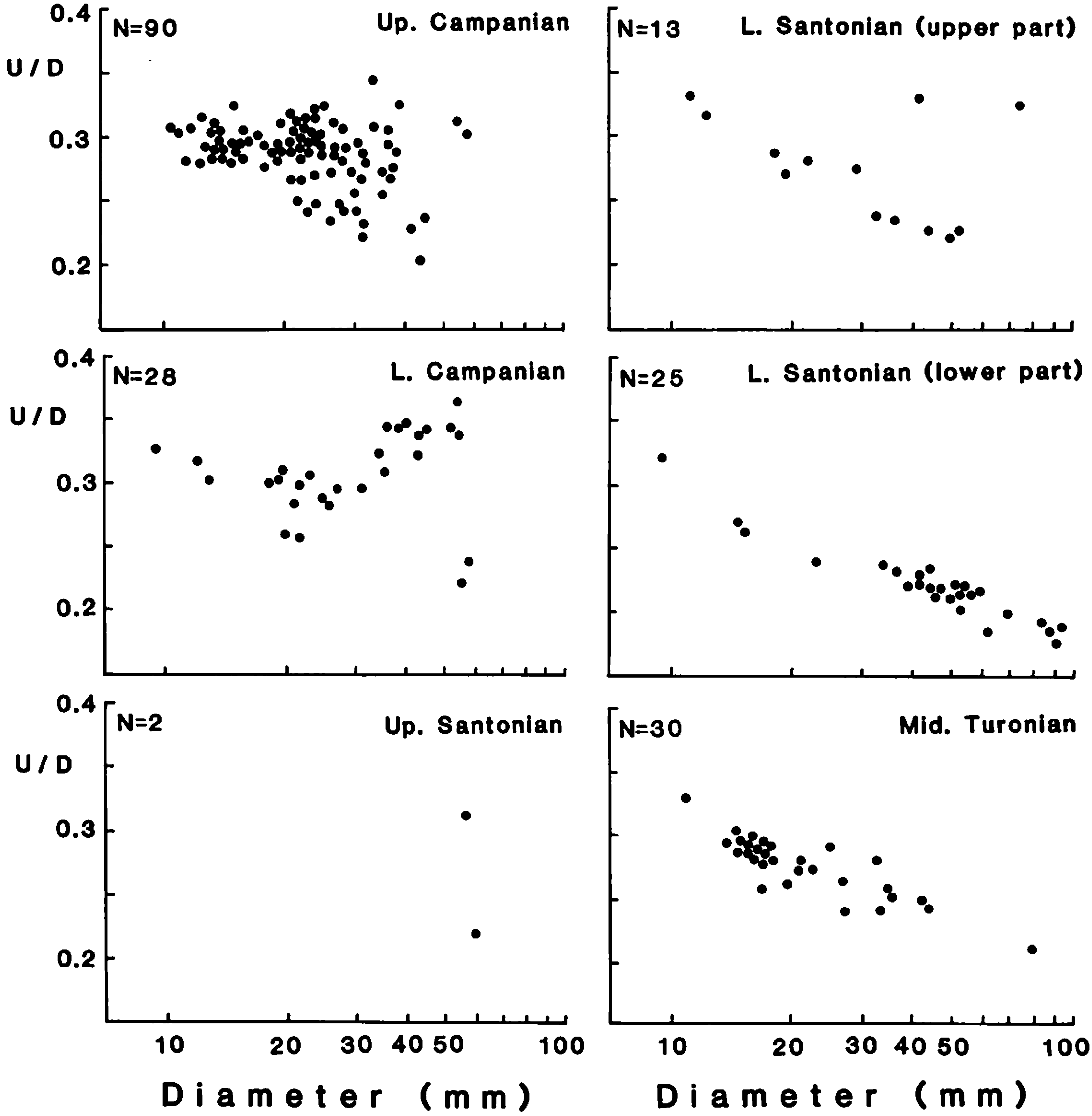


Figure 4. Semi-logarithmic diagram showing the relationship between umbilicus/diameter ratio (U/D) and shell diameter (D) for middle- to large-sized specimens of Group A from different horizons. Turonian and most Santonian specimens tend to become narrowly umbilicate with growth. Campanian specimens exhibit wide variation in U/D ratio, even in the middle to late growth stages.

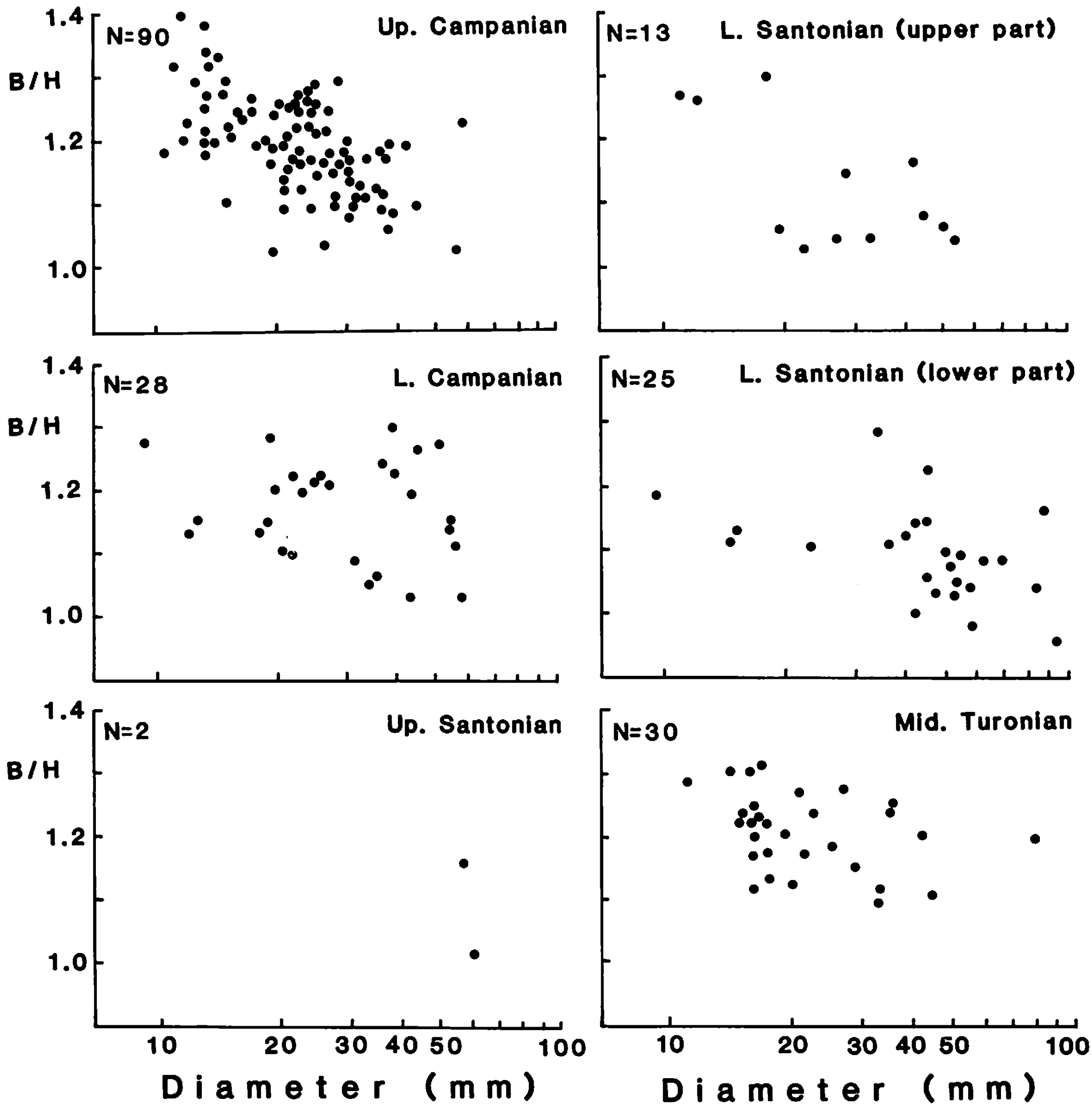


Figure 5. Semi-logarithmic diagram showing the relationship between breadth/height ratio (B/H) and the shell diameter for middle- to large-sized specimens of Group A from different horizons. The specimens of each horizon exhibit wide variation in this parameter.

recognized in the middle- to large-sized specimens of this group (Figures 4 and 5). The Turonian specimens are narrowly umbilicate (U/D=0.20-0.28) with more or less round whorl sections (B/H=1.1-1.3) in the growth stages of more than 30 mm in diameter. Almost all specimens lack conspicuous ribs and a keel-like elevation.

Although the sufficient Coniacian specimens could not be observed, their shell shape and surface ornament essentially resemble those of the Turonian specimens.

Most Santonian specimens have also a narrow umbilicus (U/D=0.18-0.25) and a round whorl section (B/H = 1.0-1.3) without a keel in the middle to late growth stage (D > 30 mm), but two specimens (UMUT MM 18652-1, MM 18654-1) from the upper Lower Santonian and one (UMUT MM 18649-1) from the Upper Santonian have a relatively wide umbilicus (U/D = 0.30-0.35) even in the stage of more than 40 mm in diameter. In such specimens the whorls are subrectangular in cross section, with a keel-like elevation on the relatively flat venter.

Shell shape variation is conspicuous in the Campanian specimens, especially in the Late Campanian ones (UMUT MM 18638-1 ~ 90). Even in the specimens of similar size, the shells are widely to narrowly umbilicate (U/D = 0.20-0.37) with a round to subrectangular whorl section (B/H = 1.0-1.3). A keel-like elevation is fairly common in the Early Campanian specimens, although the state of development varies from specimen to specimen. Such a morphotype is rare in the Late Campanian specimens.

Ontogenetic shell variation — At about 2 mm in diameter, every specimen has a wide umbilicus in relation to shell diameter (U/D = 0.4) (Figure 7). Thereafter the shell becomes narrowly umbilicate up to 10 mm in diameter. In the stage larger than 10 mm in diameter the whorl umbilication is fairly variable from specimen to specimen.

In every specimen the whorl cross-section is relatively depressed in the early stage (B/H = 1.2-1.4) (Figure 7). Except for specimen no. 4 in Figure 7 (UMUT MM18638-3), it generally becomes more compressed (B/H = 1.05-1.15) in growth stages of more than 20 mm in diameter.

Group B : The specimens belonging to this group are small in size, less than 30 mm in diameter even in the adult stage, being characterized by the early internal morphology of IB type, adorally convex aperture on the venter, round to subrectangular whorl section and fairly narrow to wide umbilicus. They are found less commonly in the Middle Turonian to the Lower Campanian sequence of the Yezo Group. Although sufficient material could not be analyzed, the morphological features of this group are summarized below.

Variation in juvenile stage — Initial chamber size, ammonitella size and its spiral length in median section are from 500 to 600 μm, from 900 to 1,050 μm and 320 to 340°, respectively (Figures 8 and 9). The ranges of variation of these characters among the specimens of different stages largely overlap one another.

Variation in the middle to late growth stage — Both Turonian and Coniacian specimens have a wide umbilicus (U/D = 0.27-0.36) and a round whorl section (B/H = 1.1-1.3) with a keel-like elevation in the stage of

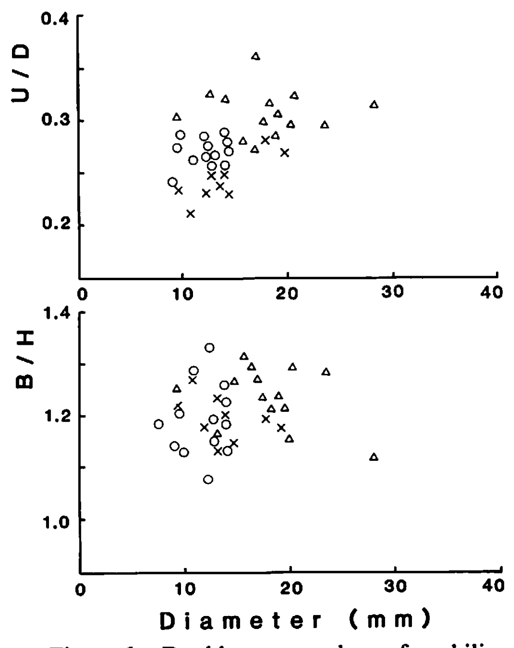


Figure 6. Double scatter plots of umbilicus/diameter ratio (U/D) and breadth/height ratio (B/H) versus shell diameter (D) for specimens of Groups B and C. Triangle: Turonian and Coniacian specimens of Group B. Circles: Santonian and Campanian specimens of Group B. Cross mark: Specimens of Group C. Both Turonian and Coniacian specimens of Group B have a relatively wider umbilicus than the Santonian and Campanian specimens of Group B.

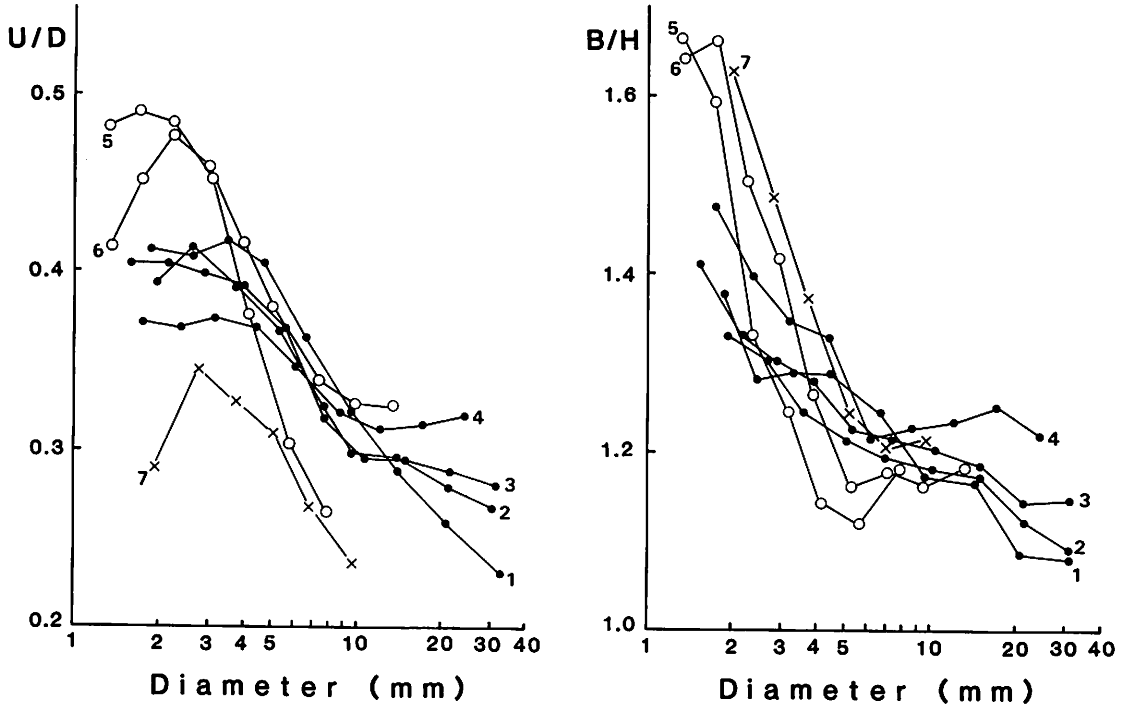


Figure 7. Ontogenetic changes of umbilicus/diameter ratio (U/D) and breadth/height ratio (B/H) versus shell diameter (D) for specimens of Groups A, B and C. Black circle: Specimens of Group A (1: UMUT MM18638-1, 2: UMUT MM18638-2, 3: UMUT MM18638-4, 4: UMUT MM18638-3, sample AW1001A, the Upper Campanian). White circle: Specimens of Group B (5: UMUT MM18642-5, sample AS2038B, the Lower Campanian; 6: UMUT MM18678-4, sample AT1578, the Middle Turonian). Cross mark: Specimen of Group C (7: UMUT MM18637-3, sample SF1104, the Lower Maastrichtian).

more than 10 mm in diameter (Figure 6). Diagnostic features of an adult stage, such as approximation of the last two septa, and thickening of the last septum, are observable at 20 mm in phragmocone diameter of some specimens.

The Santonian and Campanian specimens are narrowly umbilicate (U/D=0.24-0.29) with more or less round whorl section (B/H=1.0-1.3) at the middle to late growth stage (D>10 mm) (Figure 6). The phragmocone diameter in adult stage is usually 10 mm, which is smaller than those of Turonian and Coniacian specimens. Also the state of development in a keel-like elevation is less conspicuous in comparison with that of the Turonian and Coniacian specimens.

Ontogenetic shell variation — In the early stage of about 2 mm in diameter, the two specimens are widely umbilicate, but thereafter they become narrowly umbilicate (Figure 7). Decreasing of U/D ratio versus diameter (D) for specimen no. 6 (UMUT MM18678-4) in Figure 7 is smaller than that for specimen no. 5 (UMUT MM18642-5). In both specimens, B/H ratio decreases from 1.7 to 1.1 as the shells grow, and the whorl becomes higher than broad in the adult stage.

Group C: The specimens of this group possess early internal morphology of IC type, adorally concave ventral sinus at aperture, round to subrectangular whorl section, flat venter, rounded umbilical shoulder and fairly narrow umbilicus. The shell surface is generally smooth but some specimens have numerous rib-like elevations. A keel-like elevation on the venter is obsent. All specimens possess an unusually large initial chamber (925-1,050 μm in median diameter) and ammonitella (1,700-1,900 μm in diameter) (Figure 8). Ammonitella length ranges from 330 to 345° (Figure 9). The specimens of this group are restricted to the Lower Maastrichtian.

The shell at 3 mm in diameter is widely umbilicate (U/D=0.35) but it becomes narrowly umbilicate (U/D=0.24) with growth (Figure 7). The relative whorl thickness (B/H) is initially large (=1.6), but gradually decreases with growth up to 5 mm in diameter (Figure 7). The parameter remains constant in the stage of more than 5 mm in diameter (Figure 6).

Taxonomic relationship

Group A: All specimens of this genus hitherto described from Hokkaido and Sakhalin are characterized by the possession of an adorally concave aperture on the venter, a round to subrectangular whorl section and fairly narrow to wide umbilicus (Table 3). Such features agree with the characteristics of Group A. As already stated, the specimens of this group exhibit remarkably wide varia-

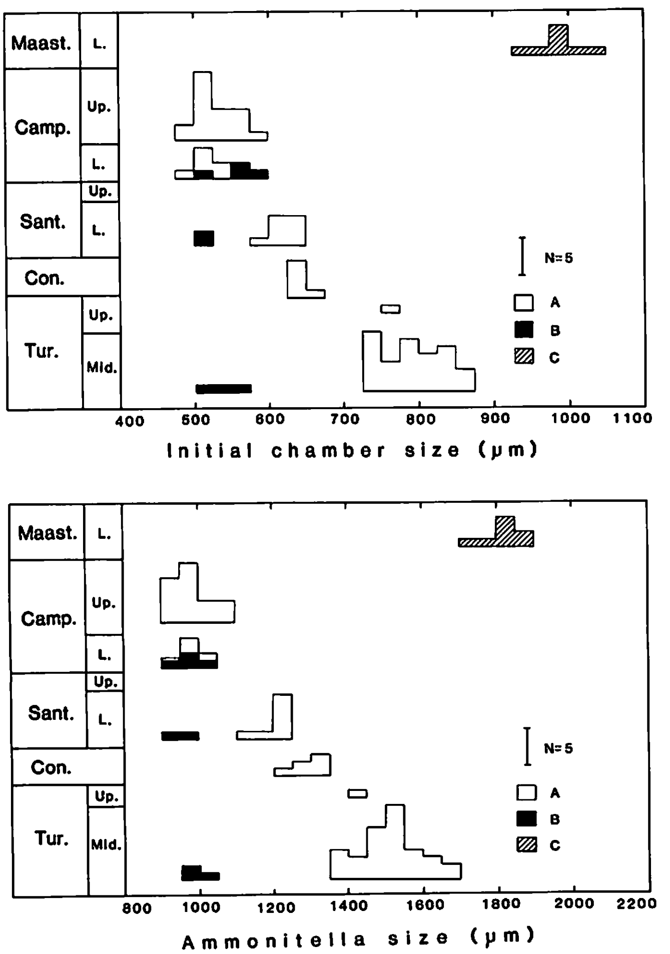


Figure 8. Variation in initial chamber size and ammonitella size for specimens of Groups A, B and C from different horizons. In Group A both sizes tend to decrease toward the upward sequence.

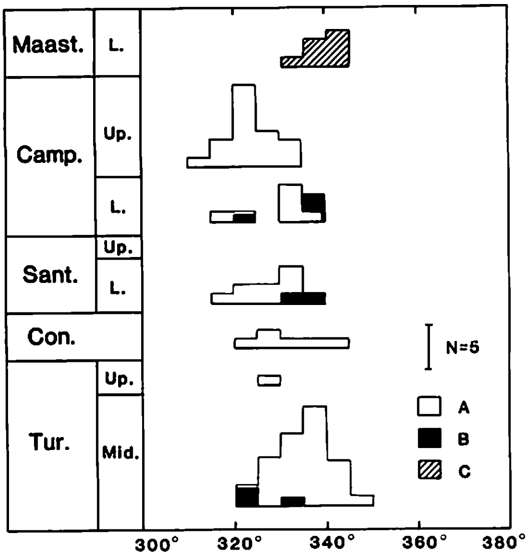


Figure 9. Variation in ammonitella length for specimens of Groups A, B and C from different horizons. There is no significant difference in the ammonitella length among the three groups.

tion in the external shell shape. They cannot be divided into subgroups by the shell form ratios because of the wide and continuous range of the variation. Sample AW1001A from the Upper Campanian of Soya area is a typical example showing wide shell shape variation. Furthermore, the shell form ratios (U/D, B/H) of the type and previously illustrated specimens are mostly included in the range of variation of the specimens in the sample (Figure 10). This evidence strongly suggests that these specimens merely represent the variants in a single species. Although the internal structure of these specimens cannot be examined, all the previously described species, *T. glabrus* (Jimbo), *T. sphaeronotus* (Jimbo), *T. crassus* (Jimbo), *T. popetensis* Yabe and *T. glabrus problematicus* Matsumoto, show an adorally concave aperture on the venter. These species should be, therefore, treated as synonymous, and are all included in Group A. The oldest species name, *T. glabrus*, is used here for these specimens in Group A. Judging from the apertural features and shell sizes of the figured specimens, *T.* cf. *epigonus* (Kossmat) and *T. superstes* Van Hoepen illustrated respectively by Yabe (1903) and Matsumoto and Miyauchi (1984) can also be identified as *T. glabrus*.

Group B: This group is represented by small-sized specimens with an adorally con-

Table 3. Measurements (in mm) of previously described or illustrated specimens of *Tetragonites* from the Upper Cretaceous of Hokkaido.

Authors	No.	Species	D	U	B	H	U/D	B/H	Remarks
Jimbo(1894)	(1)	Lytoceras glabrum	51.1	11.3	21.5	24.2	0.22	1.09	MM7513
	(2)	L. shaeronotum	40.8	8.9	21.6	19.8	0.22	1.17	MM7494
	(3)	L. crassum	24.9	6.8	13.2	11.6	0.27	1.14	MM7515
Yabe(1903)	(4)	Tetragonites glabrus	35.0	8.0	19.0	17.0	0.24	1.17	MM7461
	(5)	T. glabrus	65.0	14.0	36.0	32.0	0.22	1.12	
	(6)	T. shaeronotus	145.0	30.0	72.0	70.0	0.21	1.02	
	(7)	T. shaeronotus	68.9	13.5	36.7	34.3	0.18	1.07	MM7540
	(8)	T. popetensis	34.0	10.5	15.0	14.5	0.31	1.03	MM7460
	(9)	T. popetensis	20.5	5.5	9.0	9.0	0.27	1.00	MM7541
	(10)	T. cf. epigonus	34.4	9.4	16.1	14.7	0.27	1.09	MM7459
Matsumoto (1942b)	(11)	Epigoniceras glabrum var. problematica	87.0	21.0	37.3	40.7	0.24	0.92	MM5529
Matsumoto & Miyauchi(1984)	(12)	T. superstes	41.3	11.2	18.6	12.7	0.28	1.05	MNH.502
	(13)	T. popetensis	66.6	21.2	27.0	26.4	0.32	1.02	MNH.501

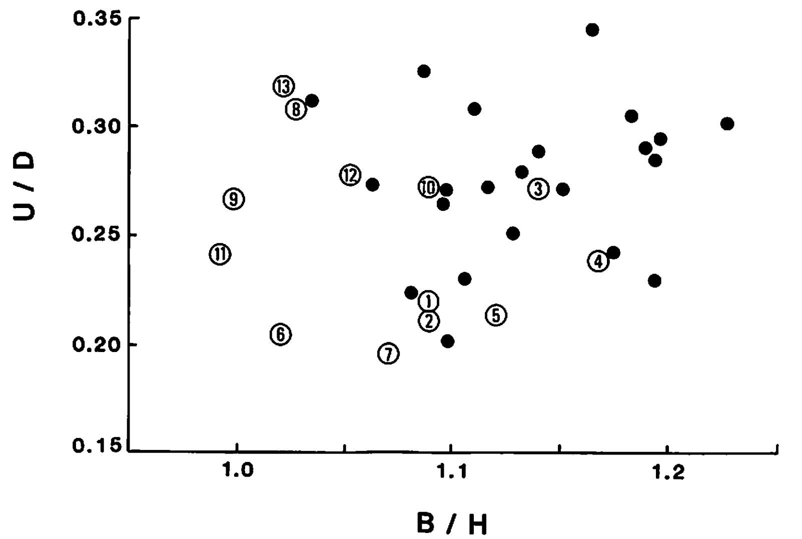


Figure 10. Scatter plot of umbilicus/diameter ratio (U/D) versus breadth/height ratio (B/H) for 22 specimens of Group A (black circle; more than 30 mm in diameter) in the Upper Campanian sample AW1001A from Soya area and 13 previously described or illustrated specimens of *Tetragonites* from Hokkaido (white circle). Number in each white circle corresponds to that in Table 3. The shell form ratios of type and illustrated specimens largely overlap with those of the specimens in the sample AW1001A.

vex aperture on the venter. Such a morphotype has not yet been described from the Upper Cretaceous of the North Pacific region including Hokkaido. Although the adult shell form and size more or less differ between the specimens from the Turonian — Coniacian and those from the Santonian — Campanian, because of the similarity in other shell characters, it is considered that the difference should be attributed to the phyletic transition within a lineage. A new species name, *T. minimus*, n. sp., is therefore given to this group.

Group C: Matsumoto (1942b, 1943) listed *Epigoniceras poptense* var. *frequence* from the Lower Maastrichtian of Tomiuchi area. Judging from Matsumoto's (1942b, p. 673) description, this variety appears to resemble some specimens of Group C in having numerous rib-like elevations on the whorls and a fairly narrow umbilicus. However, he did not describe the diagnostic characters of the variety, nor illustrated any material. Therefore, Group C is treated as a new species, *T. terminus*, n. sp.

Phylogeny

Although the phylogenetic relationships of the post-Cenomanian *Tetragonites* species have not been studied, those of Aptian to Cenomanian species have been discussed by Murphy (1967a) and Wiedmann (1973). Murphy (1967a) classified seventeen species into three morphological groups, based on their apertural shape, suture line and shell form. The *T. timotheanus* group was characterized by species with an adorally convex aperture on the venter, and has as its ancestor the Upper Aptian species, *T. subbeticus*. This group includes *T. timotheanus* from the Upper Albian, and *T. spathi* from the Lower Cenomanian.

T. minimus, n. sp. also possesses an adorally convex aperture on the venter, and therefore, according to Murphy's classification, it belongs to the *T. timotheanus* group. Furthermore, the Turonian specimens of this species resemble *T. spathi*, in having a wide umbilicus and a keel-like elevation on the venter. Therefore, *T. minimus* is considered to have originated from a species of this group, and its probable ancestor is *T. spathi*.

Other morphological groups proposed by Murphy (1967a) are the *T. rectangularis* group and the *T. kichini* group, both of which are represented by species with an adorally concave sinnous aperture on the venter. The former group was possibly the dominant stock of *Tetragonites*, and includes most species of mid-Cretaceous representatives. According to Murphy's (1967a) definition, *T. glabrus* can be assigned to this group. Many Albian and Cenomanian species of this group have been described by previous authors (*e.g.* Wiedmann, 1962; Kennedy and Klinger, 1977), but details of the intra- and interpopulational variation of shell form and phylogenetic relationships have not yet been realized. *T. glabrus* seems to have originated from a species of this group. However, it is at present difficult to identify its ancestor.

Santonian and Campanian *Tetragonites* having an adorally concave sinuous aperture on the venter consist of the following species: *T. margaritatus* Marshall, *T. simplex* (Marshall), *T. marshalli* (Collignon), *T. superstes* Van Hoepen, *T. mitraikyensis* Collignon, *T. beantalyensis* Collignon, *T. garudus* Forbes, *T. epigonus* Kossmat and *T. glabrus* (Jimbo) (Collignon, 1956; Kennedy and Klinger, 1977). *T. terminus*, n. sp., with the same apertural type, may have been derived from a species of this group. The exact ancestor of this species is, however, unknown because of the insufficiency of data on intra- and interpopulational variation and exact stratigraphical distribution for the above foreign species.

On the other hand, the three species of *Tetragonites* examined are well defined by their unique early internal shell features. The significance of early internal shell structure in the major classification of the Mesozoic Ammonoidea have been demonstrated by several paleontologists (Druschchits and Khiami, 1970; Druschchits and Doguzhayeva, 1974; Zakharov, 1974; Druschchits *et al.*, 1977; Tanabe *et al.*, 1979; Tanabe and Ohtsuka, 1985; Ohtsuka, 1986). According to Ohtsuka (1986), the Gaudryceratidae are characterized by the following early internal morphology in median section: nearly circular initial chamber, semi-circular caecum with a weakly constricted base, one to three short prosiphons and ventrally located siphuncle in most of the post-ammonitella growth stages. Such features are commonly observed in *T. glabrus*. The Tetragonitidae are now regarded as having been derived in the Aptian from the Gaudryceratidae (Wiedmann, 1962; Murphy, 1967b). If this interpretation is correct, it is apparent that *T. glabrus* preserves more ancestral characters in the early stage than *T. minimus* and *T. terminus*. The present study also suggests that *T. terminus*, n. sp. and *T. minimus*, n. sp. might have been derived from the stock with the early internal morphology of IA type including *T. glabrus*. Because of the similarity of apertural shapes, such a stock may correspond to the *T. rectangularis* group of Murphy (1967a).

According to Wiedmann (1973), *Tetragonites* rapidly diversified throughout the Tethyan realm during the Albian and Cenomanian, and thereafter had a distinct decline from Turonian to Maastrichtian. However, in Hokkaido in the northwestern Pacific region generally, the diversity of the Albian and Cenomanian members remained nearly constant until the end of Campanian or Maastrichtian.

Concluding remarks

This study reveals that the intrapopulational variation of shell form in *Tetragonites glabrus* is relatively wide, especially in the middle to later growth stage, and that many of the previously described species under the name of *Tetragonites* are synonymous with

T. glabrus. Moreover, the seemingly small variability of shell form in the previously described "species" was a result of extreme taxonomic splitting. More than twenty species of *Tetragonites* have hitherto been described from the Aptian to Cenomanian of the world. Their taxonomic and phylogenetic relationships should be re-examined by adequate evaluation of taxonomic characters from the viewpoint of population concept.

The smooth and featureless external morphology in *Tetragonites* causes difficult problems for phylogenetic reconstruction. However, three morphological types of early internal shell structure are clearly distinguished in *Tetragonites*. It is believed that such early characters are stable within a given species irrespective of time and may be strongly controlled by phylogenetic (genetic) factors. They may serve as a key for phylogenetic reconstruction not only in *Tetragonites* but also in other ammonoids.

Systematic description

Order Ammonoidea Zittel, 1884
Suborder Lytoceratina Hyatt, 1889
Superfamily Tetragonitaceae Hyatt, 1900
Family Tetragonitidae Hyatt, 1900
Genus *Tetragonites* Kossmat, 1895

Type species. — *Ammonites timotheanus* Pictet, 1848

Tetragonites glabrus (Jimbo)

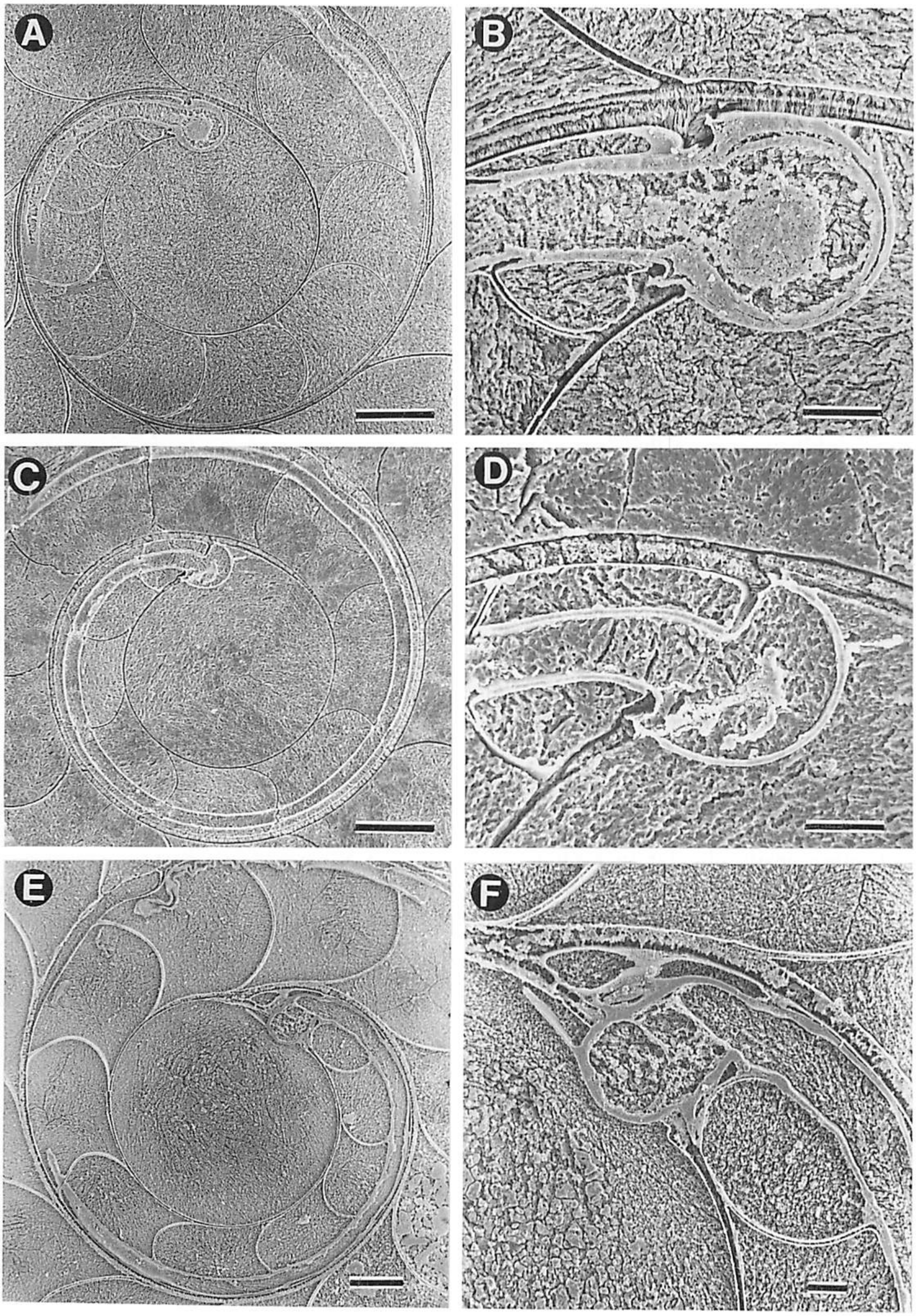
Figures 11A—B, 12

Lytoceras glabrum Jimbo, 1894, p. 180, pl. 22, figs. 2, 2a.
Lytoceras sphaeronotum Jimbo, 1894, p. 181, pl. 22, fig. 4.
Lytoceras crassum Jimbo, 1894, p. 181, pl. 22, figs. 5, 5a, 5b.
Tetragonites glabrus: Yabe, 1903, p. 43, pl. 7, figs. 2, 5; Tanabe and Kanie, 1978, p. 8, pl. 1, figs. 2a, 2b.
Tetragonites sphaeronotus: Yabe, 1903, p. 45, pl. 7, figs. 1a, 1b.
Tetragonites popetensis Yabe, 1903, p. 48, pl. 7, figs. 4, 6; Matsumoto and Miyauchi, 1984, p. 52, pl. 23, figs. 3a, 3b.
Tetragonites cf. *epigonus*: Yabe, 1903, p. 49, pl. 7, fig. 3.
Epigoniceras glabrum var. *problematica* Matsumoto, 1942, p. 672, fig. 1.
Tetragonites superstes: Matsumoto and Miyauchi, 1984, p. 52, pl. 23, fig. 2.

Type. — The holotype (UMUT MM7513; Jimbo, 1894, pl. 22, figs. 2, 2a) is a large-sized specimen with a deformed body chamber from the Upper Cretaceous of Ikandai, Urakawa area.

Material. — In addition to the holotype, 267 specimens [UMUT MM18638 (N=110), UMUT MM18640 (N=18), UMUT MM18641 (N=7), UMUT MM18643 (N=3), UMUT MM18645 (N=1), UMUT MM18646 (N=3), UMUT MM18647 (N=2), UMUT MM18648 (N=1), UMUT MM18649 (N=2), UMUT MM18650 (N=7), UMUT MM18651 (N=3), UMUT MM18652 (N=2), UMUT MM18653 (N=1), UMUT MM18654 (N=1), UMUT MM18656 (N=3), UMUT MM18557 (N=2), UMUT MM18658 (N=1), UMUT MM18660 (N=14), UMUT MM18661 (N=1), UMUT MM18662 (N=10), UMUT MM1863 (N=1), UMUT MM18664 (N=1), UMUT MM18665 (N=2), UMUT MM18666 (N=2), UMUT MM18668 (N=6), UMUT MM18669 (N=3), UMUT MM18670 (N=15), UMUT MM18672 (N=6), UMUT MM18673 (N=11), UMUT MM18674 (N=

→ **Figure 11.** Scanning electron micrographs of the early internal shell structure of three *Tetragonites* species in median section. Scale bars in A, C and E: 200 μm. Scale bars in B, D and F: 50 μm. **A-B.** *Tetragonites glabrus* (Jimbo), the Coniacian, Haboro area, Sample AH4087, UMUT MM 18665-1. **C-D.** *Tetragonites minimus*, n. sp., the Lower Campanian, Saku area, Sample AS2038B, UMUT MM18642-6, paratype. **E-F.** *Tetragonites terminus*, n. sp., the Lower Maastrichtian, Tomiuchi area, Sample SM1041, UMUT MM18636-2, paratype.


A
B
C
D
E
F

2), UMUT MM18675 (N=5), UMUT MM18676 (N=13), UMUT MM18677 (N=5), UMUT MM18679 (N=1), UMUT MM18680 (N=2)] are referable to the present species. The localities and ages of them are summarized in Table 1.

Diagnosis. — Large-sized species of *Tetragonites* characterized by adorally concave sinuous aperture on venter, nearly circular initial chamber in median section, subellipsoid caecum with weakly constricted base, and ventrally located siphuncle except for earliest first to fourth chamber stage.

Description. — Shell large, sometimes, exceeding 80 mm in diameter, rather evolute to moderately involute, with a fairly narrow to wide umbilicus even in the stage of more than 30 mm in diameter. Whorl round to subrectangular in cross section, with a rounded to flat venter, nearly flat to gently convex flanks, subangular to rounded umbilical shoulder and nearly vertical to subvertical umbilical wall. Shell surface nearly smooth, with fine and dense growth lines, and infrequent conspicuious rib-like elevations. They are prorsiradiate on the flanks, curved adapically at the peripheral shoulder and cross the venter with a shallow backward sinus. A keel-like elevation sometimes occurs in middle to late stage of the Santonian and Campanian specimens. Initial chamber nearly circular in median section. Caecum subelliptical in lateral view with a weakly constricted base, and its adapical end connects with the initial chamber wall by one to three short, adorally concave prosiphons. Flange weakly developed. Siphuncle occupies a central position near the proseptum, and then immediately shifts toward the venter in second to forth chamber stage. Thereafter it keeps a ventral position. Initial chamber and ammonitella medium- to large-sized (ranging 475-875 μm and 900-1;700 μm in median diameter, respectively), both showing a clear chronocline in size decrease in the Upper Cretaceous seqeunce of Hokkaido. Variation of ammonitella length is rather small (310 to 350° in volution), never marking a conspicuous historical trend.

Dimensions. —

	D (mm)	U (mm)	B (mm)	H (mm)	U/D	B/H
Holotype	51.1	11.3	26.5	24.2	0.22	1.10

For the measurements of other specimens, see Figures 4, 5, 7, 8 and 9.

Remarks. — In overall shell morphology *T. glabrus* (Jimbo) closely resembles some foreign species such as *T. epigonus* Kossmat (1895, p. 135, pl. 17, figs. 4, 5, 10), *T. superstes* Van Hoepen (1921, p. 10, pl. 2, figs. 17-20), *T. garudus* (Forbes) (1846, p. 102, pl. 7, fig. 1), *T. mitraikyensis* Collignon (1956, p. 86, pl. 11, fig. 2), *T. beantalyensis* Collignon (1956, p. 83, pl. 10, fig. 1), *T. marshalli* (Collignon) (1956, p. 86), *T. margaritatus* Marshall (1926, p. 151, pl. 20, fig. 5, pl. 30, figs. 5, 6) and *T. simplex* (Marshall) (1926, p. 150, pl. 20, figs. 11, 11a, pl. 32, figs. 3, 4). The narrowest and the widest umbilicate forms of *T. glabrus* also suggest affinities with *Pseudophyllites indra* Forbes (1846, p. 105, pl. 11, fig. 7) and *Saghalinites nuperus* (Van Hoepen) (1921, p. 13, pl. 3, figs. 3, 4).

The taxonomic relationship between *T. glabrus* and the above foreign species is, however, at present uncertain because of insufficient data on the intra- and interpopulational variation and exact stratigraphical distribution of the later.

Occurrence. — This species occurs abundantly from the Middle Turonian to the Upper Campanian of the Yezo Group in Hokkaido and south Sakhalin. This species is also known from the Turonian-Campanian of California (Matsumoto, 1959).

Tetragonites minimus, n. sp.

Figures 11C—D, 13-1—7b

Type. — A small-sized specimen (UMUT MM18667-1) from the Coniacian outcrop exposed along the middle course of the Obirashibe River (Loc. T1220 of Sekine *et al.*,

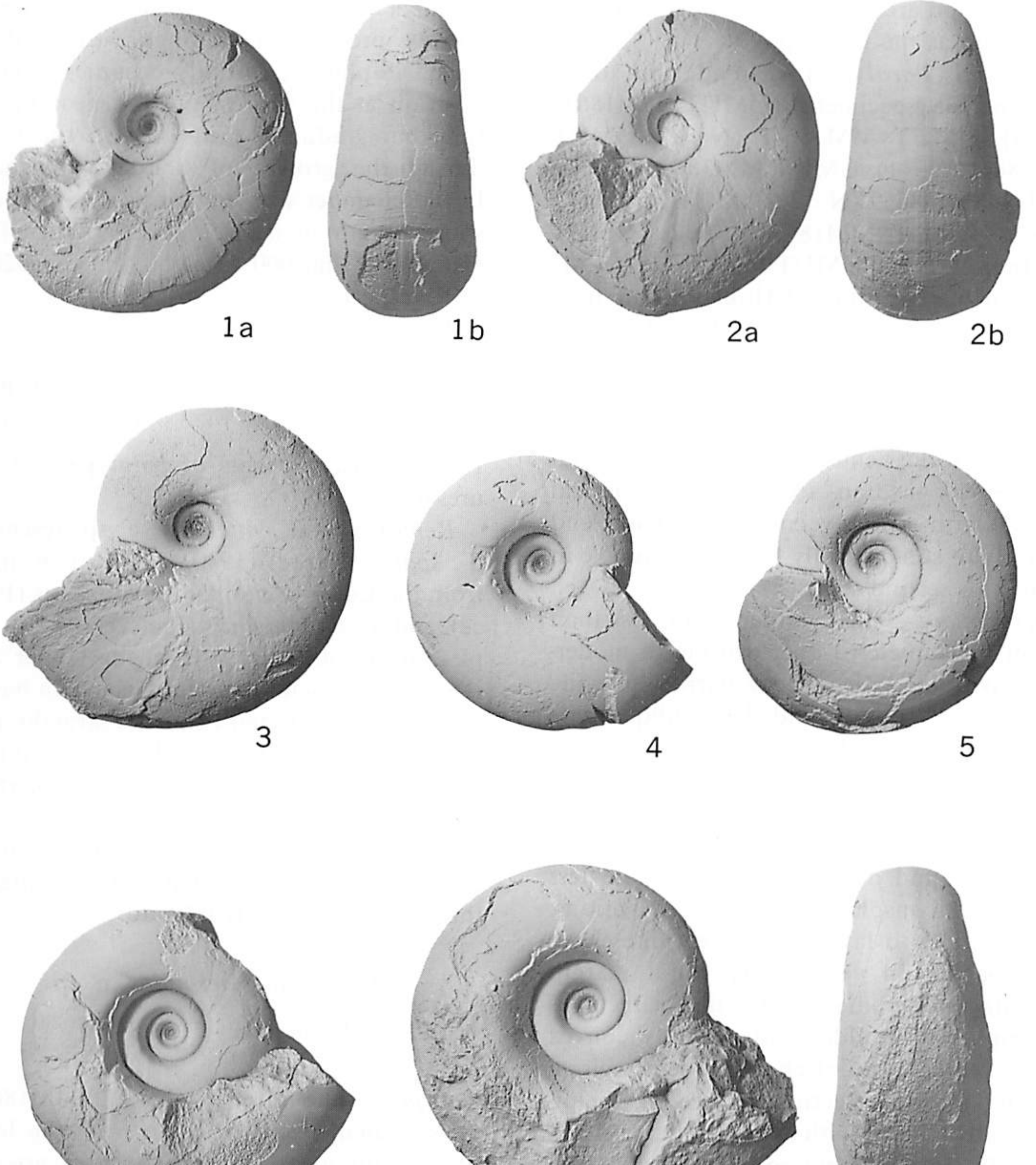


Figure 12. *Tetragonites glabrus* (Jimbo). For localities see Table 1. **1a–b.** UMUT MM18662-5, Sample AT1514, the lower Lower Santonian, Tappu area, ×0.8. **2a–b.** UMUT MM18653-1, Sample AH6033P, the upper Lower Santonian, Haboro area, ×0.8. **3.** UMUT MM18638-16, Sample AW1001A, the Upper Campanian, Soya area, ×1.0. **4.** UMUT MM18638-15, Sample AW1001A, the Upper Campanian, Soya area, ×1.0. **5.** UMUT MM18638-13, Sample AW1001A, the Upper Campanian, Soya area, ×1.0. **6.** UMUT MM18640-3, Sample AW1003, the Lower Campanian, Soya area, ×0.8. **7a–b.** UMUT MM18654-1, Sample AK1029A, the upper Lower Santonian, Kotanbetsu area, ×0.7.

1985), Tappu area, northwestern Hokkaido is designated as the holotype.

Material (*Paratypes*). — In addition to the holotype, 35 specimens [UMUT MM18639 (N=3), UMUT MM18642 (N=9), UMUT MM18644 (N=1), UMUT MM18655 (N=4), UMUT MM18659 (N=2), UMUT MM18671 (N=3), UMUT MM18678 (N=7), UMUT MM18681 (N=2), UMUT MM18682 (N=4)] from various localities of Hokkaido are used in the following description. Their localities and ages are summarized in Table 1.

Diagnosis. — Small-sized species of *Tetragonites* characterized by adorally convex aperture on the venter, nearly circular initial chamber in median section, hemispherical caecum with strongly constricted base, and centrally to sub-centrally located siphuncle in the first to second whorls.

Description. — Shell rather small, less than 30 mm in diameter, rather evolute to moderately involute, with a fairly narrow to wide umbilicus. Whorl rounded to subquadrate in cross section with a round venter, nearly flat to gently convex flanks, round umbilical shoulders and a nearly vertical umblilical wall. Shell surface sculptured with regularly spaced fine and dense growth lines and less frequent, inconspicuous rib-like elevations. In the middle to late stage, a keel-like elevation appears on venter. Apertural margin markedly prorsiradiate on the flanks, recurves at peripheral shoulder and adorally convex on the venter. Initial chamber nearly circular in median section. Caecum hemispherically shaped with a strongly constricted base. Its adapical end connects with initial chamber wall by one to three short, adorally convex prosiphons. Flange weakly developed. Siphuncle initially occupies a central position at the earliest portion near proseptum, but gradually shifts toward the venter during the growth of first-second whorls. Initial chamber size, ammonitella size and its spiral length in median section range from 500 to 600 μm, 900 to 1,050 μm and 320 to 340°, respectively.

Dimensions. —

	D (mm)	U (mm)	B (mm)	H (mm)	U/D	B/H
Holotype	28.1	8.9	12.3	11.0	0.32	1.12

For the measurements of paratypes see Figures 6-9.

Remarks. — *T. minimus*, n. sp. resembles *T. spathi* (Fabre) (1940, p. 214, pl. 6, fig. 1) from the Lower Cenomanian of Cassis (France), and *T. timotheanus* (Pictet) (1848, p. 295, pl. 2, fig. 6, pl. 1, fig. 9) from the Upper Albian of the French Alps near Geneva in having an adorally projected or nearly straight aperture on the venter, but it is distinguished from these taxa in having an arch-shaped apertural margin on the venter.

Occurrence. — This species ranges from the Lower Turonian to the Upper Campanian of the Yezo Group in Hokkaido.

Tetragonites terminus, n. sp.

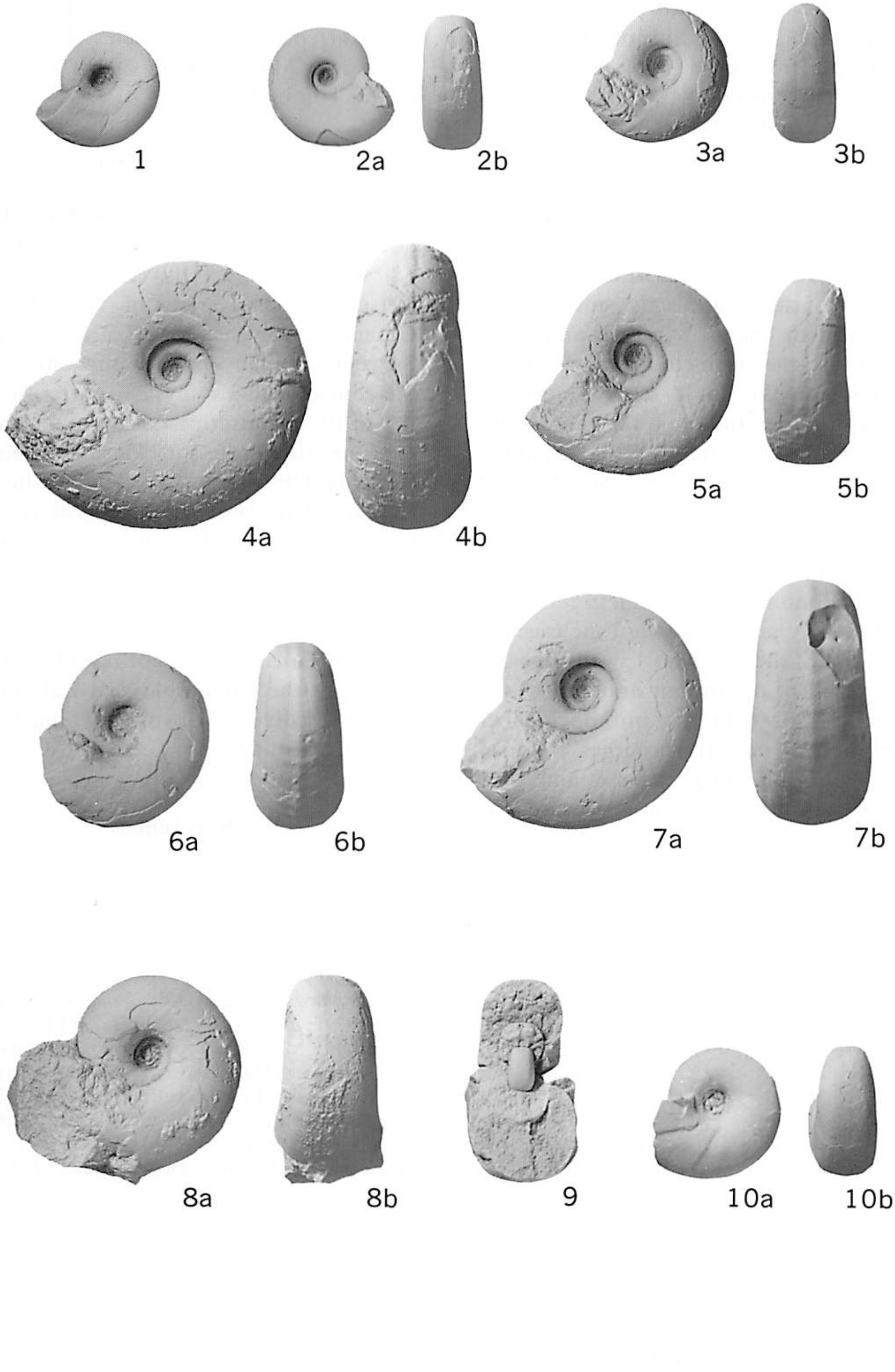
Figures 11E—F, 13-8—10

Type. — The holotype (UMUT MM18635-1) is a small-sized specimen from the lower Maastrichtian of the Ichiyanagi-no-sawa

→ **Figure 13. 1—7:** *Tetragonites minimus*, n. sp., ×1.5. For localities see Table 1. **1.** UMUT MM18642-1, Sample AS2038B, the Lower Campanian, Saku area, paratype. **2a-b.** UMUT MM18655-1, Sample AK1029B, the upper Lower Santonian, Kotanbetsu area, paratype. **3a-b.** UMUT MM18678-1, Sample AT1578, the Middle Turonian, Tappu area, paratype. **4a-b.** UMUT MM18667-1, Sample AT1551, the Coniacian, Tappu area, holotype. **5a-b.** UMUT MM18671-1, Sample AT1201B, the Middle Turonian, Tappu area, paratype. **6a-b.** UMUT MM18682-1, Sample AT2100, the Lower Turonian, Tappu area, paratype. **7a-b.** UMUT MM18681-1, Sample AW2001P, the Lower Turonian, Soya area, paratype. **8—10:** *Tetragonites terminus*, n. sp., ×1.5. **8a-b.** UMUT MM18635-1, Sample SM1048, the Lower Maastrichtian, Tomiuchi area, holotype. **9.** Sectional view, UMUT MM18635-2, Sample SM1048, the Lower Maastrictian, Tomiuchi area, paratype. **10a-b.** UMUT MM18635-4, Sample SM1048, the Lower Maastrichtian, Tomiuchi area, paratype.

(Loc. H12d in Matsumoto 1942a), Tomiuchi area, southern central Hokkaido.

Material (*Paratypes*). — In addition to the holotype, 7 specimens [UMUT MM18635-2 ~8] from the type locality and 9 specimens [UMUT MM18636 (N=3), UMUT MM18637 (N=6)] from other localities are used in the following description. Their



localities and ages are summarized in Table 1.

Diagnosis. — Small-sized species of *Tetragonites* characterized by adorally concave sinuous aperture on venter, unusually large-sized initial chamber, elongate subellipsoid caecum without any conspicuous constriction at its base, relatively long and straight prosiphon, and abrupt shift of siphuncular position from dorsum to venter within the first camera.

Description. — Shell rather small, less than 20 mm in diameter even in adult, involute, with a fairly narrow umbilicus. Whorls round to subrectangular in cross section, with a flat venter, gently convex flanks, rounded umbilical shoulder and subvertical umbilical wall. Shell surface seemingly smooth, but ornamented with fine growth lines and wide-spaced rib-like elevations, both of which are prorsiradiate on the flank, recurve near the peripheral shoulder and cross the venter with a shallow backward sinus. Initial chamber elliptical in median section. Subellipsoid caecum lacks a conspicuous constricted base. Its adapical end connects with the inner surface of initial chamber by a long and nearly straight prosiphon. Proseptum is relatively long and acutely projects toward the caecum. Early portion of the first whorl swells remarkably as a result of discordant underlay of the ammonitella wall with the initial chamber wall. Siphuncle initially occupies a dorsal position within the first camera, and then immediately shifts its position toward the ventral side. Marginal approximation is completed in the third camera, and thereafter, it retains a ventral position. The first septum is adorally concave, but subsequent septa are adorally convex. Median diameter of initial chamber, and maximum diameter and spiral length of ammonitella range from 925 to 1,050 μm, 1,700 to 1,900 μm and 330 to 345°, respectively.

Dimensions. —

	D (mm)	U (mm)	B (mm)	H (mm)	U/D	B/H
Holotype	19.4	5.2	10.1	8.6	0.27	1.17

For the measurements of other paratypes see Figures 6-9.

Remarks. — *T. terminus*, n. sp. resembles the narrowly umbilicate form of *T. glabrus* (Jimbo) in the external shell shape, but the two species are easily distinguished by the difference in the early internal shell features.

Occurrence. — This species is restricted to the Lower Maastrichtian of the Yezo Group in the Tomiuchi area.

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Haboro 羽幌, Ikandai 井寒台, Kotanbetsu 古丹別, Nukibetsu 貫気別, Obira 小平, Saku 佐久, Soya 宗谷, Tappu 達布, Tomiuchi 富内, Toyoshimizu 豊清水, Urakawa 浦河.

北海道上部白亜系産 *Tetragonites* 属アンモナイトの分類：北海道の白亜系蝦夷層群より産出する Tetragonites 属アンモナイトについて，既存種の模式•図示標本を加えた豊富な標本をもとに諸形質の分類学的評価を行った。その結果に基づき，T. glabrus (Jimbo) を再定義するとともに 2 新種を識別し，*T. minimus*, *T. terminus* と命名し記載した。

これら 3 種は初期殻体内部構造や殻口縁の形など不連続な形質によって容易に識別される。*T. glabrus* はチューロニアン階中部からカンパニアン階上部に産し，螺環の形や表面装飾などに大きな変異がみられる。従来記載された *T. sphaeronotus* (Jimbo), *T. crassus* (Jimbo), *T. popetensis* Yabe などは本種内の変異型とみなせる。*T. minimus* は小型の種で，チューロニアン階下部からカンパニアン階上部に産する。*T. terminus* はマストリヒチアン階下部のみに産し，巨大な胚殻を有する。 重田康成
