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On a Maastrichtian (Cretaceous) inoceramid species *Sphenoceramus hetonaianus* (Matsumoto) from the Hobetsu district, Hokkaido

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Abstract
Inoceramus hetonaianus Matsumoto, 1952 was established on the syntypes from the Fukaushi Sandstone at several localities in the Hobetsu district. Based on our cooperative study of a large collection in the Hobetsu Museum from another locality of the same formation, as well as the syntypes in Kyushu University, we redescribe this species under the genus *Sphenoceramus* Böhm, giving its diagnosis and features of variation. Its main part of valve is obliquely sphenoid with broader angle of umbonal inflation; its posterior wing is flat and fairly large with a longer hinge line and more obtuse posterior hinge angle, as compared with well known species of the same genus in the Coniacian to Lower Campanian of the North Pacific region. It resembles *S. haboroensis* Toshimitsu in the entire outline of shell but differs by its less uniform ribbing, with more or less stronger or coarser major ribs developed in later growth-stages. With respect to the ornament a resemblance between a certain form of *S. naumanni* and *S. hetonaianus* cannot be overlooked. The phylogenetic relationships of this species with the ancestral species are hardly concluded on account of the absence of linking material and the considerable time gap. Anyhow, this species is so far a unique representative of *Sphenoceramus* in the Maastrichtian stage. It defines a zone together with *Pachydiscus* (*Neodesmoceras*) *gracilis*, indicating most probably the upper part of the Lower Maastrichtian in Japan.

Key words — *Sphenoceramus*, *S. hetonaianus*, Maastrichtian, Fukaushi Formation, Hobetsu

I Introduction

Inoceramus hetonaianus Matsumoto was established in an appendix to a geological paper on the late Cretaceous Izumi Group of Awaji Island (Tanaka *et al.*, 1952). The original description by Matsumoto was based mainly on a number of specimens from the Upper Hakobuchi Subgroup of Hokkaido but it was very short and written in Japanese.

For several reasons a more precise description of this species in English has been delayed. Fortunately the repair work of the road cutting in 1990 at a locality in the Hobetsu district had brought a large collection of this species to the Hobetsu Museum and we have been afforded facilities to study them in the Museum. Moreover, representative specimens were on loan for further study. The previously handled specimens were mostly collected by T.M. from the Hobetsu district (including the Hetonai area in an older administrative place name, now called Tomiuchi) and have been deposited in Kyushu University. They are of course restudied on this occasion. Some other specimens of subsequent (later than 1952) collection in Kyushu University are also added to the material of this study.

The present study has revealed the specific characters, features of variation and affinities of this species as an interesting Maastrichtian representative of *Sphenoceramus*.

II Note on stratigraphy

The stratigraphy of the Cretaceous deposits in the southern part (previously called Hetonai area) of the Hobetsu district was described by Matsumoto (1942) who followed Otatsume (*in* Uwatoko and Otatsume, 1933) in major division. This is cited here with a slight alteration as follows in ascending order:

Upper subgroup of the Yezo Group (Coniacian to earliest Campanian)

Lower subgroup of the Hakobuchi Group (Campanian)

Upper subgroup of the Hakobuchi Group (Maastrichtian)

- Lower Sandy Siltstone [unnamed]: 300m
- Fukaushi Sandstone Formation : 150-160m
- Upper Sandy Siltstone [unnamed]: partly lacking
- Sanushibe Sandstone Formation : lacking in the south

The name Hakobuchi was derived from the Hakobuchi gorge, farther north in the Oyubari area, but the fossil faunas of the group occur more frequently in the southern Hobetsu area. Hence the Hetonaian was proposed for the upper unit of the tripartite biostratigraphic division of the Upper Cretaceous in Japan (Matsumoto, 1943). It is mainly Campanian and Maastrichtian.

The Fukaushi Formation is best exposed near the curved part (Ohmagari) of the Mukawa River between Tomiuchi and Fukaushi and also along the creek called the Panke-rusa-no-sawa (=Panke-tosa-no-sawa by Matsumoto, 1942), a branch of the Mukawa. It is subdivided into 6 members, marked as IVc1 to IVc6, according to the detailed features of the sandstone. Fossil mollusks and others occur abundantly in several parts of the formation. *S. hetonaianus* is one of them.

III Palaeontological description

Family Inoceramidae Zittel, 1881
Genus *Sphenoceramus* J. Böhm, 1915

Type species — *Inoceramus cardissoides* Goldfuss, 1835.

Remarks. — *Sphenoceramus* was introduced by Böhm (1915, p. 183) as a "Formenreihe" (morphological series or group) of the inoceramids which has an obliquely extended sphenoid main part of the valve falling down to a posterior wing often demarcated by a long groove. It is equivalve. In some species a more or less strong radial groove runs on the posterior part of the main valve. Böhm has already noticed an anterior ear giving a notch for the byssus in such species as *S. nasutus* (Wegner) (1905, p. 167, pl. 10, fig. 3).

Seitz (1965) ascribed *Sphenoceramus* to a subgenus of *Inoceramus*, describing a number of interesting species with fine illustration. Since Matsumoto *et al.* (1982), many of Japanese authors have treated *Sphenoceramus* as an independent genus. In addition to concentric ribs of the first and second orders oblique and/or divergent ribs or radial ribs or riblets and/or radial grooves are developed in a considerable number of species.

Glasunov (1967) proposed *Schmidticeramus, Sachalinoceramus* and *Pennatoceramus*, but we do not use them because we refrain from too much splitting.

Various species from the northern Pacific region have been established by Yokoyama (1890), Michael (1899) and Sokolow (1914). Nagao and Matsumoto (1940), Glasunov (1967), Pergament (1974) and Toshimitsu (1988), among others, have added more species, some of which are, however, synonyms of previous ones (see Noda, 1988).

Sphenoceramus hetonaianus
(Matsumoto, 1952)

Plate I, Figs. 1-12; 15, 16; Plates II-IV

Inoceramus hetonaianus Matsumoto, *in* Tanaka *et al.*, 1952, p. 72, fig. 2; Matsumoto, 1959, p. 87, pl. 11, fig. k; Noda and Matsumoto, 1976, 45-268, 45-269-fig. 12; Zonova, 1992, p. 186, pl. 98, figs. 8-10; 11, 12-13.

Material. — *Inoceramus hetonaianus* Matsumoto, 1952 was established on a

Table 1. Illustrated specimens of *Sphenoceramus hetonaianus* and *S.* aff. *hetonaianus*

Register No.	V	Locality	Pl.	Fig.	Remarks	Register No.	V	Locality	Pl.	Fig.	Remarks
GK.H626a	L	H33d	I	3, 4	LT, x1.2	HMG 937	B	H311	II	1-4	Hy, x1
GK.H629a	L	H33d	I	1	ST, x1	HMG 938	B	H311	II	5-8	Hy, x1
GK.H629b	L	H33d	I	5	ST, x1	HMG 939	R	H311	III	4,6,7	Hy, x1
GK.H634a	R	H36b	I	2, 6	ST, x1	HMG 940	B	H311	III	4-7	Hy, x1
GK.H634b	L	H36b	I	9	ST, x1.5	HMG 942	R	H311	III	1-3	Hy, x1
GK.H634c	R	H36b	I	7, 8	ST, x1	HMG 942	R	H311	IV	9	Part, x2
GK.H634e	B	H36b	I	11	ST, x2	HMG 953	L	H311	III	8-10	Hy, x1
GK.H8400	L	K65p	I	10	Hy, x1.2	HMG 953	L	H311	IV	8	Part, x1.5
GK.H8402a	B	K57	I	12	Hy, x1.2	HMG 959	R	H311	III	11,12	Hy, x2
						HMG 993	B	H311	IV	4-6	Hy, x1
GK.H8401	L	Awaji	I	15,16	cf., x1	HMG 994	R	H311	IV	7	Hy, x1.9
GK.H633a	R	H15a	I	14	aff.,x1	HMG 998	B	H311	IV	1	Hy, x1
GK.H633b	L	H15a	I	13	aff.,x1.2	HMG 999	L	H311	IV	2, 3	Hy, x1

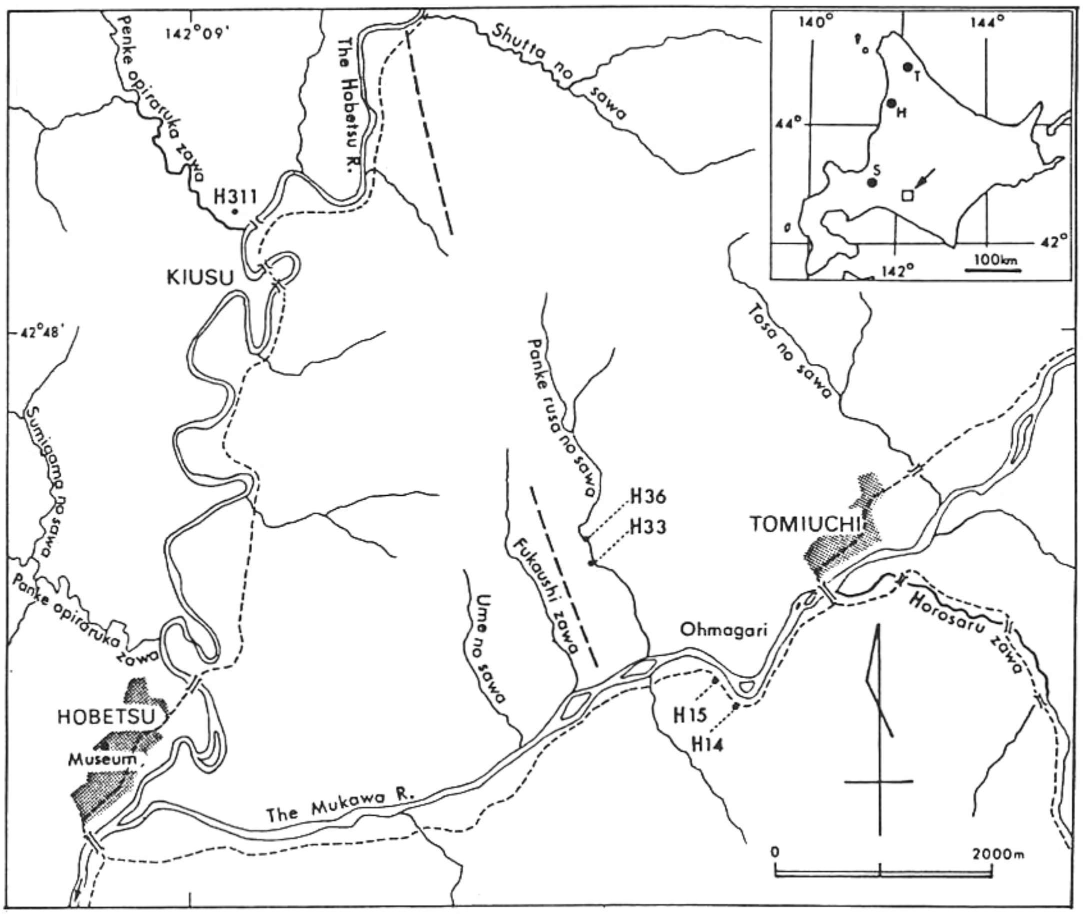
Abbreviations — V = Valve(s), B = Both, L = Left, R = Right; Pl. = Plate, Fig. = Figure(s); LT = Lectotype, ST = Syntype, Hy = Hypotype; GK. = Geological Collection, Department of Earth and Planetary Sciences, Kyushu University, HMG = Hobetsu Museum Geological Collection.

number of syntypes from Member IVc3, more or less silty, fine-grained sandstone in the middle part of the Fukaushi Sandstone Formation, exposed at localities H33d and H36b on the Panke-rusa-no-sawa and locality H14a, b, Ohmagari, all in the Hobetsu district, collected by T.M. in 1938. Text-fig. 2 of Matsumoto (1952) was a synthetic drawing based on the syntypes. GK.H626a from loc. H33d (Pl. I, Figs. 3, 4) is hereby designated as the lectotype. This and some other syntypes are illustrated in this paper (Pl. I, Figs. 1-11) (see also Table 1).

In addition to the above syntypes, a large number of specimens were excavated in 1990 at locality H311 from a member of silty fine-grained sandstone in the Fukaushi Formation and are now held by the Hobetsu Museum. As they are contained mostly in sandy calcareous nodules, some of them are well-preserved and the diagnostic characters are observable by careful cleaning. The representative specimens are illustrated in Plates II-IV and listed in Table 1. The localities mentioned above are shown in Text-fig. 1 (see also maps in Matsumoto, 1942, pls. 16, 17).

Specific characters. —Shell small to medium-sized, equivalve and inequilateral; the entire shell outline including posterior wing is subrhomboid; the main part of valve (here called disk) subtrigonal, with beak angle (β) about 90° (sometimes more obtuse or slightly acute), almost straight obliquely to the extremity of asymmetrically rounded ventral margin, forming a broadly sphenoid shape.

Hinge line (s) fairly long, about or somewhat over half of shell length (l). Posterior wing flat and triangular, with obtuse apex ($\gamma = 130°$ or more) and very long basal line which forms a demarcation from the moderately to gently convex main part of the valve. Only in the postero-ventral part the main disk merges gradually to the flat wing, whereas the major part of the wing is supported by moderately thick hinge plate. Ligamental pits numerous, with moderate density and depth. Antero-dorsal portion of the umbonal part somewhat more inflated than other parts, falling rapidly down to the antero-dorsal margin



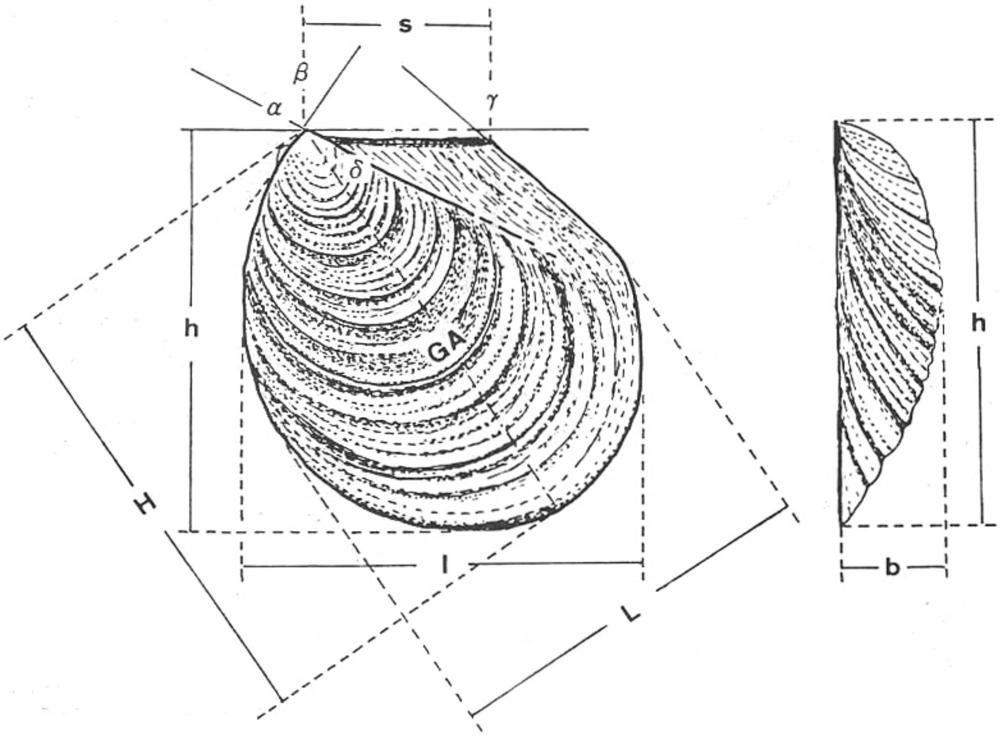
Text-fig. 1. Map of the Hobetsu area, showing sites of the fossil-localities (small solid circles) where *Sphenoceramus hetonaianus* and *S.* aff. *hetonaianus* were collected.

Thick broken line is a fault. For the geological map see Matsumoto (1942, pl. 16) and Matsumoto and Toshimitsu (1992, text-fig. 1). Inset at the upper right corner is the outline map of Hokkaido in which an arrow indicates the Hobetsu area; S: Sapporo, H: Haboro and T: center of the Tonbetsu Valley.

where tiny anterior ear is annexed below the beak.

Surface of the young part of disk ornamented with narrow and sharp-headed concentric ribs. In the succeeding middle or main growth-stage major low elevations or stronger ribs developed and combined with minor or weaker ones, often showing irregularity in appearance. Very faint radial ornament may occur in some individuals. Surface of the posterior wing ornamented with very fine, nearly straight, very oblique, subparallel lirae and striae. In the late growth-stage some of the lirae can be traced as extensions from the concentric ribs on the disk.

Biometry. —On the well-preserved specimens from locality H311, the selected characters h, l, b, H, L, s, α, β, γ, δ, l/h, b/h, L/H and s/l are measured as in Table 2. The specimens HMG 937, 938, 940, 993 and



Text-fig. 2. Basic morphology for measurements.

b: shell breadth, h: shell height, l: shell length, s: length of hinge line, H: maximum linear dimension from umbo to ventral extremity, L: maximum linear dimension perpendicular to H, GA: growth axis, α: anterior hinge angle, β: beak angle (angle of umbonal inflation), γ: posterior hinge angle, δ: obliquity, angle between hinge line and GA.

Table 2. Measurements of *Sphenoceramus hetonaianus*. Linear dimension in mm.

specimen	V	h	l	b	H	L	s	α	β	γ	δ	l/h	b/h	L/H	s/l
HMG 937	L	36.4	38.8	8.9	39.8	31.2	20.0	115°	90°	133°	55°	1.07	0.24	0.78	0.52
	R	33.5	35.5	8.5	38.0	30.7	18.1	114°	90°	132°	56°	1.06	0.25	0.81	0.51
HMG 938	L	43.3	45.1	11.0	49.4	41.8	23.4	114°	95°	146°	57°	1.04	0.25	0.85	0.52
	R	31.0	32.5	7.9	34.5	29.2	16.6	115°	93°	146°	56°	1.05	0.25	0.85	0.51
HMG 940	L	29.4	32.0	8.5	32.6	28.3	16.1	122°	101°	138°	59°	1.09	0.29	0.87	0.50
	R	38.2	43.4	11.8	46.4	36.2	24.5	116°	101°	139°	45°	1.14	0.31	0.78	0.57
HMG 942	R	35.0	35.5	10.2	39.5	35.2	17.7	109°	90°	129°	63°	1.01	0.29	0.89	0.50
HMG 959	R	17.2	18.5	4.1	19.5	16.8	-	120°	98°	-	55°	1.08	0.24	0.86	-
HMG 993	L	29.5	31.4	7.8	32.7	29.1	18.0	118°	99°	132°	57°	1.06	0.26	0.89	0.57
	R	29.4	31.4	7.8	34.0	29.3	18.0	118°	95°	131°	53°	1.07	0.27	0.86	0.57
HMG 998	L	20.4	20.6	4.8	25.9	17.5	11.5	98°	89°	130°	45°	1.01	0.24	0.68	0.56
	R	20.3	20.6	4.6	25.6	17.4	11.5	98°	90°	132°	44°	1.01	0.23	0.68	0.56
HMG 999	L	37.6	36.4	8.4	44.2	30.0	20.6	99°	89°	132°	52°	0.97	0.22	0.68	0.57

Reference. V : valve, L : left valve, R : right valve,
l/h : simple ratio of l vs. h, b/h : simple ratio of b vs. h,
L/H : simple ratio of L vs. H, s/l : simple ratio of s vs. l.
For others readers may refer to Text-fig.2.

Table 3. Biometric characters of *Sphenoceramus hetonaianus*.

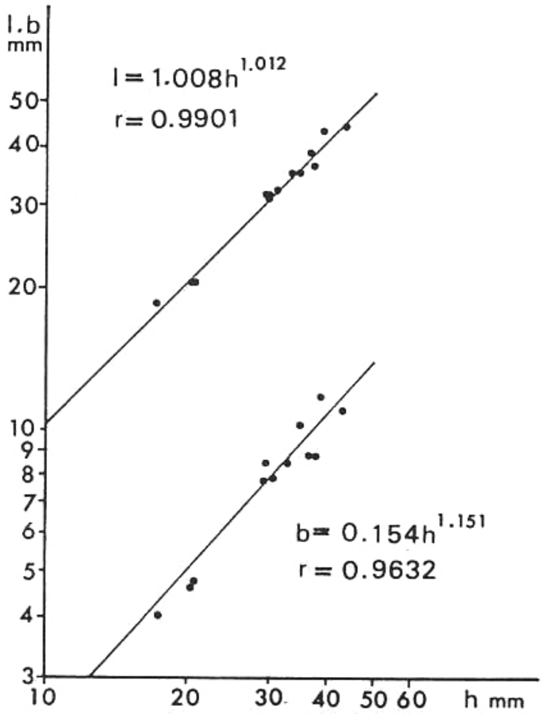
	α	β	γ	δ	l/h	b/h	L/H	s/l
N	11	11	10	11	11	11	11	10
m	110.7	92.5	134.3	53.9	1.039	0.249	0.803	0.539
s	8.45	3.67	6.27	5.43	0.0345	0.0192	0.0849	0.0292
v	7.63	3.97	4.67	10.07	3.32	7.71	10.57	5.42

Reference. *N* : sample size, *m* : mean value, *s* : standard deviation,
v : Pearson's coefficient of variation

998 are conjoint valves, which show nearly equal dimensions respectively, except for HMG 940.

The statistics, therefore, have been taken for the above tabulated specimens, excluding HMG 940 which may have been deformed secondarily. The mean value *m*, standard deviation *s* and Pearson's coefficient of variation *v* are shown in Table 3. The characters δ and L/H are considerably variable, whereas those of others are fairly stable.

The average relative growth of shell length (l) vs. shell height (h) and shell breadth (b) vs. shell height (h) are demonstrated in Text-fig. 3. The growth index (α), Y intercept (β) of the reduced major axis and the coefficient of correla-



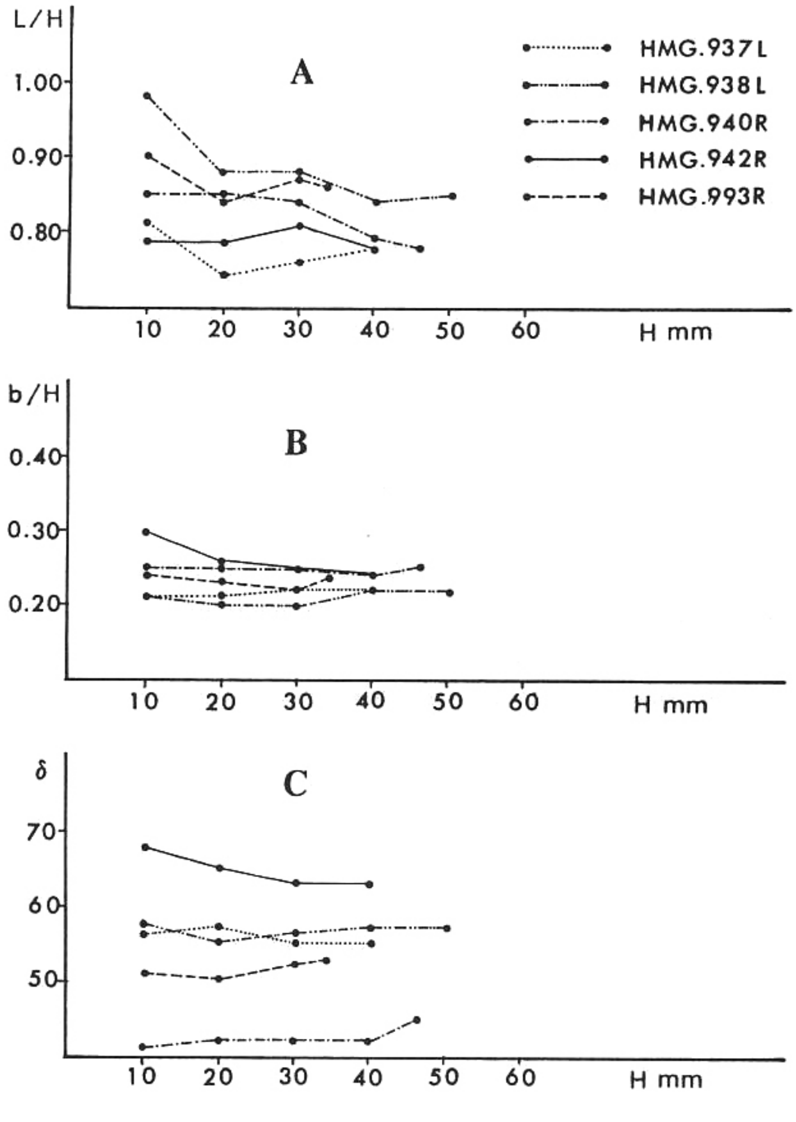
Text-fig. 3. Diagram showing the average relative growth of *Sphenoceramus hetonaianus.*

Table 4. Relative growth of *S. hetonaianus* and other species of *Sphenoceramus.*

species	N	$\alpha_{l.h}$	$r_{l.h}$	evaluation	$\alpha_{b.h}$	r_{bh}	evaluation
S. hetonaianus	13	1.012	0.9901	isometry	1.151	0.9632	isometry
S. naumanni	9	0.824	0.9931	negative allometry	1.035	0.9765	isometry
S. yokoyamai	8	0.730	0.9894	negative allometry	1.051	0.9831	positive allometry
S. nagaoi	10	0.833	0.9959	negative allometry	0.888	0.9937	negative allometry
S. transpacificus	8	0.859	0.9956	negative allometry	0.929	0.9846	isometry
S. orientalis	9	0.822	0.9906	negative allometry	0.658	0.9791	negative allometry
S. schmidti A	10	0.872	0.9916	negative allometry	0.679	0.9540	negative allometry
S. schmidti B	10	0.837	0.9902	negative allometry	0.802	0.9571	negative allometry
S. sachalinensis A	10	0.819	0.9868	negative allometry	0.898	0.9387	isometry
S. sachalinensis B	8	0.920	0.9959	negative allometry	0.992	0.9143	isometry

Reference. N : sample size, $\alpha_{l.h}$: growth index of l vs. h, $r_{l.h}$: correlation coefficient of l vs. h, $\alpha_{b.h}$: growth index of b vs. h, $r_{b.h}$: correlation coefficient of b vs. h, A : high form, B : broad form.

tion (r) are calculated. In reference to the basic criteria by Hayami and Matsukuma (1970, p. 601, text-fig. 12; also 1971, p. 150, table 2; p. 151, fig. 8), the relative growth l vs. h and b vs. h are both within a scope of isometry. Table 4 is the relative growth of the above bivariate characters of *S. hetonaianus* in comparison with that of some other



Text-fig. 4. Diagram showing the ontogenetic change in selective characters of *Sphenoceramus hetonaianus*.
A: simple ratio L/H, B: simple ratio b/H, C: obliquity.

Sphenoceramus species (cited from Noda, 1988). *S. hetonaianus* shows an isometry in both of l vs. h and b vs. h, whereas the other species show negative allometry in the relative growth l vs. h and show isometry or positive and/or negative allometry in that of b vs. h.

The ontogenetic change of L/H, b/H and obliquity (δ) of selected five specimens are demonstrated in Text-figs. 4A, B and C respectively. As is clear from Text-fig. 4, the simple ratio b/H is nearly constant throughout growth and its individual difference is not great, whereas the obliquity is also nearly constant with growth but somewhat different between individuals and the simple ratio L/H varies considerably with growth and also between individuals.

Observation. —A large collection of the Hobetsu Museum from one and the same locality has enabled us to make clear the diagnostic characters and also the variable features of this species.

The typical form, so called in this paper, is represented by such specimens as HMG 937 and HMG 938. The posterior wing is well exhibited in them and some others of HMG. The lectotype and several other syntypes also show the wing. In many cases, however, the posterior wing is partly exposed or concealed by rock matrix or even broken away.

The anterior ear is present in this species, although it was missed previously. Through careful trimming and cleaning (by S. T.), the ear is revealed on several specimens, e.g. HMG 937, HMG 993, HMG 998 and HMG 1004, or its basal section is shown when the ear itself was cut away, as in HMG 938, HMG 940, HMG 942, HMG 953 and HMG999.

The shell size of the typical form is 50 to 60 mm in the dimension (H) along the growth axis. The lectotype (with H=37 mm) is probably middle-aged, for its ventral part is broken. Smaller specimens are numerous but many of them are juveniles. The largest among the specimens at our disposal is 80 mm in H as in HMG 953, or nearly 90 mm in H as in HMG 965, although these examples are somewhat deformed secondarily.

The shell-form is variable to some extent. This is shown by a large range of the simple ratio L/H or that of the degree of obliquity (δ) (see Table 2). The curvature along the anterior margin is also variable, with a considerable convexity in the typical form but less so in some others. There is furthermore a change of L/H with growth. Should the stage of change be retarded or accelerated (see Text-fig. 4), the difference in the outline of shell between individuals would become multiple. As the characters l/h, b/h, s/l and γ are stable and the ranges of angles α and β are moderate, the shell-form does not vary at random in this species, showing the features as if certain ancestral characters have been retained or modified.

The ornament of this species is considerably variable. In the typical form mentioned above moderately coarse major ribs are developed on the main part of valve in the main growth stage and combined with minor ribs which are often finer and denser than the simple ribs of younger part.

In some other specimens, e.g. HMG 942 (rather small example), HMG 999 (medium-sized) and HMG 953 (fairly large), minor ribs predominate over very faint major undulations and are regularly fine for a long period of life.

There is so to speak the ornament of an intermediate state between the above two cases. For example, in GK.H629a and GK.H634c, the major ribs on the main or middle-aged part are less elevated than those of the typical form, whereas the minor ribs are more distinct, often doubled and at periodic intervals some of them are somewhat stronger than others with accompanied deeper interspaces. There are low major elevations corresponding to these periods. Similar features with stronger ribs and deeper interspaces at rather irregular intervals are not uncommon in the material at our disposal. In the case when an internal mould alone is available (e.g. GK.H629b and GK.H634b) major ribs are distinct but minor ones are faint, only partly discernible or scarcely perceptible.

Another irregularity in ornament is occasionally observed in connection with a probable injury, as exemplified by HMG 959 and HMG 996 in which concentric ribs form chevrons or a kind of discontinuity.

The radial ornament mentioned in the diagnosis is represented by faint radial riblets on some major concentric ribs. The form with such weak riblets occupies a fraction of a population.

Comparison and discussion. —This species is assigned to *Sphenoceramus,* because it has a flat posterior wing which is demarcated clearly from the convex main part (here called disk) of the valve and because the disk is sphenoid in outline in having a trigonal umbonal part and extending obliquely backward toward the extremity of ventral margin.

As compared with the well known species of *Sphenoceramus* of Coniacian to early Campanian ages, such as *S. naumanni* (Yokoyama), *S. nagaoi* (Matsumoto & Ueda), *S. orientalis*

(Sokolow), *S. schmidti* (Michael), *S. cardissoides* (Goldfuss) etc., *S. hetonaianus* shows a broader sphenoid outline of the disk, with larger beak angle (90° or more) and its hinge line is clearly longer with obtuse posterior hinge angle (γ =130° or more); hence its posterior wing is broad or large. Fairly broad posterior wing occurs in some forms of *S. naumanni*, *S. orientalis*, *S. angustus* (Beyenburg) and even *S. schmidti*, but their posterior hinge angle is not so much obtuse or their ratio l/h is not so great as in *S. hetonaianus*.

The anterior ear, with a byssal opening, is by no means particular to *S. hetonaianus*. A similar structure has been noticed already by Böhm (1915, 1920) and Seitz (1965) in several species of *Sphenoceramus* and also quite recently by Toshimitsu *et al.* (1992) in *S. schmidti*.

In having a broadly sphenoid main part of the valve and a subrhomboid outline of the entire shell with a broad posterior wing mentioned above, *S. hetonaianus* resembles *S. haboroensis* Toshimitsu (1988, p. 148, pl. 27, figs. 12a, b) from the sandy siltstone in the upper part of the Upper Haborogawa Formation, the Lowest Campanian according to Toshimitsu (*op. cit.*), of northern Hokkaido. The holotype of the latter has a more convex disk which falls down more steeply to the flat posterior wing as compared with the average form of the former. In this respect GK.H8400 (Pl. I, Fig. 10), an example of *S. hetonaianus*, is comparable with the holotype of *S. haboroensis*, although it is an internal mould and may have been secondarily distorted.

The difference in ornament between the above two species is undoubted. *S. haboroensis* has simple and regular concentric ribs of moderate intensity throughout life. In *S. hetonaianus* the ribbing similar to the above is only seen on younger shells and in later growth-stages some ribs are stronger than others or major ribs appear in combination with finer or minor ribs.

The available material of *S. haboroensis* is too few to know its varieties in shell-form and ornament and the time-gap between *S. haboroensis* and *S. hetonaianus* is too great to trace their evolutionary relationship, if any.

The ornament with regularly combined major and minor concentric ribs characterizes *S. orientalis*. In the typical form of *S. hetonaianus* there are major and minor ribs but their combination is not so regular as in *S. orientalis*.

S. naumanni, a rather primitive and long ranging species from Coniacian to early Campanian, has no major ribs, showing several types of minor ribs appearing with growth in various ways, as Nagao and Matsumoto (1940, p. 33-36, text-fig. 4) have pointed out. In a certain morphotype of *S. hetonaianus*, as represented by GK.H629a and GK.H634c (Pl. I, Figs. 1, 7), the ornament of the disk resembles that of such examples of *S. naumanni* as IGPS.53305-1 (Nagao and Matsumoto, 1940, pl. 14, fig. 5; Noda, 1988, pl. 1, fig. 5) and IGPS. 63348 (Noda, 1988, pl. 1, fig. 10 [misprinted fig. 11 in his plate]).

A variety of the ornament in *S. hetonaianus* as exemplified by HMG 953 and HMG 999 (mentioned in the foregoing page 10 and illustrated in Pl. III, Fig. 8 and Pl. IV, Fig. 2 of this paper) is similar to another type of ornament in *S. naumanni* shown by IGPS.22737 (Nagao and Matsumoto, 1940, pl. 14, fig.2).

The strong resemblance in the above cases cannot be overlooked. This could be interpreted as a feature in which a hereditary character in a remote ancestor may have survived. It occurred, however, in a fraction of the whole population.

Even in these cases *S. hetonaianus* is distinguished from *S. naumanni* by its broader posterior wing with a longer hinge line, greater ratio l/h, more oblique growth-axis and its better traceable ornament from the main valve to the wing in the late growth-stage.

As indicated clearly in Table 4, the relative growth of *S. hetonaianus* shows an isometry in shell length (l) vs. shell height (h), whereas that of the other examined species of *Sphenoceramus* (e.g. *S. naumanni, S. nagaoi, S. orientalis, S. schmidti* etc.) all show negative allometry. This is concerned with shape and size of the shells. Should the material be obtained from a successive sequence of strata, the phylogenetic relationships of *S. hetonaianus* with *S. naumanni, S. haboroensis, S. nagaoi, S. orientalis* etc. could be examined by way of the allometric analyses, although such material is not available at present.

A similar idea could be applied in principle to the characters of ornament, although they are not treated numerically.

The faint radial riblets which occur also in another fraction of the population can be regarded as an incipient character, because the specimens from a higher level, represented by more than a dozen specimens (GK.H622 and GK.H633) from the uppermost member (IVc6) of the Fukaushi Formation at locality H15a, have better marked radial ribs and also numerous minor radial riblets and/or striae which cross the concentric ribs, although these radial elements of the ornament are by no means strong. The same kind of radial ornament occurs also in the specimens obtained at locality K79p and K83 on the Heitaro-zawa (see Matsumoto *et al.*, 1980 for the location), a branch of the Tonbetsu [Tombets] River in northern Hokkaido. These specimens are tentatively called *Sphenoceramus* aff. *hetonaianus*, as the material at our disposal is not sufficient. It is, however, noted that an incipient radial ornament which appeared in a fraction of the population of *S. hetonaianus* seems to have become more stable in a succeeding species (or ? subspecies).

The radial (instead of divergent) ornament occurs more frequently in many European species of *Sphenoceramus*, as exemplified by *S. cardissoides* (Goldfuss), *S. pachti* (Archangelski), *S. pinniformis* (Willet), *S. steenstrupi* (de Loriol) etc. (see Seitz, 1965). They are, however, of Santonian or early Campanian age. Our examples are found in the Maastrichtian beds and have dissimilar shell-form. The similarity in radial ornament is probably a homeomorphy within the same genus.

Occurrence. —Syntypes were obtained from Member IVc3, silty fine-grained sandstone of the Fukaushi Formation exposed on the cliff at localities H33d and H36b along the creak called Panke-rusa-no-sawa, about 2.2 km west from the center of Tomiuchi, Hobetsu district. They are contained abundantly in calcareous nodules but often broken; conjoined valves are found there rather infrequently.

A large collection of Hobetsu Museum (HMG) came from the silty fine-grained sandstone (about 15 m thick) of the Fukaushi Formation at locality H311. Many of the specimens from this place are opened but completely or almost conjoined. Fragmentary pieces of the inoceramid shells are also met with in the same nodule. Minute vegetable drifts are contained in the nodules sometimes in parallel or at random. Body chambers are preserved in many of the associated ammonites, although they are often partly broken. Thus, the sedimentary condition of the host rock must have been fairly calm and the inoceramids may have been living almost in situ or in the place not far from the embedded position.

The formation of the sandy siltstone below the Fukaushi Formation is characterized by *Inoceramus* (*Endocostea*) *shikotanensis* Nagao & Matsumoto and *Pachydiscus* (*Neodesmoceras*) *japonicus* Matsumoto, forming a well-defined zone which is referable to the Lower Maastrichtian, (Matsumoto, 1959), most probably the lower part of the Lower Maastrichtian.

Now the main part of the Fukaushi Formation, in which *S. hetonaianus* occurs abundantly, contains *Pachydiscus* (*Neodesmoceras*) *gracilis* Matsumoto. This ammonite species has been yielded very commonly at locality H311 and was found also at Fukaushi by K. Muramoto (who kindly showed three specimens to T.M.). In addition to it, *Pachydiscus* (*Pachydiscus*) *kobayashii* (Shimizu) has been recently reported from locality H311 by Matsumoto and Toshimitsu (1992) who correlated the fossiliferous zone to the upper part of the Lower Maastrichtian rather than to the lower part of the Upper Maastrichtian. In other words the Lower Maastrichtian is bipartite in Japan, with the Zone of *Inoceramus* (*Endocostea*) *shikotanensis*-*Pachydiscus* (*Neodesmoceras*) *japonicus* below and the Zone of *Sphenoceramus hetonaianus*- *Pachydiscus* (*Neodesmoceras*) *gracilis* above.

More study is needed for the Cretaceous biostratigraphy in the Tonbetsu Valley. Examples of *S. hetonaianus* and *S.* aff. *hetonaianus* mentioned in this paper came from the rock unit which is somewhat higher than the bed with *I.* (*E.*) *shikotanensis*.

S. cf. *hetonaianus* listed by Tanaka *et al.* (1952) is said to have come somewhere in the upper part of the Izumi Group in Nada-mura, island of Awaji. Its plaster cast is in Kyushu University as illustrated in this paper (Pl. I, Figs. 15, 16). It does show the diagnosis of *S. hetonaianus* and also very weak radial (in part divergent?) riblets. Further study is needed for this species from the Cretaceous of Awaji and adjacent areas.

Outside Japan Zonova (1992, p. 186, pl, 98, figs. 8-10, 11, 12-13) reported the occurrence of this species from the Zone of *Inoceramus* [*Shahmaticeramus* in her paper] *kusiroensis* in Sachalin. The illustrated specimens are small and without examining the actual ones it is difficult to give adequate comments. Anyhow *I. kusiroensis* at its type locality in eastern Hokkaido occurs commonly in the tuffaceous sandstone of the Monshizu Formation which overlies the shale (often siliceous) of the Otamura Formation. As the shale contains *I.* (*E.*) cf. *shikotanensis*, the cooccurrence of *S. hetonaianus* with *I. kusiroensis* would be reasonable.

IV Conclusions

(1) *Inoceramus hetonaianus* Matsumoto, 1952 is described in this paper on the basis of numerous specimens from the sandstones of the Fukaushi Formation, the lower second

of the quadripartite Upper Hakobuchi Subgroup, in the Hobetsu district. Its diagnosis and features of variation are shown.

(2) On the ground of the described characters this species is assigned to the genus *Sphenoceramus* Böhm, 1915.

(3) *S. hetonaianus* is compared with certain other species of the same genus, with discussion of the similarity and distinction. Its affinities with *S. naumanni* (Yokoyama) and *S. haboroensis* Toshimitsu are noted but the precise phylogenetic relationships are hardly concluded on account of the lack of successive material and the great time gap inbetween.

(4) Faint radial riblets occur in some individuals of this species. Whether or not this incipient feature would develop into a distinct character, evolving a new species of later age, is a problem to be worked out further.

(5) *S. hetonaianus* occurs abundantly in the main part of the Fukaushi Formation. Its appearance is seemingly abrupt, forming the Zone of *Sphenoceramus hetonaianus*-*Pachydiscus* (*Neodesmoceras*) *gracilis*, which is probably a correlative of the upper part of the Lower Maastrichtian. It is found also in the Upper Hakobuchi equivalent of the Tonbetsu Valley of northern Hokkaido and also somewhere in the Izumi Group of Awaji Island, Southwest Japan. Further work is needed to make clear its true stratigraphic range and biogeographic distribution. Anyhow, *S. hetonaianus* is so far an unique Maastrichtian species of *Sphenoceramus*.

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