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Cover : A terminally resorbed maxillary tooth of iguanodontids (Ornithischia : Ornithopoda). The specimen is from the Kuwajima Formation, the Neocomian section of the Tetori Group, in Shiramine-mura, Ishikawa County, Ishikawa Prefecture, the west coast of Central Honshu, Japan (Shiramine-mura Board of Education, Coll. Cat. No. SBEI 001, 23 mm in dorsoventral length).

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Five inoceramids (Bivalvia) from the Upper Cretaceous of Hokkaido with some phylogenetic and taxonomic considerations, Part 1. Introductory remarks, method and systematic descriptions of one species of *Inoceramus* (*I.*) and one of *I.* (*Volviceramus*)

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Abstract. Some of the inoceramid specimens from the upper Turonian to lower middle Coniacian of the Obira and Ikushunbetsu areas, Hokkaido, are identical or well comparable with certain species, *viz.,* *Inoceramus* (*I.*) *lusatiae* Andert, *I.* (*Volviceramus*) *koeneni* Müller, *I.* (*Cremnoceramus*) *deformis* Meek, *I.* (*Cr.*) *ernsti* Heinz and *I.* (*Cr.*) *lueckendorfensis* Tröger, all of which are cosmopolitan species that, however, have not been recorded in Japan. In this paper, I describe these specimens, subject them to some biometric analyses, and discuss their phylogeny and taxonomic position. Some specimens show intermediate, or transitional characters between *Inoceramus* and *Cremnoceramus*, *Cremnoceramus* and *Cordiceramus*, and *Cordiceramus* and *Volviceramus*, suggesting their phylogenetic relationships. The probable succession for the concerned taxa is preliminarily discussed and the taxonomic ranking of *Inoceramus*, *Cremnoceramus* and *Volviceramus* is also discussed. The above taxa are here regarded as subgenera of *Inoceramus*. Meanwhile, the widespread occurrence of these species in East Asia has application to international correlation and elucidation of paleobiogeography in the upper Turonian to lower middle Coniacian. In Part 1, *I.* (*I.*) *lusatiae* and *I.* (*V.*) *koeneni* are described and discussed.

Key words : *Inoceramus*, Cretaceous, Upper Yezo Group, phylogeny, subgenus

Introduction

I. (*I.*) *uwajimensis* Yehara, 1924 and *I.* (*Cr.*) *mihoensis* Matsumoto, 1957, which are good zonal indices of the upper lower to middle and upper Coniacian, respectively, were for a long while the only Coniacian inoceramids reported from Japan. Subsequently, *I.* (*Cr.*) *rotundatus* Fiege, 1930, a cosmopolitan zonal index of the lower lower Coniacian was described by Matsumoto and Noda (1985) on the basis of a sample from the Ikushunbetsu area, Hokkaido. *I.* (*Co.*) *kawashitai* Noda, 1986, from the upper Coniacian, *I.* (*Pl.*) *troegeri* Noda, 1992, from the lower to lower middle Coniacian, and *I.* (*Pl.*) *szaszi* Noda and Uchida, 1995, from the upper middle Coniacian were later also recorded. These species, except for *I.* (*Cr.*) *rotundatus*, are endemic to East Asia or unknown in other regions, possibly because they were established only recently.

In 1988, during the construction of the Obira Dam, a large number of inoceramid fossils were collected from lower to lower middle Coniacian sediments on the riverside and riverbed by cutting and dredging. Most of the specimens examined were obtained by Toshio Shimanuki. The specimens are mostly well preserved, without secondary deformation. Since then, I inspected the localities together with Shimanuki and, on another occasion, with Matsumoto and Shimanuki, along the main course of the River Obirashibe, and some supplementary specimens were obtained from fresh outcrops. Another field workers, Kenji Sanada, offered additionally some questionable specimens obtained from the lower Coniacian of the Ikushunbetsu Valley.

My preliminary observation suggested that some of them were conspecific with well-known and widespread species of the upper Turonian through middle Coniacian, but were as yet undescribed in Japan. Further study led to discrimination of five inoceramid species.

The occurrence of these cosmopolitan species from the upper Turonian to lower middle Coniacian of East Asia is important for international correlation and for the consideration of paleobiogeography in those stages.

Method

In addition to general observation, some biometric analyses applied for selected characters. The basic linear measurements and angles are shown in Figure 1. For the procedure of biometric examination, readers may refer to Hayami and Matsukuma (1971) and Noda (1992). Evaluations of the normal distribution by means of the chi-square test and related statistics are omitted here because of the insufficient size of the samples.

The phylogenetic relationships of the species are preliminarily discussed on the basis of intermediate or transitional characters shown between *Inoceramus* (*Inoceramus*) and *I.* (*Cremnoceramus*), *I.* (*Cr.*) and *I.* (*Cordiceramus*), and *I.* (*Co.*) and *I.* (*Volviceramus*) and their stratigraphic occurrences.

Systematic description

Family Inoceramidae Zittel, 1881
Genus ***Inoceramus*** Sowerby, 1814
Subgenus ***Inoceramus*** Sowerby, 1814
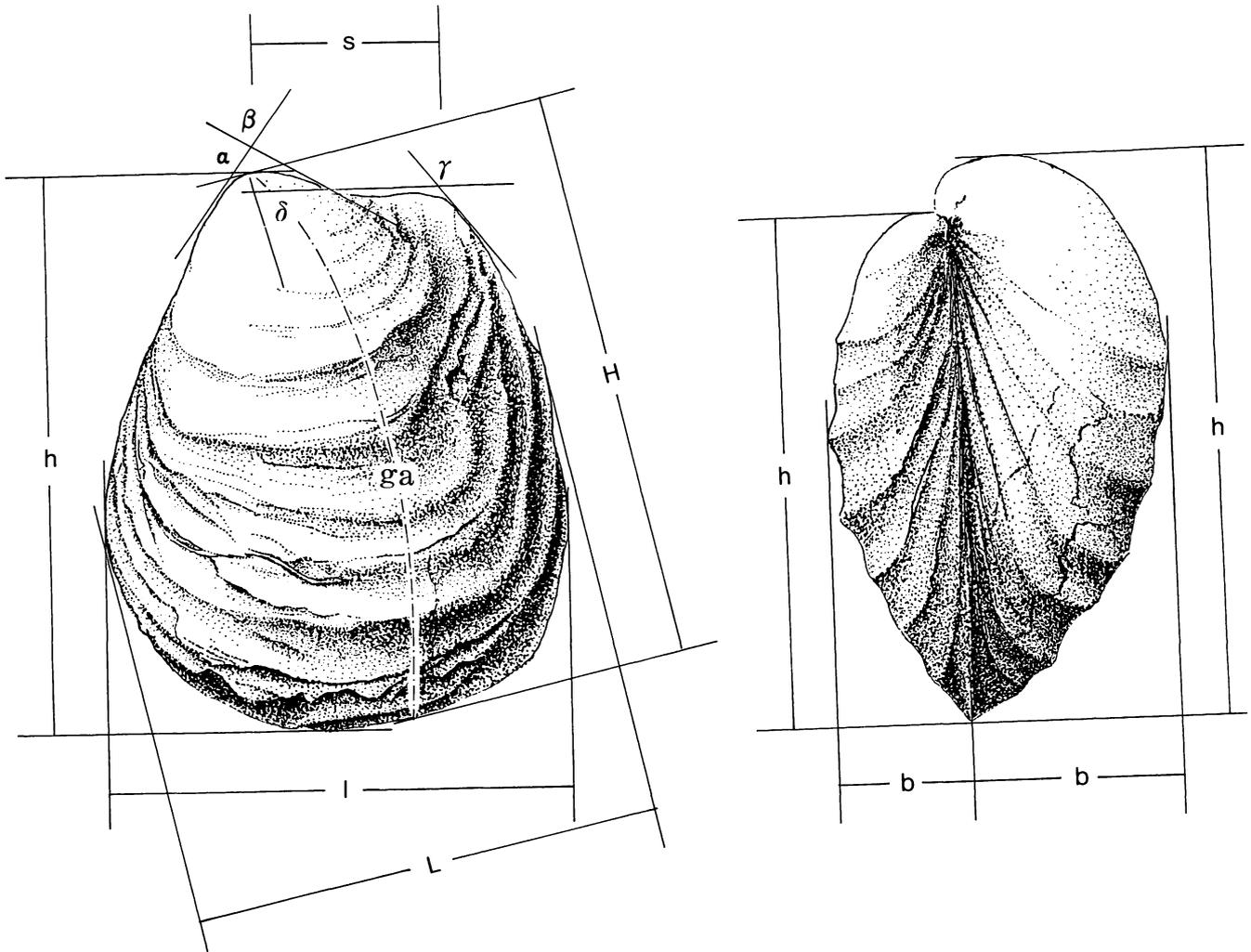
Figure 1. Basic linear measurements and angles. h : shell height, 1 : shell length, b : shell breadth, s : length of hinge line, H : maximum length between umbo and ventral extremity, L : maximum length perpendicular to H, α : anterior hinge angle, β : beak angle, angle of umbonal inflation, γ : posterior hinge angle, δ : obliquity, angle between hinge line and H.

Figure 2. *Inoceramus* (*Inoceramus*) *lusatiae* Andert, all figures natural size. **1a-e.** JG.H3095 from loc. Ik 7002. 1a : right valve, 1b : left valve, 1c : anterior view, 1d : posterior view, 1e : dorsal view (coll. K. Sanada, 1983). **2a-e.** JG.H3096 from loc. Ik 7001, 2a : left valve, 2b : right valve, 2c : dorsal view showing anterior ear, 2d : posterior view, 2e : anterior view (coll. K. Sanada, 1983).

1a 1b 1c 1d 1e 2a 2b 2c 2d 2e
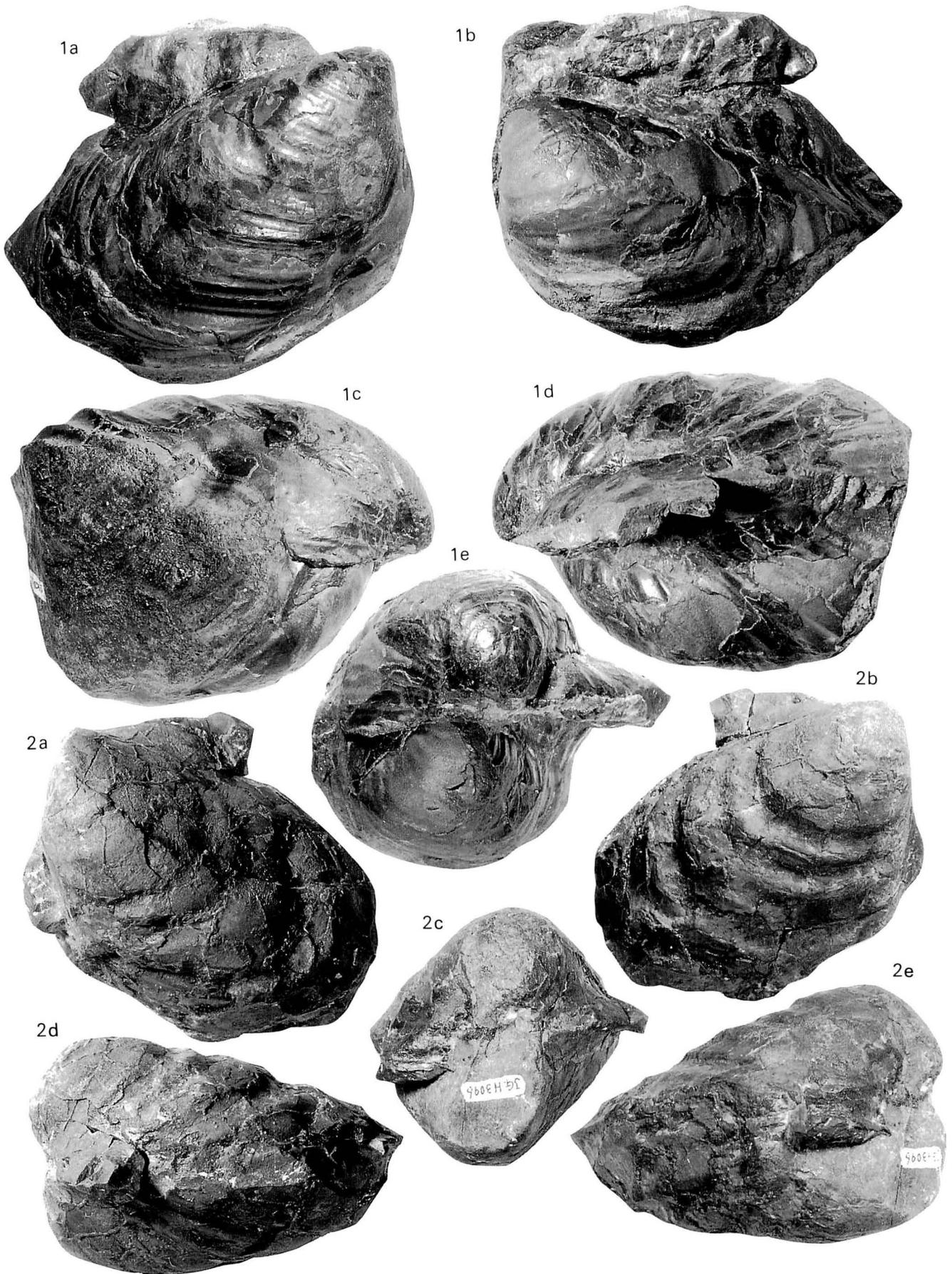
Type species.—*Inoceramus cuvierii* Sowerby, 1814, by subsequent designation by Cox (1969).

Diagnosis.—See Cox (1969, p. N315), Herm *et al.* (1979, p. 52, 53) and Walaszczyk (1992, p. 29).

Inoceramus (*Inoceramus*) *lusatiae* Andert, 1911

Figures 2-1a—e, 2a—e ; 3-1a—c, 2—4

Inoceramus lusatiae Andert, 1911, p. 54, 56, pl. 2, figs. 1a, b, pl. 3, fig. 3, pl. 8, figs. 3-5 ; Andert, 1934, p. 126, pl. 7, figs. 1-3, text-figs. 14a, b ; Dobrov and Pavlova, 1959, pars, p. 151, pl. 4, figs. 5, 6a, b ; Tröger, 1967, p. 73-76, pl. 8, figs. 2, 3 ; Keller, 1982, p. 87-89, pl. 6, fig. 3 ; Szàsz, 1985, p. 172, pl. 4, figs. 2, 3 ; Tröger, 1991, p. 29, pl. 3, fig. 6 ; Tarkowski, 1991, p. 113, pl. 7, fig. 4 ; Walaszczyk, 1992, p. 32, 33, pl. 27, figs. 1-3, 5, 6.

Mytiloides lusatiae (Andert). Kauffman, 1977, p. 240, 243, pl. 9, figs. 17, 23 ; Kauffman, Cobban and Eicher, 1978, p. XXXIII-9, pl. 9, figs. 17, 23.

Mytiloides ? lusatiae (Andert). Kauffman, 1978b, pl. 2, fig. 5, pl. 4, fig. 5.

not *Inoceramus lusatiae* Andert. Pergament, 1971, p. 94, 95, pl. 23, fig. 1.

Lectotype.—The specimen figured by Andert (1911, pl. 2, figs. 1a, b ; Tröger, 1967, pl. 8, figs. 2a, b) was designated as the lectotype by Tröger (1967, p. 73).

Material.—JG.H3095, 3096, 3100, 3101, 3102, 3201 and 3202 from the Ashiyachi-zawa (so-called Yoshiashi-zawa) in the Ikushunbetsu area, central Hokkaido.

Repository.—JG : Collections of the Jonan Geological Association, Oita, kept tentatively in Noda's personal laboratory, Oita.

Description.—Shell of medium size, nearly equivalve and highly inequilateral, with very oblique outline. Valve considerably inflated with some variation, from anterior to posterior, and uniformly or geniculately convex along growth axis. Anterodorsal part steep or perpendicular to commissure plane, posterior one also steep. Posterior auricle well developed, nearly regularly triangular and demarcated clearly from disk with a shallow sulcus. A small anterior auricle devoloped in some specimens. Umbo situated at anterior end and projected slightly above hinge line. Growth axis straight, with a considerably large obliquity. Anterior margin straight or slightly concave, continuing to broadly curved ventral one ; posteroventral part narrowly bent and passing into a guitar-shaped or hourglass-like concave posterior margin, which forms an acute angle with hinge line. Hinge line is longer than half of shell length.

Surface ornamented with commarginal undulations and commarginal rings ("commarginal" may be a more appropriate term than "concentric" for ornamentation of intricate outline as in this species) in combination, but in umbonal region major ornament inconspicuous. Commarginal undulations gradually more predominant with growth, fairly irregular in size, interspacing and intensity, weaken in anterior wall and continue to posterior auricle. Commarginal rings superimposed on major ornament and also irregular in size, interspace and intensity.

Biometry.—Measurements are shown in Table 1.

The individual relative growth of shell length (1) vs. shell height (h) and shell breadth (b) vs. shell height (h) in each valve of the specimen JG.H3095 is shown in Figure 4. In reference to the basic criteria of Hayami and Matsukuma (1971, p. 150, table 2, p. 151, fig. 8), the relative growth of l vs. h shows a negative allometry in both valves, and that of b vs. h is regarded as a positive allometry.

Ontogenetic changes in l/h, b/h and obliquity (δ) are demonstrated in Figures 5A, B and C, respectively. As is clear from Figure 5A, the simple ratio l/h decreases with growth and b/h changes abruptly at a certain stage of growth which is variable among individuals as shown in Figure 5B. The obliquity is nearly constant throughout the growth with about 66 on average.

Profiles of two specimens in two directions are illustrated in Figure 6. In the cross section A of specimen JG.M3096, the posterior part is steeper than the anterior slope, and a posterior auricle is clearly demarcated from the disk, and a small anterior ear is clearly developed.

Remarks.—The specimens JG.H3095 and 3096 are both closed valves. JG.H3095 is scarcely deformed secondarily but the valves are displaced along the commissure plane and the left valve has been somewhat eroded. JG.H3096 is slightly deformed obliquely, missing the left umbo, with small anterior ear. JG.H3100 is a right valve, fairly well preserved with original margin, and somewhat less convex. JG.H3101 in the same nodule as JG.H3100 is a left valve of a different individual, with a well preserved umbonal portion but lacking the ventral part. JG.H3102 is an imperfect specimen. JG.H3201 and 3202 from the upper Turonian near the Coniacian localities are fairly large, somewhat imperfect individuals, lacking the ventral and anterior parts, respectively. The former is characterized by its broad outline, which somewhat resembles *I.* (*I.*) *lamarcki stümckei* Heinz, 1926, whereas the latter is an elongate form like JG.H3095, 3096, 3100 and 3101.

Comparison and discussion.—The specimens figured by Andert (1911, 1934) show a large extent of variation in marginal curvature, shape of auricle and obliquity as originally noticed by Andert himself and then by Tröger (1967). The triangular auricle well defined from the disk, guitar-shaped curvature of the posterior margin, strongly vaulted shell and coarse and irregular commarginal ornamentation are regarded as the essential criteria of *I.* (*I.*) *lusatiae.*

These specimens are agree well with all aspects of *I.* (*I.*) *lusatiae* described by Andert (1911, 1934) and by Tröger (1967), but the development of a small anterior auricle in JG.H3096 may be exceptional.

According to Tröger (personal communication, Oct. 5, 1993) there are two extreme forms in the German specimens, i.e., an elongate form and a subquadrate one, both are linked by various grades of intermediates. Tröger (personal letter of Oct. 5, 1993) attempted a precise comparison between the original specimens of Andert and the plaster replica of the Japanese ones. The data (Figures 7, 8) are taken from Tröger's letter with his approval.

Ontogenetic changes in Na/Ha (=L/H), Vo/Ha (length of anterior margin/H) and Wa (= δ) are shown in Figures 7A, B and C, respectively. Solid line represents the original speci-
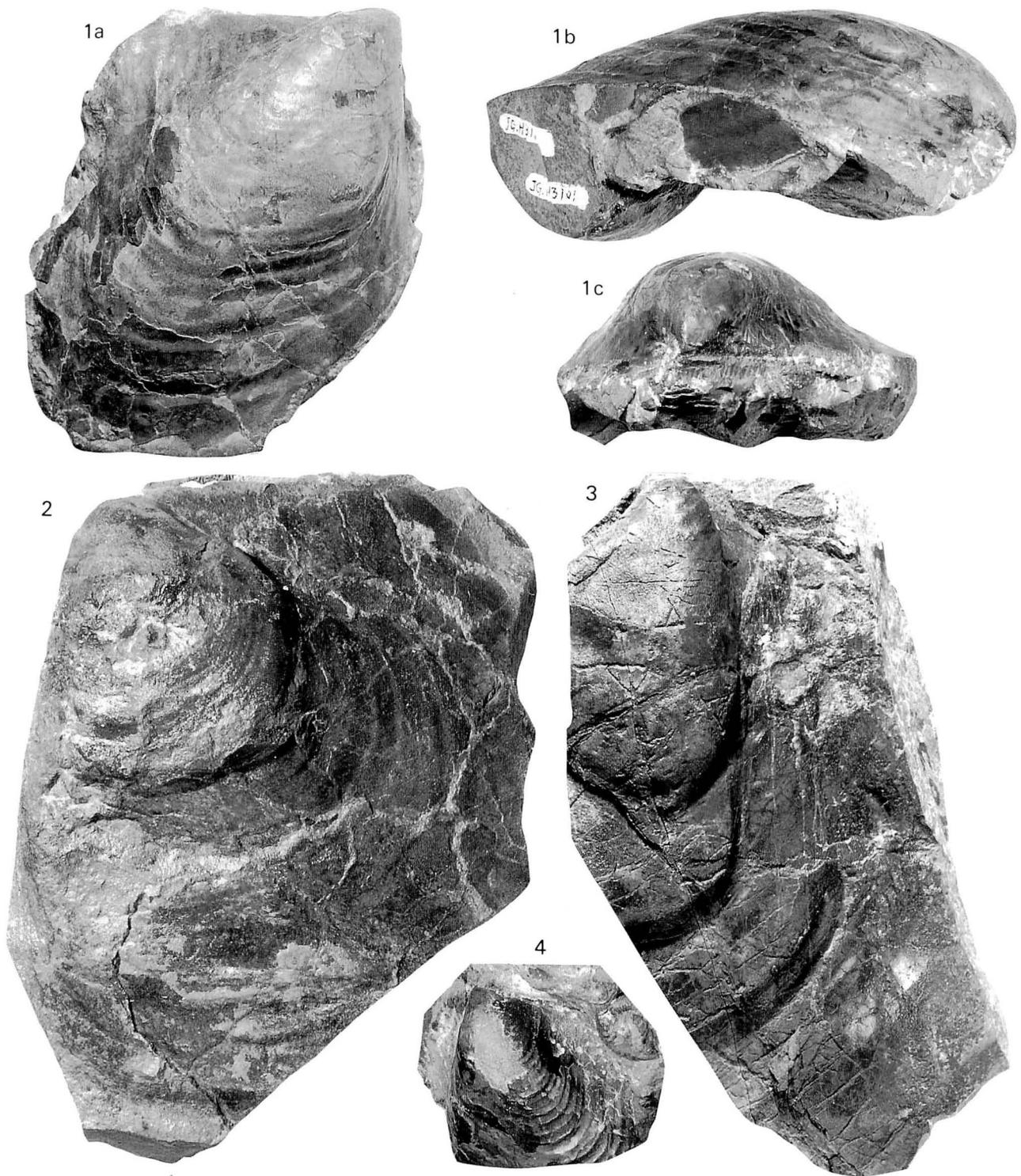
Figure 3. *Inoceramus* (*Inoceramus*) *lusatiae* Andert, all figures natural size. **1a-c.** JG.H3100 from loc. Ik7003, 1c shows ligament structure (coll. K. Sanada, 1982). **2.** JG.H3201 from loc. Ik7000 (coll. K. Sanada and M. Noda, 1994). **3.** JG.H3202 from the same locality (coll. K. Sanada and M. Noda, 1994). **4.** JG.H3101 from loc. Ik7003 (coll. K. Sanada, 1982).

Table 1. Measurements of *Inoceramus (Inoceramus) lusatiae* Andert from Hokkaido.   Linear dimensions in mm.

specimen	valve	h	l	b	s	H	L	α	β	γ
JG. H3095	L.	73.0	62.0	25.0	—	79.0	63.0	—	89°	—
	R.	81.0	66.0	26.8	—	86.0	68.0	120°	86°	60°
JG. H3096	L.	70.0	61.4	24.5	33.0	75.0	57.0	120°	79°	—
	R.	70.0	61.4	23.0	33.0	75.0	57.0	114°	84°	—
JG. H3100	R.	76.0	62.7	21.3	43.8	89.0	70.0	100°	76°	87°

specimen	valve	δ	l/h	b/h	L/H	s/l	remarks
JG. H3095	L.	64°	0.85	0.34	0.80	—	closed valves, posterior auricle partially
	R.	66°	0.81	0.33	0.79	—	missing
JG. H3096	L.	67°	0.87	0.35	0.76	0.54	closed valves, anterior auricle present
	R.	67°	0.87	0.33	0.79	0.54	
JG. H3100	R.	57°	0.83	0.28	0.79	0.70	somewhat less convex

Abbreviations.   L. : left valve, R. : right valve, l/h : simple ratio l versus h, b/h : simple ratio b versus h, L/H : simple ratio L versus H, s/l : simple ratio s versus l.
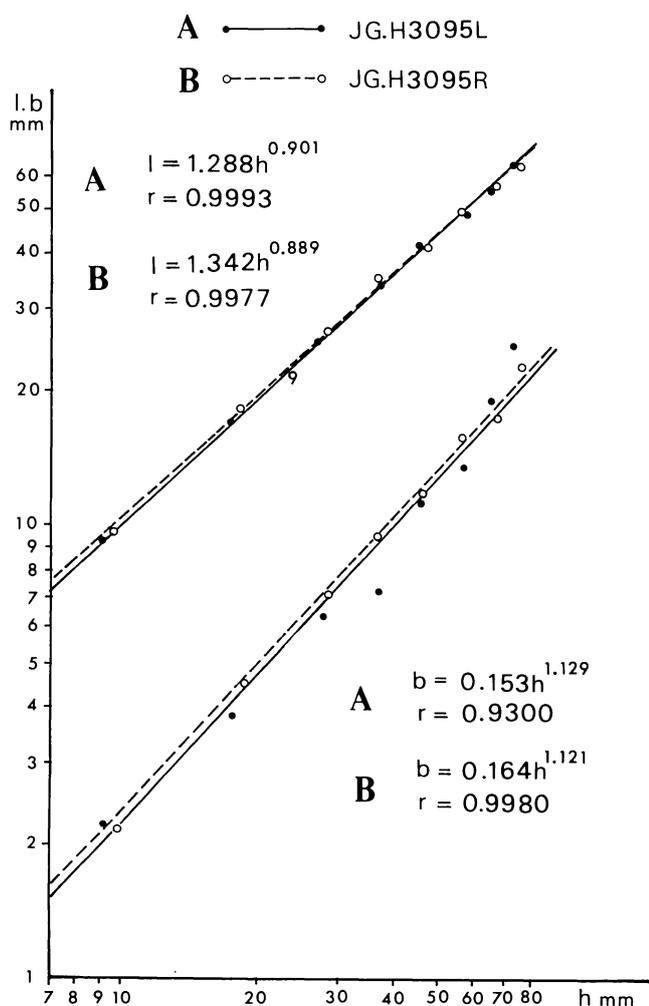

Figure 4. Diagram showing individual relative growth between l and h, and b and h (in mm) of *Inoceramus (I.) lusatiae*. (Specimen JG. H3095).

mens of Andert, and broken and chain lines the Japanese ones.   As is clear from Figure 7, the original specimens from the type locality (Sennenberg, Saxony near the Bohemian border) show a large extent of variation in the characters examined, and the Japanese specimens lie within the range of variation.

As shown in Figure 8A, at the growth stage 30 mm-50 mm in H, the size of commarginal undulations of the specimens examined is indistinguishable between the German and Japanese specimens, whereas in the subsequent stage, more than 50 mm in H, as is clear from Figure 8B, the size of commarginal undulations broadens rapidly in the German specimens in contrast to their remaining nearly constant in the Japanese ones.   This is the most conspicuous difference between the German and Japanese specimens.   On the basis of the above examination, Tröger suggested to me that the Japanese specimens may be conspecific with *Inoceramus (I.) lusatiae* Andert, or a special new subspecies.

The specimens from the Coniacian of the Babadag Basin, Romania, figured by Szàsz (1985, pl. 4, figs. 2a, b, 3) are somewhat less convex and predominant in minor ornament in comparison with the specimens examined.

Keller's specimen (1982, pl. 6, fig. 3) from the upper middle Turonian of Sack-Mulde of Germany resembles the Japanese specimens in marginal curvature, obliquity, shell convexity and surface ornamentation, but the stratigraphic position of his specimen is substantially lower than the others.

Moskvina's specimen (1959) from the uppermost Turonian of Crimea figured in her pl. 4, fig. 4 also resembles specimen JG.H3100 (Figure 3-1a c) in the oblique outline, moderately convex shell and surface ornamentation, but another one (pl. 4, fig. 5) from the uppermost Turonian of Dagestan it is more or less questionable to assign strictly to *I. (I.) lusatiae* so far as I can observe from the photograph.

The specimen from the upper Turonian of the Opole Trough of Poland figured by Tarkowski (1991, pl. 7, fig. 4) is comparable with the specimen JG.H3102 in the much higher outline, small posterior auricle, less obliquity and major
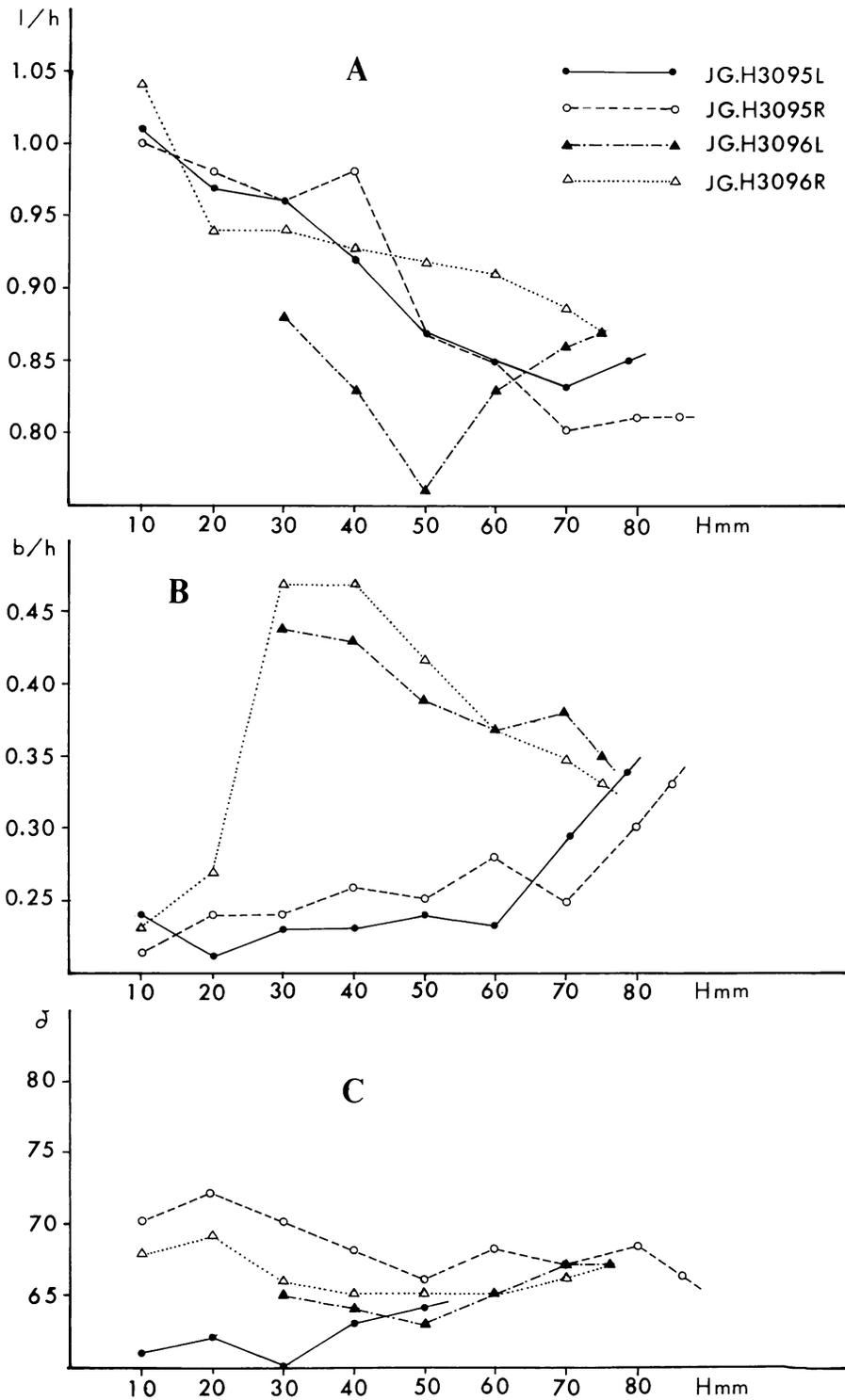
Figure 5. Diagram showing ontogenetic changes in selected characters of *Inoceramus* (*I.*) *lusatiae*. A : l/h, B : b/h, C : obliquity.

**A**   **B**
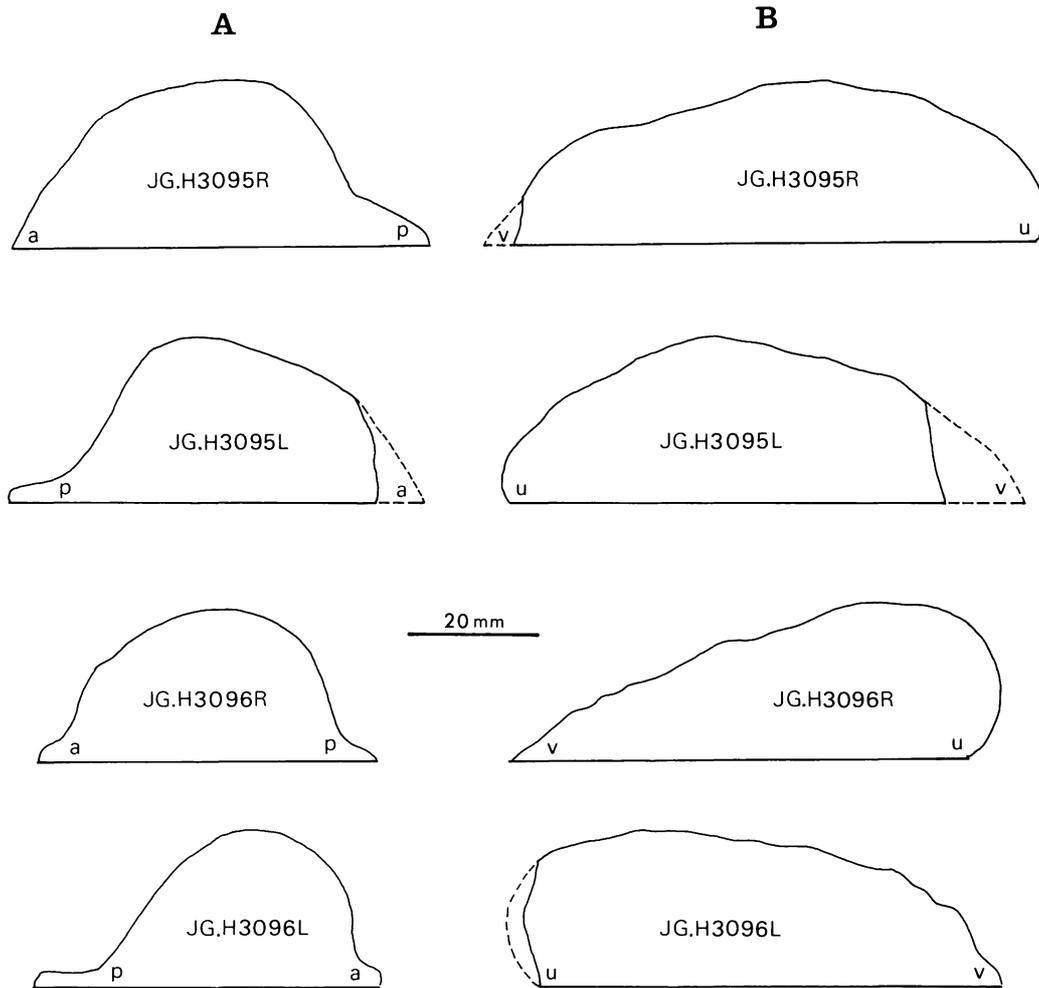
Figure 6.   Profiles of two selected specimens of *Inoceramus* (*I.*) *lusatiae* in two directions.   A : cross section at the highest point of shell convexity, B : vertical section along the growth axis.   a : anterior, p : posterior, u : umbo, v : venter.

ornament less predominant.

Walaszczyk's specimens (1992, pl. 7, figs. 1-3, 5, 6) from the uppermost Turonian through middle Coniacian of the Central Polish Upland are similar to those of Andert and those from Japan in the obliquely elongate shell and surface ornamentation, but unfortunately, as he mentioned (1992), the posterior auricle which is one of the important characters of the species is lacking.   A guitar-shaped, sinuous curvature of major commarginal undulations is partially perceptible on the specimen ME : ML1216 (Walaszczyk, 1992, pl. 27, fig. 2), which suggests clearly the presence of a triangular auricle.

Specimens of *Mytiloides lusatiae* (Andert) from the uppermost Turonian of the Western Interior figured by Kauffman (1966, pl. 9, figs. 17, 23) and Kauffman *et al.* (1978, pl. 13, figs. 17, 23) accord well with Andert's specimens in the outline and triangular and clearly defined posterior auricle, and the specimen USNM240318 (fig. 17) resembles closely JG.H3100 in the marginal curvature and surface ornamentation with less conspicuous major undulations.   Another specimen

USNM240338 (pl. 14, fig. 5) from the same horizon is fairly distinct from the type specimens, as Kauffman *et al.* (1978) noted as a less oblique variety, which closely resembles the specimen JG.H3102.

The specimen of *M.* ? *lusatiae* from the lower lower Coniacian of Bohemia, figured by Kauffman (1978b, pl. 2, fig. 5), is also somewhat distinct from the type specimens by a less oblique outline, as he remarked.

Pergament's specimen no. 3588-540-123 (Pergament, 1971, pl. 23, fig. 1) from the upper Turonian (lower Coniacian after Pergament) of northwestern Kamchatka is quite doubtfully assigned to *I.* (*I.*) *lusatiae* as Walaszczyk (1992, p. 33) pointed out, because of its posterior margin without a guitar-shaped sinus and the shape of the posterior auricle with no sharp boundary of the disk.   The specimen appears to be closer to *I.* (*I.*) *lamarcki* Parkinson and/or its variety.   In connection with this, Tröger (personal letter of Oct. 5, 1993) suggested that Pergament's specimen is referable to *I.* (*I.*) *lusatiae*.
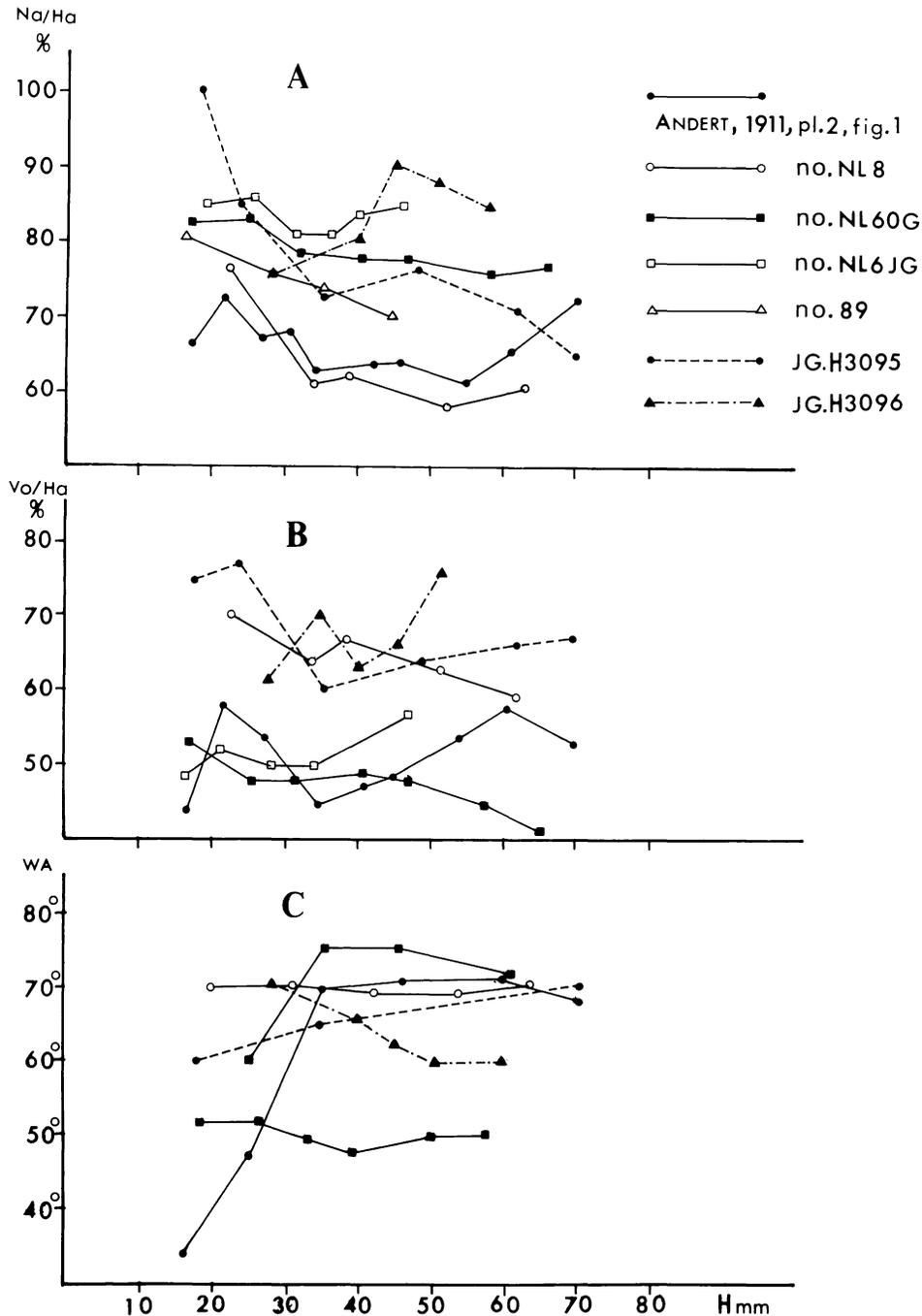
Figure 7. Diagram showing ontogenetic changes in selected characters of *Inoceramus* (*l.*) *lusatiae*. Comparison with German specimens (by the courtesy of Prof. Dr. K.-A. Tröger). Na/Ha=L/H, Vo/Ha= length of anterior margin/H, WA = δ.

Phylogeny.—On the basis of morphological and stratigraphical evidence, *I.* (*l.*) *lusatiae* from the uppermost Turonian through lower Coniacian (upper Turonian in the German scale before Seibertz, 1979) is regarded by Tröger (1969) as an immediate descendant derived from *I.* (*l.*) *lamarcki stümckei* Heinz, 1926, of the upper middle Turonian. Besides, specimens comparable with *I.* (*l.*) *lamarcki stümckei*,

not described in Japan yet, are obtained from the middle Turonian of some areas of Hokkaido. JG.H3201 (Figure 3-2) from the uppermost Turonian of Ikushunbetsu and Pergament's specimen from the same stage of Kamchatka resemble the type specimens of *I.* (*l.*) *lamarcki stümckei*. This evidence would help to support the Tröger's scheme (1969, fig. 8). According to Tröger (1969), descendants of *I.* (*l.*)
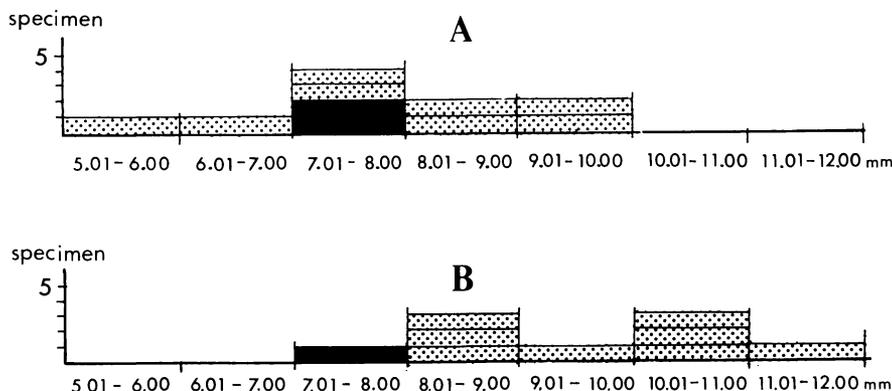
Figure 8. Diagram showing the wave length of commarginal undulation of *Inoceramus* (*I.*) *lusatiae*. A : growth stage 30 mm-50 mm in H, B : growth stage 50 mm-70 mm in H, black : Japanese specimens, dotted : German specimens (by the courtesy of Prof. Dr. K.-A. Tröger).

lusatiae are unknown, as is the case in Japan, which can be ascribed either to its terminal extinction or to insufficient collection up to the present. The species may possibly represent an offshoot of the main stocks of inoceramids as schematized by Tröger (1969).

On the other hand, Kauffman (1977) regarded the present species as being closer to the genus *Mytiloides* than to *Inoceramus* (*Inoceramus*). The specimens I have observed, however, seem to show that the species is more closely related to *I.* (*Inoceramus*) than to the group of *Mytiloides* on account of the triangular and clearly defined posterior auricle, fairly thick hinge plate and coarser and irregular commarginal undulations.

Occurrence.—The locality map is shown in Figure 9.

Loc. Ik7000.—Topographic map "Katsurazawako", Scale 1 : 25,000. A cliff at the confluence of the Ashiyachi-zawa (so-called Yoshiashi-zawa) and the Hatsudenshono-sawa, in usual, under the water level of Lake Katsurazawako. Sandy siltstone bed of Unit IIIa (Matsumoto, 1965), uppermost part of the lower Upper Yezo Group. Associated with *I.* (*I.*) *teshioensis* Nagao and Matsumoto, *I.* (*I.*) *tenuistriatus* Nagao and Matsumoto and *Otoscaphites* sp.

Loc. Ik7001.—Topographic map, ditto. Scree of the small left branch of the Ashiyachi-zawa. Sandy siltstone bed of Unit IIIb, lower part of the middle Upper Yezo Group (Matsumoto, 1965).

Loc. Ik7002.—Topographic map, ditto. A left bank of the lower reaches of the Ashiyachi-zawa, about 270 m upstream from the Kumaoi Power Station, submerged at full water seasons.

Loc. Ik7003.—Topographic map, ditto. A stream floor of the Ashiyachi-zawa, about 220 upstream from loc. Ik7002, also submerged at full water seasons. Associated with *Mesopuzosia yubarensis* (Jimbo), *Gaudryceras denseplicatum* Jimbo and *Scaphites* sp. No effective zonal index is known, but at a horizon about 20 m above, *I.* (*I.*) *uwajimensis* Yehara, a good index of the upper lower to middle Coniacian, occurs abundantly.

Range.—The described specimens were obtained from the mentioned horizons. Loc. Ik7000 represents the uppermost

Turonian, and Ik7001, 7002 and 7003 are probably the lower Coniacian. The Tu/Co boundary is regrettably unclear because it is below the surface of Lake Katsurazawako.

As discussed above, the present species is recorded from the middle Turonian to middle Coniacian of various regions of Euramerica, with some time lag in each area, but mostly from the uppermost Turonian to lower Coniacian. The stratigraphic position of this species in Japan is well in accordance with these occurrences.

Subgenus *Volviceramus* Stoliczka, 1871

Type species.—*Inoceramus involutus* Sowerby, 1828 (*In* Cox, 1969) was originally designated by Stoliczka (1871).

Diagnosis.—See Stoliczka (1871), Meek (1876) and Cox (1969).

Remarks.—*Volviceramus* was proposed by Stoliczka (1871) as a full genus, and the original diagnosis was given for the type species *I. involutus*. Hattin and Cobban (1977) and Kauffman (1977) followed Stoliczka and adopted it as a full genus, whereas Müller (1887) and Scupin (1913) regarded *Volviceramus* as a subgenus of *Inoceramus* without any comment. Heinz (1932) separated a group of *I. epigonus* Heinz, 1932, which is not so highly inequivalve as *I. involutus*, from the genus *Volviceramus* and established the full genus *Tactoceramus*, designating *I. epigonus* (*V. epigonus* of Heinz's sense) as the type species, with a brief definition. Thus the generic name is available under Art. 13 of the I.C. Z.N. Vokes (1967, 1980) regarded *Tactoceramus* as an available name, while Cox (1969) regarded it as a junior synonym of *Volviceramus*. Heinz (1932) also proposed *Cymatoceramus* as an independent genus and designated *I. koeneni* Müller, 1887, as the type species, but gave no diagnosis. It is surely invalid. Cox (1969) regarded *Cymatoceramus* as a junior synonym of *Volviceramus*. *Tethyoceramus* is another full genus proposed by Heinz (1932), who designated *I. emigrans* Heinz, 1932, as the type species, but it is also invalid, because given diagnosis of the type species is insufficient, with no designation of type specimen or any illustration.
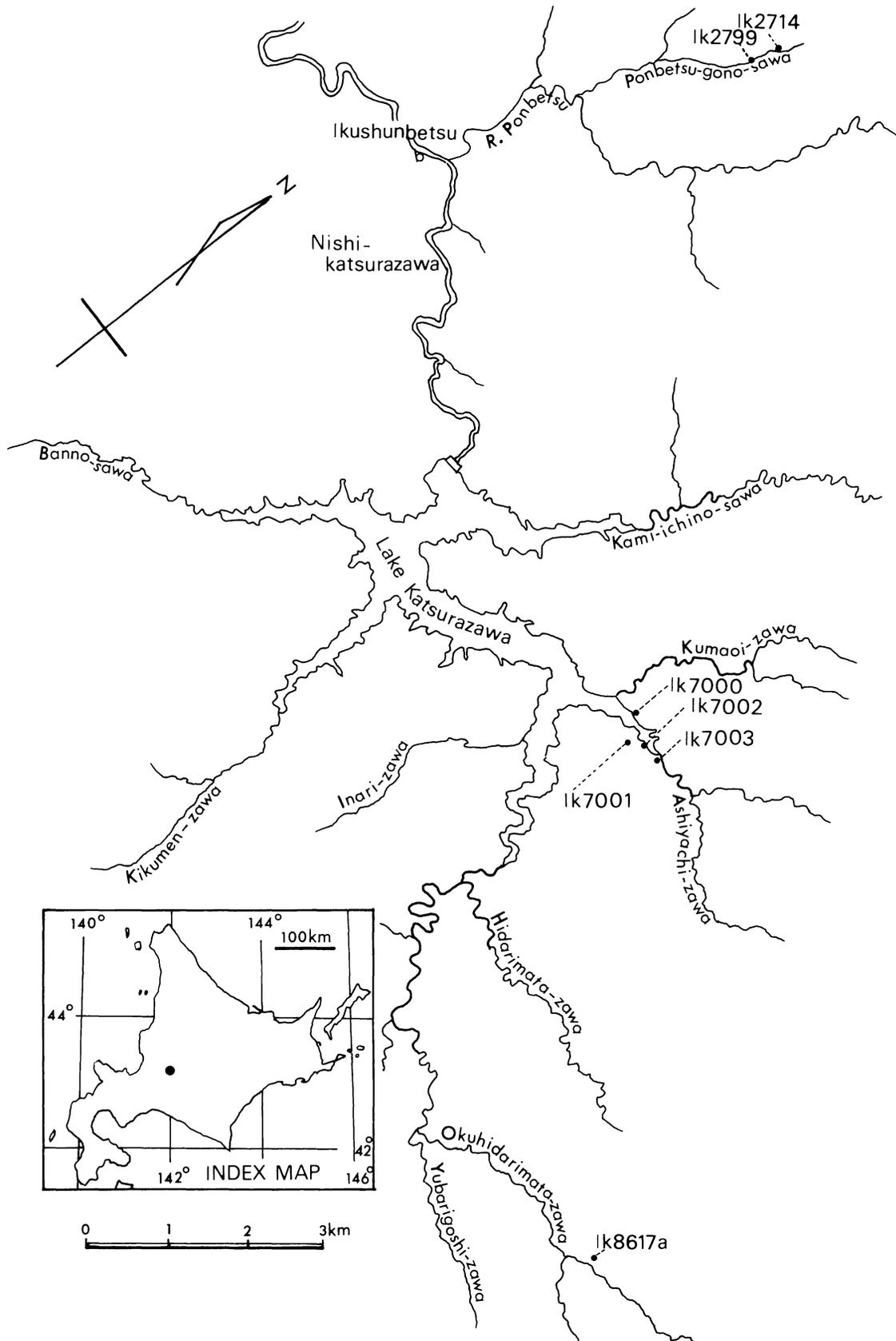
Figure 9. Locality map of the Ikushunbetsu area.

Sornay (1980) gave a revised precise definition, positioning *Tethyoceramus* as a subgenus of *Inoceramus* and designating *I. basseae* Sornay, 1980 (= *Tethyoceramus* aff. *emigrans* Heinz) from the lower Coniacian of Madagascar as the type species. At that date, *Tethyoceramus* came to be valid under Art. 13.

As seen in the synonym list of Sornay (1980), some specimens of *I.* (*Cr.*) *ernsti* and *I.* (*V.*) cf. *involutus* were included in *Tethyoceramus*. In reality there are various intermediate forms between *Volviceramus* and *Tethyoceramus*.

I. (*Cremnoceramus*) is slightly or moderately inequivalve (Herm *et al.*, 1979) whereas *I.* (*Volviceramus*) and *I.* (*Tethyoceramus*) are highly inequivalve. This is taken as the most important criterion for separating these subgenera, but the distinction between *I.* (*Volviceramus*) and *I.* (*Tethyoceramus*) is quite obscure in practice. In my opinion, the distinction between these two subgenera may be rather unnecessary, then *Tethyoceramus* should be included in *Volviceramus* as a junior synonym.

Woods (1912b, figs. 42, 43) connected a highly inequivalve variety of *Inoceramus lamarcki* with *I. involutus*. This suggests emphatically that *I.* (*Inoceramus*) is closely related to *I.* (*Volviceramus*). These forms are hardly assignable either to *Inoceramus* or to *Volviceramus*.

From the above discussion, it would appear natural that *Volviceramus* be ranked as a subgenus of *Inoceramus*.

Inoceramus (*Volviceramus*) *koeneni* Müller, 1887

Figures 10-a—d

Inoceramus (*Volviceramus*) *koeneni* Müller, 1887, p. 412, 413, pl. 17, fig. 1.

Inoceramus lamarcki Parkinson (pars). Woods, 1912a, pl. 52, figs. 4, 6.

Inoceramus connecting *Inoceramus lamarcki* Parkinson with *Inoceramus involutus* Sowerby. Woods, 1912b, p. 9, figs. 42, 43.

Inoceramus koeneni Müller. Heinz, 1928b, p. 37, pl. 3, fig. 2; Heine, 1929, p. 98-100, pl. 15, fig. 63, pl. 17, fig. 66, pl. 18, fig. 67; Andert, 1934, text-fig. 16, pl. 8, figs. 2b, c; Tröger, 1969, p. 69-87, pls. 1, 2; Ivanikov, 1979, p. 13, list; Cieśliński and Blaszkiewicz, 1984, p. 364, pl. 159, fig. 1; Cieśliński and Blaszkiewicz, 1989, p. 255, pl. 160, fig. 1.

Cymatoceramus (*Cymatoceramus*) cf. *koeneni* (Müller). Heinz, 1934, p. 253, 254, pl. 19, fig. 3.

Inoceramus (*Cremnoceramus*) *koeneni* Müller. Hattin and Cobban, 1977, p. 191, 192, fig. 9-3.

Volviceramus ? *koeneni* (Müller). Kauffman, 1978a, p. IV-8, list.

Volviceramus koeneni (Müller). Kauffman, 1978b, p. XIII-2, list.

Lectotype.—The specimen figured by Müller (1887, pl. 17, fig. 1) was designated as the lectotype by Tröger (1969).

Material.—A single specimen (JG. H3019) from loc. Ob0013 in the Obira area, Hokkaido.

Description.—Shell large-sized, highly inequivalve, inequilateral, much higher than long. Left valve strongly convex from anterior to posterior and along growth axis. Anterior wall angularly bent from disk and deeply concave to commissure plane. Posterior half of flank steeply sloped to posterior margin and hinge part, and almost perpendicular near umbo. Umbo terminal, and left one highly projected above hinge line, strongly involuted and twisted forwards. Three radial elevations developed, of which anterior one demarcates clearly between anterior wall and disk, median one is prominent and runs posteriorly along growth axis, and
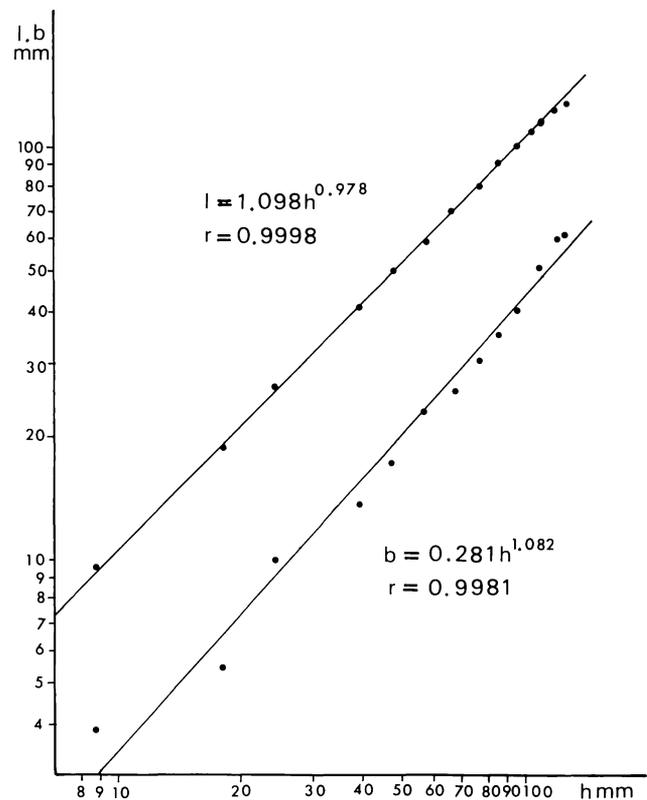

Figure 11. Diagram showing individual relative growth between l and h, and b and h of *Inoceramus* (*V.*) *koeneni*. (Specimen JG.H3019).

Table 2. Measurements of *Inoceramus* (*Volviceramus*) *koeneni* Müller fom Hokkaido.   Linear dimensions in mm.

specimen	valve	h	l	b	s	H	L	α	β	γ	$\delta_{H=60mm}$
JG. H3019	L.	130.0	127.7	60.6	46.0	135.6	93.6	152°	121°	108°	96°

specimen	valve	l/h	l/h$_{H=60mm}$	b/h	b/h$_{H=60mm}$	L/H	s/l
JG. H3019	L.	0.98	0.97	0.46	0.37	0.69	0.34

Figure 10.   *Inoceramus* (*Volviceramus*) *koeneni* Müller.

Masayuki Noda
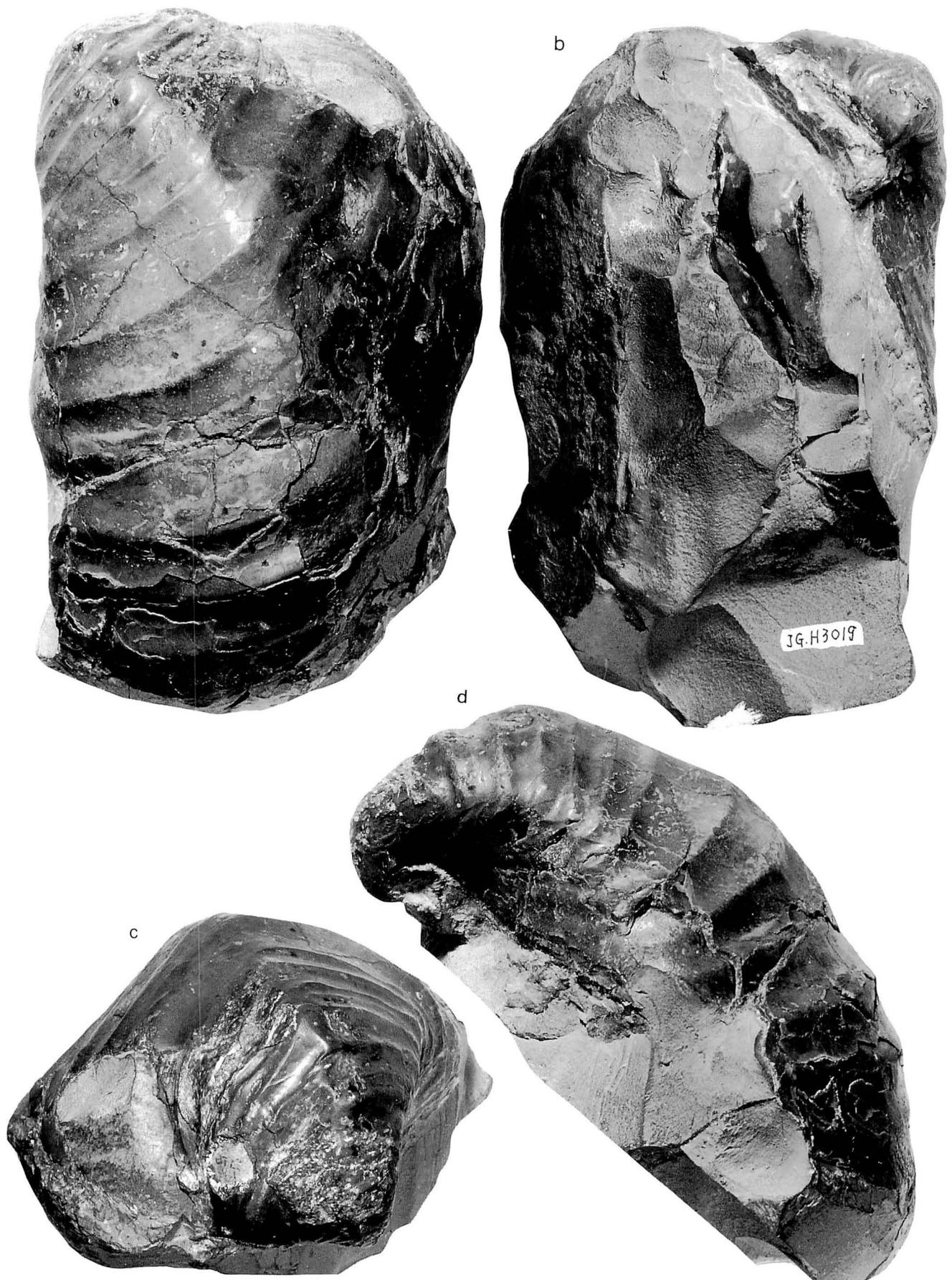
posterior one is blunt. Anterodorsal margin long and straight continuing to broadly rounded anterior one, and narrowly curved, passing into asymmetrically arcuate ventral margin; posterior margin fairly short, forming an obtuse angle with hinge line which is short, about one-third shell length. Posterior wing narrow and small. Hinge plate fairly thick, ligament pits rectangular with round ridge.

Surface ornamented with concentric ribs which are fairly crowded near umbo, prominent, sharp-topped and irregular in strength, and concave interspaces which broaden with growth. Minor ornament scarcely perceptible.

Biometry.—Measurements are shown in Table 2.

The individual relative growth of l vs. h and b vs. h are demonstrated in Figure 11. The former shows isometry and the latter positive allometry.

Ontogenetic changes in l/h, b/h and obliquity (δ) are shown in Figures 12A, B and C, respectively. As is clear from Figure 12A, l/h is nearly constant throughout growth, while b/h increases gradually with growth. The obliquity increases rapidly in the early stage of growth and then gradually, which suggests a spirally twisted growth axis.

Profiles in two directions are illustrated in Figure 13.
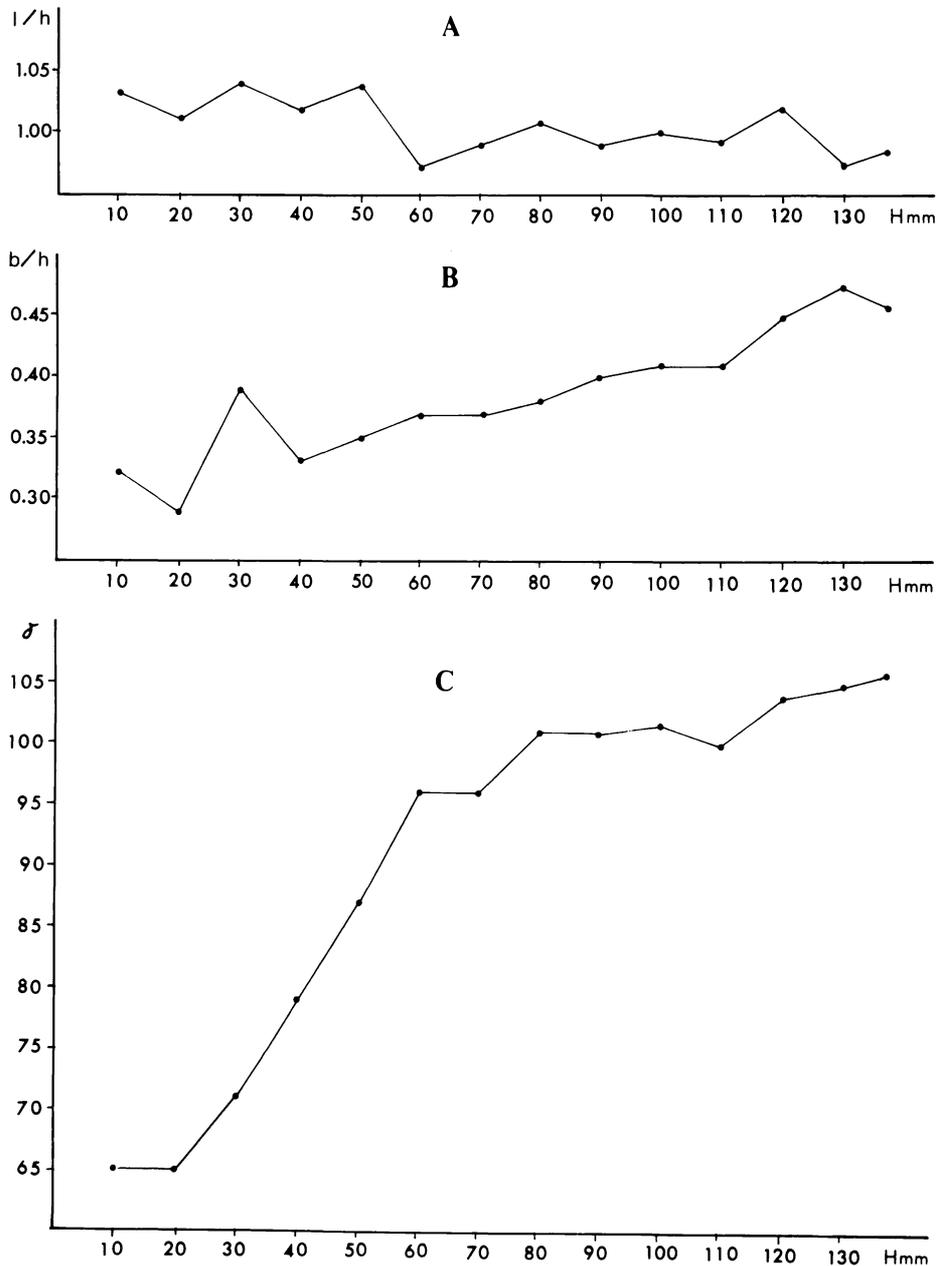
Figure 12. Diagram showing ontogenetic changes in selected characters of *Inoceramus* (V.) *koeneni*. A: l/h, B: b/h, C: obliquity.

A　　　　　　　　　　**B**
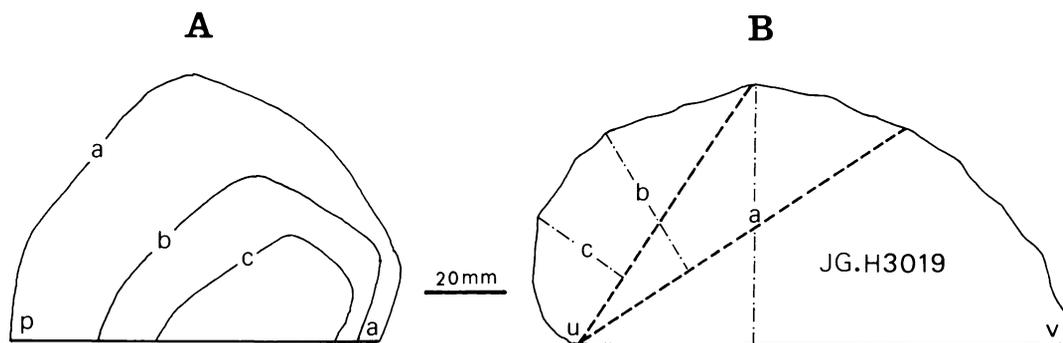
Figure 13. Profiles of *Inoceramus* (*V.*) *koeneni* (specimen JG.H3019) in two directions A-a : cross section at the highest point of shell convexity, A-b and A-c : cross sections at certain growth stages shown by broken lines in B. B : vertical section along the growth axis.

Three cross sections a, b and c of Figure 13A correspond to chain lines a, b and c of Figure 13B, which are perpendicular to the commissure plane at three different growth stages as shown by the broken lines.

Remarks.—The specimen JG. H3019 is a well preserved left valve and a fragment of the right valve without secondary deformation. The prismatic layer is preserved only near the beak and posterodorsal parts. The precise ornamentation, therefore, is uncertain. The right valve is visible on the opposite side of the left valve, but it is too imperfect to assume the original outline. From the left umbo being strongly involute and twisted forwards, the right umbo is presumed to have been not so prominent and the shell convexity may have been weaker than that of the left valve.

Comparison and discussion.—JG. H3019 is characterized by the strongly involuted left umbo, considerably inflated shell and twisted growth axis, which are in common with features of the subgenus *Volviceramus*. It surely resembles closely the specimens of *I.* (*V.*) *koeneni* described by Müller (1887) and Tröger (1969). In addition, the radial elevations situated somewhat posteriorly along the growth axis and blunt posterior one in JG.H3019 are closely similar to those figured by Tröger (1969, p. 72, fig. 4), and the sharply concave anterior wall resembles closely that of the specimen figured by Tröger (1969, pl. 2, fig. 5). Moreover, the cross sections at three growth stages illustrated in Figure 13A agree well with those of type I of Tröger (1969, p. 72, fig. 3). From the above comparison, JG. H3019 is referable to *I.* (*V.*) *koeneni*, even though having somewhat weaker convexity than the German specimens.

The type species of *Volviceramus, I.* (*V.*) *involutus* Sowerby, is clearly distinct from the present species in its extreme inequivalveness as Müller (1887) discussed originally.

I. (*V.*) *umbonatus* Meek and Hyden, 1858 also resembles the present species, as Müller (1887) pointed out. According to the description by Meek (1876) the former shows a much higher outline than the latter.

The specimen figured by Woods (1912a, pl. 52, figs. 4a, c) somewhat resembles *I.* (*V.*) *koeneni* in the highly inequivalve shell and vaulted outline in anterior view and the well developed posterior wing.

I. (*Cr.*) *ernsti* somewhat resembles the present species in

the vaulted shell with a concave anterior wall and coarse and irregular major ornament, but the former is discriminated from the latter in subequivalveness in contrast to the latter being highly inequivalve and having twisted left umbo.

Phylogeny.—Woods (1912a, b) suggested that *I.* (*V.*) *involutus* derived from *I.* (*I.*) *lamarcki* through a connecting form figured by himself (1912a, pl. 52, figs. 4, 5 ; 1912b, p. 9, figs. 42, 43) is surely comparable with *I.* (*V.*) *koeneni.* Tröger (1969, p. 74, fig. 6) demonstrated schematically the phylogenetic relationships of *I.* (*V.*) *koeneni* as an immediate descendant of *I.* (*Cr.*) *ernsti* and the ancestor of *I.* (*V.*) *involutus.* I support his scheme fully. Collom (1993, personal communication) suggests another lineage in the phylogeny. *I.* (*V.*) *koeneni* in common with *I.* (*Co.*) spp. has a vaulted shell, concaved anterior wall, and twisted umbo, and develops radial elevations. The essential distinction, though, is that the subgenus *Volviceramus* became highly inequivalve with time, whereas the subgenus *Cordiceramus* is nearly equivalve. *I.* (*V.*) *involutus,* however, has not been found in Japan.

As is clear from the above discussion, *I.* (*Cr.*) *ernsti* is regarded as a common ancestor of *I.* (*V.*) *koeneni* and *I.* (*Co.*) *kawashitai* Noda, 1986, from the upper Coniacian of Hokkaido and Kyushu (Teraoka *et al.*, 1992 ; Noda, 1994), and the characters of the three species suggest undoubtedly the relationships among *I.* (*Cremnoceramus*), *I.* (*Volviceramus*) and *I.* (*Cordiceramus*).

Occurrence.—For the locality map of the Obira area, the readers may refer to Noda (1992, p. 1312, fig. 1). Loc. Ob0013 (=loc. NH79 of Tanaka, 1963). Topographic map "Takishita", Scale 1 : 25,000. A left bank about 150 m below Bridge Takimi-Ohashi, now below the surface of artificial Lake Obireshibeko. Silty sandstone bed at the base of Unit Ub (Tanaka, 1963 ; Tsushima *et al.*, 1958). Associated with *I.* (*Cr.*) *deformis* Meek, *I.* (*I.*) *uwajimensis, I.* (*I.*) aff. *pedalionoides, Didymotis akamatsui* (Yehara), *Damesites damesi* (Jimbo), *Neophylloceras subramosum* Spath, *Tetragonites glabrus* (Jimbo) and *Mesopuzosia yubarensis* (Jimbo).

Range.—The specimen handled was obtained from Unit Ub, associated with *I.* (*Cr.*) *deformis* and *I.* (*I.*) *uwajimensis.* According to Kennedy and Cobban (1991), *I.* (*Cr.*) *deformis*

indicates the lower middle Coniacian of the Western Interior, to Kauffman (1978a, b) and Tröger (1981b, 1989) the species represents the middle Coniacian of Europe, while Seitz (1959) positioned the species in the middle Coniacian (Unterconiac before Seibertz, 1979), and Collom (1993, personal communi-cation) in the upper lower Coniacian. Unit Ub is regarded as lower middle Coniacian deposits (Noda, 1992, p. 1313). The stratigraphic range of the species in Japan should be made clear on the basis of further field work in various regions.

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Five inoceramids (Bivalvia) from the Upper Cretaceous of Hokkaido with some phylogenetic and taxonomic considerations, Part 2. Systematic descriptions of three species of *Inoceramus* (*Cremnoceramus*) and concluding remarks

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Abstract. Described along with phylogenetic and taxonomic considerations are three species of *Inoceramus* (*Cremnoceramus*) from the Upper Turonian to lower middle Coniacian of the Obira and Ikushunbetsu areas of Hokkaido: *Inoceramus* (*Cremnoceramus*) *deformis* Meek, *I.* (*Cr.*) *ernsti* Heinz and *I.* (*Cr.*) *lueckendorfensis* Tröger. Concluding remarks on the significance of occurrence of cosmopolitan species (including two species described in part 1) from Japan are also made.

Key words: *Inoceramus*, Cretaceous, Upper Yezo Group, phylogeny, subgenus

Introduction

In the present part, three inoceramids from the upper Turonian to lower middle Coniacian of the Upper Yezo Group of Hokkaido are described.

Systematic descriptions

Family Inoceramidae Zittel, 1881
Genus *Inoceramus* Sowerby, 1814
Subgenus *Cremnoceramus* Cox, 1969

Type species.—*Inoceramus inconstans* Woods, 1912a, designated by Cox (1969).

Diagnosis.—See Cox (1969, p. N314) and Herm *et al.* (1979, p. 58).

Remarks.—The name "*Cremnoceramus*" was originally proposed as a full genus of the Inoceramidae Heinz fam. nov., 1932, by Heinz (1932) who gave a brief diagnosis and designated "*Cremnoceramus absolutus* Heinz, 1932" as the type species. The name was invalid, as Vokes (1967) pointed out, because neither diagnosis nor illustration was given for the type species. Cox (1969) validated *Cremnoceramus* as a subgenus of *Inoceramus* Sowerby, 1814 (in Cox, 1969), with a clear revised diagnosis and designated *I. incon-*

stans as the type species. At that date *Cremnoceramus* became an available name, with Cox as its author, under Art. 50 of the I.C.Z.N. In spite of this situation, Vokes (1980) wrongly regarded the name as still invalid. Herm *et al.* (1979) ranked *Cremnoceramus* as a full genus of the Inoceramidae with supplemental description and remarks. However, they (1979) pointed out the question of whether the group of "*I.*" *rotundatus* Fiege and "*I.*" *weltersdorfensis* Andert should be assigned to *Inoceramus* or *Cremnoceramus*. Besides this work, in some other papers (Kauffman, 1978a, b ; Walaszczyk, 1988 ; Wiedmann and Kauffman, 1978), *Cremnoceramus* is regarded as a full genus, and in still others (Cox, 1969 ; Hattin and Cobban, 1977 ; Ivanikov, 1979 ; Tröger, 1981a ; López, 1989, 1990, 1992 and Kennedy and Cobban, 1991) as a subgenus of *Inoceramus*. In my opinion, it is adequate that *Cremnoceramus* be ranked as a subgenus of *Inoceramus* because there is a group of transitional forms which is hardly assignable either to *Inoceramus* or *Cremnoceramus*, as Herm *et al.* (1979) mentioned. According to Heinz (1932), Cox (1969) and Herm *et al.* (1979), the geniculation of the shell is an important criterion for *Cremnoceramus*. In contrast Tröger (1981a) pointed out that the geniculation should not be used for taxonomic purposes because it is a highly flexible feature varying with mode of life.

Inoceramus (*Cremnoceramus*) *deformis* Meek, 1871

Figures 1-1a—d, 2a—c ; 7-4

Inoceramus sp. ? Hall, 1845, p. 310, pl. 4, fig. 2.

Inoceramus deformis Meek, 1871, p. 296 ; White, 1875, p. 179, 180, pl. 15, fig. 1 ; Meek, 1876, p. 146, pl. 14, figs. 4a, b ; Stanton, 1893, p. 85, pl. 15, fig. 2 ; Heinz, 1928b, p. 34, pl. 2, fig. 1, Seitz, 1959, p. 118 ; Dobrov and Pavlova, 1959, p. 138, pl. 8, fig. 3 ; Scott and Cobban, 1964, pl. 1 ; Tröger, 1967, p. 130-132, pl. 14, fig. 7 ; Hattin and Cobban, 1977, p. 191, 192, fig. 9 ; Ivanikov, 1979, p. 48, 49, pl. 6, figs. 2, 3 ; Cieśliński and Blaszkiewicz, 1984, p. 364, pl. 158, fig. 1 ; Szász, 1985, p. 161, 162, pl. 6, figs. 1a, b, 2a, b ; Cieśliński and Blaszkiewicz, 1989, pl. 159, fig. 1 ; Tarkowski, 1991, p. 107, pl. 15, fig. 1.

"Inoceramus" deformis deformis Meek, Kauffman, 1978a, p. IV-8, list.

"Inoceramus" deformis n. subsp. Kauffman, 1978a, p. IV-8. list.

Inoceramus ? *deformis* Meek. Kauffman, 1978b, p. XIII-2, list.

Inoceramus (?) *deformis deformis* Meek. Kauffman, 1977, p. 245, pl. 12, fig. 3.

Inoceramus (?) *deformis* n. subsp. Kauffman, 1977, p. 245, pl. 12, fig. 2.

Inoceramus (*Cremnoceramus*) *deformis* Meek. Seibertz, 1986, p. 1177 ; Kennedy and Cobban, 1991, p. 9, 10, list.

Cremnoceramus deformis (Meek). Walaszczyk, 1988, pl. 8, figs. 1, 2 ; Kopaevich and Walaszczyk, 1990, pl. 4, figs. 4a, b ; Walaszczyk, 1992, p. 52, 53, pl. 29, fig. 4, pl. 30, fig. 4.

Cremnoceramus ? *deformis* (Meek). Walaszczyk, 1992, pl. 36, fig. 4.

Holotype.—By monotypy, the specimen drawn by Meek (1876, pl. 14, fig. 4) from the Niobrara Formation, Pueblo, Colorado, but its precise locality is uncertain.

Material.—JG.H3016 from loc. Ob0012, JG.H3058 and 3060 from loc. Ob0013 in the Obira area, northwest Hokkaido.

Description.—Shell medium-sized, subequivalve and inequilateral. Considerably inflated from anterior to posterior and also along growth axis sometimes with geniculation. Anterior side fairly broad and steep or perpendicular to commissure plane. Posterodorsal part also steep to hinge without flattened wing-like area. Umbo terminal or subterminal, left one somewhat projected over hinge line and strongly curved inwards and slightly twisted forwards. Right umbo scarcely rising above hinge line. Growth axis broadly concave to anterior. Anterior margin long, nearly straight or broadly convex, but for a portion near umbo slightly concave ; anteroventral margin somewhat narrowly bent. Ventral margin asymmetrically rounded but subangularly bent at ventral extremity (at intersecting point of growth axis to ventral margin) ; posterior margin broadly arcuate, forming an obtuse angle with hinge line which is about half shell length on average. Hinge plate fairly thick and ligament pits are deep and scooped with rounded and narrow interspaces, according to terminology by Crampton (1988, p. 987, text-fig. 3 and p. 985, table 2).

Surface ornamented with major and minor sculpture in combination ; concentric ribs coarse, sharp- or round-topped and irregular in size and interspaces, showing considerable extent of variation ; concentric rings superimposed on ribs and interspaces, weak, round-topped and regular in breadth and height. One or two radial elevations devel-

oped, one of which corresponds to growth axis or runs somewhat posteriorly, anterior one demarcates anterior wall from main part of disk.

Biometry.—Measurements are shown in Table 1.

Individual relative growth of l vs. h and b vs. h is demonstrated in Figure 2, showing left and right valves of the specimen JG.H3016. Relative growth of l vs. h shows negative allometry in both valves, whereas that of b vs. h is regarded as positive allometry.

Ontogenetic changes in l/h, b/h and obliquity (δ) are also demonstrated in Figures 3A, B and C, respectively. The simple ratio l/h decreases gradually while b/h and obliquity increase with growth, b/h changes abruptly at a certain stage of growth in some specimens, and obliquity is considerably variable among individuals.

Profiles of the specimens in two directions are shown in Figure 4. Weak geniculation is perceptible in the vertical section of the left valve of the specimens examined. The cross sections are nearly circular, being usually convex or bowl-shaped.

Remarks.—The specimen JG.H3016 (Figures 1-1a—d) consists of well preserved closed valves somewhat displaced along the commissure plane. Two blunt radial elevations develop on both valves. The anterior one demarcates indistinctly the anterior wall from the disk and posterior one runs somewhat posteriorly along the growth axis. Therefore, the shell is subrectangular in general outline. Small hemispherical pits are scattered on the internal mold of the left valve. These seem to be that the traces of blister pearls produced to cover holes made by boring barnacles (Seilacher, 1969) while the animal was alive.

Comparison and discussion.—JG.H3016 resembles closely the holotype of *I.* (*Cr.*) *paradeformis* Szász (1985, pl. 17, figs. 1a-d) and other specimens figured in the same paper, from the lower Coniacian of the Babadag Basin, Romania, in its trapezoidal to subquadrate outline, posterodorsal slope to hinge, ontogenetic change of obliquity, coarse and sharp-topped concentric ribs and the development of two weak radial elevations. According to Szász (personal communication, June 15, 1993), "the main difference exists in the shape of the umbo which is narrow in the Japanese specimen, with the apex more pointed and, in general, more highly raised above the hinge line. The shape of ribs in the first growing stage (up to 50 mm-60 mm distance from the apex of the umbo) is also different : it is almost circular in the Japanese specimen, (δ) being about 85° whereas in the specimens from Romania, the ribs are strongly elongated toward the posterior part of the valve, (δ) varying between 35°-45°. Even in specimens of *I. paradeformis* with almost circular ribs in the umbonal zone (Szász, 1985, pl. 16, fig. 1) the umbo is more massive than that of the Japanese specimen." Furthermore, Szász (1985, p. 30) remarked that *I. paradeformis* Szász, 1985, *I. dobrogensis* Szász, 1985 and *I. babadagensis* Szász, 1985 from the Babadag Basin, Dobrogea, resemble closely one another and are obviously related to *I. deformis,* all of them could constitute a single biological species. But the three morphotypes are regarded as three distinct morphological species until necessary information is available.

*I.* (*Cr.*) *deformis* was established on the basis of a single
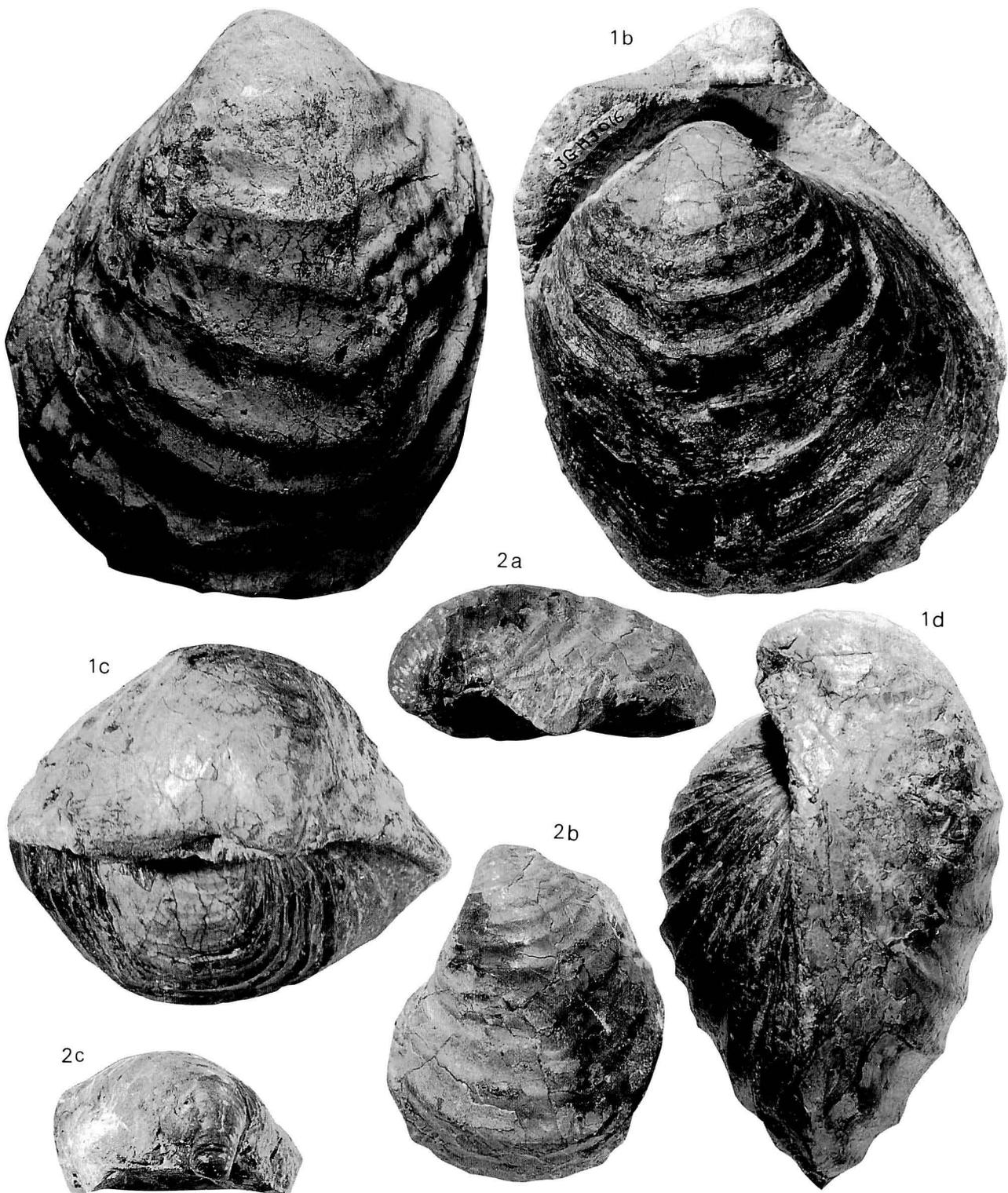
Figure 1. *Inoceramus* (*Cremnoceramus*) *deformis* Meek, all figures natural size. **1a–d.** JG.H3016 from loc. Ob0012. 1d : anterior view (coll. T. Shimanuki, 1988). **2a–c.** JG.H3060 from loc.Ob0013, 2a : anterior view (coll. T. Shimanuki and Noda, 1991).

Table 1. Measurements of *Inoceramus (Cremnoceramus) deformis* Meek from Hokkaido. Linear dimension in mm.

specimen	valve	h	l	b	s	H	L	α	γ	δ	$\delta_{H=60mm}$
JG. H3016	L.	99.2	81.8	39.8	38.3	99.6	87.0	132°	102°	86°	84°
	R.	77.4	70.4	29.7	33.0	81.8	74.8	132°	102°	76°	70°
JG. H3058	R.	51.8	53.6	14.0	29.2	52.0	59.3	123°	103°	74°	—
JG. H3060	L.	53.3	45.1	19.2	18.1	53.3	42.7	136°	104°	87°	—

specimen	valve	l/h	$l/h_{H=60mm}$	b/h	$b/h_{H=60mm}$	L/H	s/l	remarks
JG. H3016	L.	0.82	0.94	0.40	0.40	0.87	0.47	
	R.	0.91	0.86	0.38	0.31	0.91	0.47	
JG. H3058	R.	—	—	—	—	—	—	secondarily deformed
JG. H3060	L.	0.85	—	0.36	—	0.80	0.40	less than 60 mm in H

For Abbreviations, refer to Noda (1996, table 1 and fig. 1).
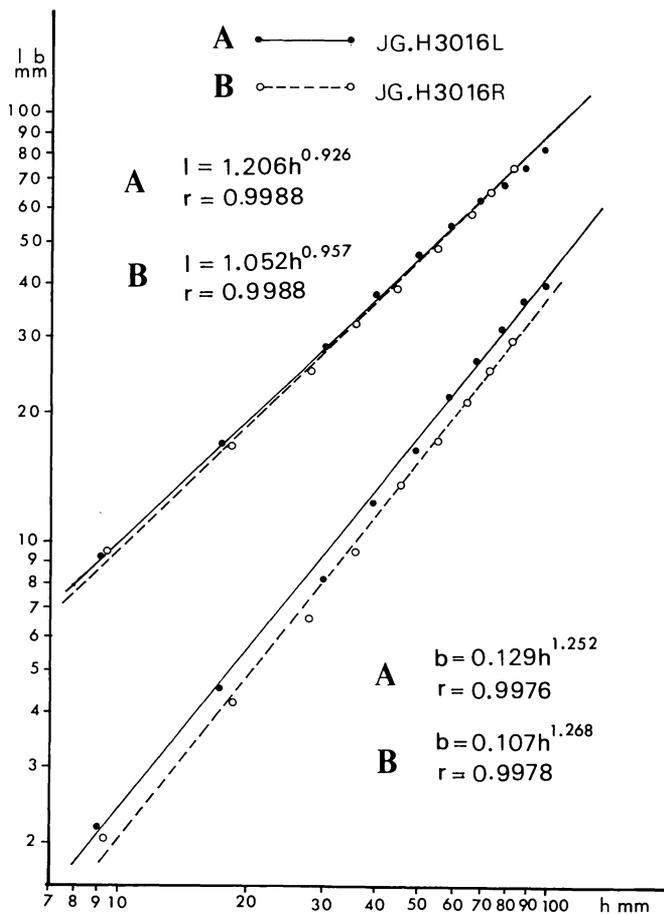
Figure 2. Diagram showing individual relative growth between l and h, and b and h of *Inoceramus (Cr.) deformis* (specimen JG.H3016).

imperfect specimen from the lower Coniacian of the Niobrara Group, Colorado. There has not been much information subsequently, in regard to this species from the type locality and adjacent areas, only some figures with no description (Hattin and Cobban, 1977 ; Kauffman, 1977) and biostratigraphic records by Scott and Cobban (1964), Hattin and Cobban (1977), Kauffman (1977, 1978a, b) and Kennedy and Cobban (1991). Thus the variability of the species is not yet clear at present. Collom (personal communication, 1993) is engaged in research on this species on the basis of a large number of specimens from several localities in Colorado. Thus the extent of variation of *I. (Cr.) deformis* will be made clear in the near future.

The specimens of *I. (Cr.) deformis* figured by Hall (1845), Meek (1876), Tröger (1967), Kauffman (1977), Hattin and Cobban (1977), Walaszczyk (1988, 1992), Szász (1985) Kopaevich and Walaszczyk (1990) and Collom (personal communication, 1993) from the upper lower to lower middle Coniacian of various regions around the world are considerably variable in general outline and surface ornamentation but have the following in common : nearly equivalve, comparatively small beak, not so prominent umbo, vaulted shell with geniculation, steep posterodorsal slope without distinct wing-like area and the concave growth axis. Although also variable in outline and ornamentation, the present specimens accord with some forms of *I. (Cr.) deformis* described or figured previously in the other characters.

The specimen JG.H3016 is distinct from the hypotype figured by Kauffman (1977). Collom (Feb. 20, 1993, personal letter with the comment for the plaster cast of JG.H3016) regarded it as a fine specimen of *I. (Cr.) deformis (Cremnoceramus* of his sense). If this assignment is pertinent, the allied species described from various regions may have to be reexamined taxonomically as Szász (1985) remarked. I have no intention of discussing that problem further because of the insufficiency of the Japanese material.

As Walaszczyk (1992, p. 55) regarded *I. (Cr.) paradeformis* as a junior synonym of *I. (Cr.) ernsti*, the holotype of *I. (Cr.) paradeformis* truly resembles the lectotype of *I. (Cr.) ernsti* illustrated by Woods (1912a, text-fig. 85 ; =Walaszczyk,
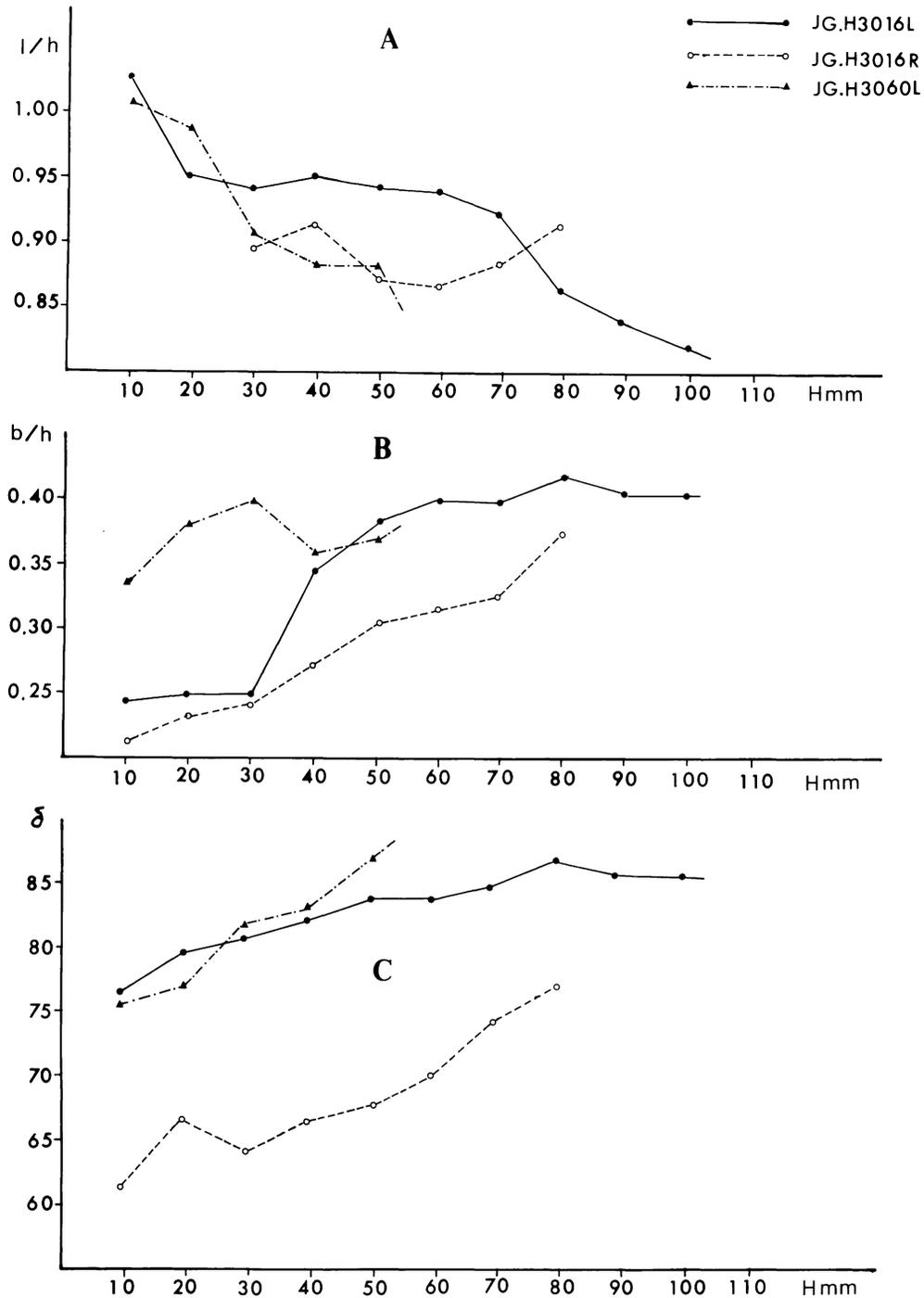
Figure 3. Diagram showing ontogenetic changes in selected characters of *Inoceramus* (*Cr.*) *deformis*. A : l/h, B : b/h, C : obliquity.

1992, pl. 32, figs. 2a, b) in general outline and surface ornamentation, but *I.* (*Cr.*) *ernsti* has a concave anterior wall, which is an essential character and an important criterion of the species as Woods (1912a) originally remarked ; the anterior wall of *I.* (*Cr.*) *paradeformis* is not so conspicuously concave except for the umbonal region, as Szász (1985)

described. The two species are thus distinct from each other.

The specimen of *I.* (*Cr.*) *schloenbachi pratjei* Heinz, 1928 figured by himself (1928b, pl. 6) was regarded as *I.* (*Cr.*) *deformis* by Seitz (1956, p. 118), but Heinz's subspecies is distinct from *I.* (*Cr.*) *deformis* in the moderately convex shell
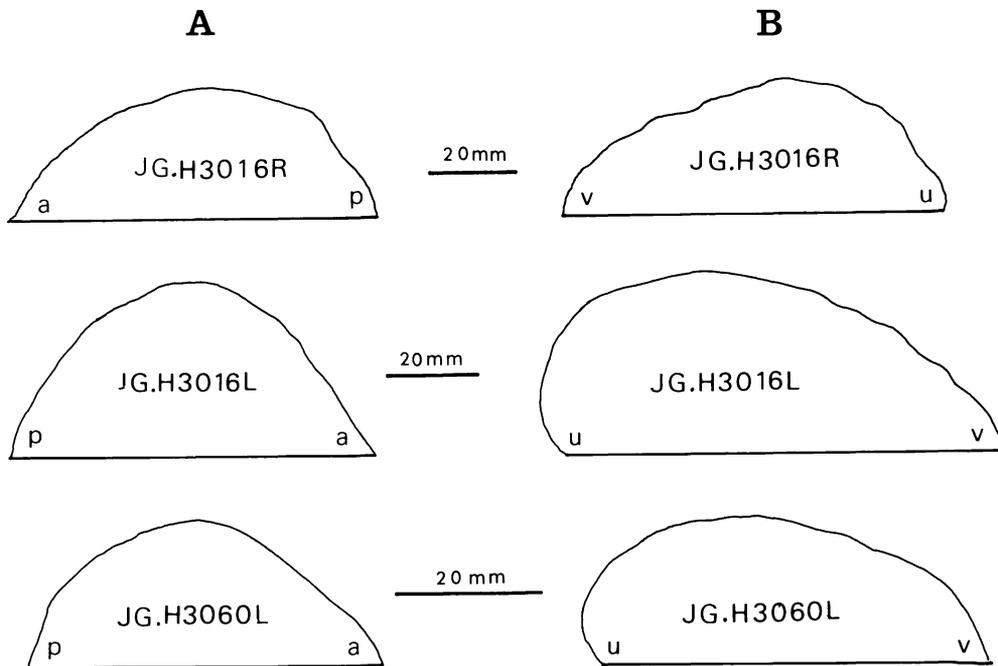
Figure 4. Profiles of selected specimens of *Inoceramus* (*Cr.*) *deformis* in two directions. A : cross section at the highest point of shell convexity, B : vertical section along the growth axis. a : anterior, p : posterior, u : umbo, v : venter.

especially in the umbonal region, even though the anterior part and left umbo, important characteristics of the species, are missing.

Phylogeny.—On the basis of the chronological change in shell size and surface ornamentation, Walaszczyk (1992, p. 53) regarded *I.* (*Cr.*) *deformis* as the last representative of the lineage of *I.* (*Cr.*) *waltersdorfensis* Andert—*I.* (*Cr.*) *brongniarti* Mantell—*I.* (*Cr.*) *deformis* Meek. Besides, Kauffman (1978b) considered the lineage of *I.* (*Cr.*) *deformis* as *I.* (*Cr.*) *rotundatus* Fiege—*I.* (*Cr.*) *erectus* Meek—*I.* (*Cr.*) *deformis* Meek—*I.* (*Cr.*) *schloenbachi* Böhm. The Japanese material is too deficient, at present, to discuss the phylogeny of *I.* (*Cr.*) *deformis*. Nevertheless the vaulted shell with blunt radial elevations shown by JG.H3016 may suggest some relationships with *I.* (*Cordiceramus*).

Occurrence.—For the locality map of the Obira area, readers may refer to Noda (1992, p. 1312, fig. 1).

Loc. Ob0012 (= loc. NH78 of Tanaka, 1963). Topographic map "Takishita", Scale 1 : 25000. A river floor of the Obira-shibe, somewhat below Bridge Takimi-Ohashi, now below the water level of artificial Lake Obirashibeko. Silty sandstone bed at the base of Unit Ub (Tanaka, 1963, Tsushima *et al.*, 1958). Associated with *I.* (*I.*) *uwajimensis* Yehara, *I.* (*I.*) aff. *pedalionoides* Nagao and Matsumoto and *I.* (*Cr.*) *ernsti* Heinz. For *Loc. Ob0013.* see Noda (1996, Part 1, p. 569)

Range.—Locs. Ob0012 and 0013 are located in Unit Ub which immediately overlies Unit Ua2 (Tanaka, 1963). Unit Ua2 contains *I.* (*Cr.*) *rotundatus* which is a good cosmopolitan zonal index of the lower lower Coniacian. Besides, one of the associated species, *I.* (*I.*) *uwajimensis*, is a representative

of the upper lower to middle Coniacian of Japan and adjacent areas. Thus the stratigraphic position of *I.* (*Cr.*) *deformis* along the River Obirashibe is limited to upper lower and/ or lower middle Coniacian. But the true range of this species in Japan should be made clear on the basis of further stratigraphic work in various regions.

Coniacian inoceramid zonation was previously proposed by Cobban (1951), Scott and Cobban (1964), Kauffman (1978a, b), Kauffman *et al.* (1978), Cobban (1986) and Szász and Ion (1988), but there is disagreement among them. According to the recent work by Kennedy and Cobban (1991) in the Western Interior, *I.* (*Cr.*) *deformis* indicates practically the lower part of the middle Coniacian. Besides, Kopaevoch and Walaszczyk (1990) regarded the species as a representative of the upper lower Coniacian of southwestern Crimea.

To sum up, opinions about the range of *I.* (*Cr.*) *deformis* slightly differ among researchers due to time lag among areas and/or different views of the specific definition, but the range largely falls within the period from lower to lower middle Coniacian.

Inoceramus (*Cremnoceramus*) *ernsti* Heinz, 1928

Figures 5-a—c ; 6-1a, b, 2a—d ; 7-1a—c, 2a—c, 3a—d

Inoceramus lamarcki Parkinson (pars). Woods, 1912a, p. 325, fig. 85.

Inoceramus ernsti Heinz, 1928a, p. 73, 74 ; Tröger, 1967, p. 128-130, pl. 14, figs. 1-6 ; Ivanikov, 1979, p. 51, 52, pl. 8, figs. 1, 2 ; Szász, 1985, p. 172, pl. 29, figs. 3a, b ; Tarkowski, 1991, p. 108, pl. 14, fig. 5.

Figure 5. *Inoceramus* (*Cremnoceramus*) *ernsti* Heinz.   JG.H3023 from loc.Ob2100,   ×ca 0.5 (coll. T. Shimanuki, 1985).

Inoceramus (Inoceramus) ernsti Heinz. Kauffman, 1977, p. 242, 244, pl. 11, fig. 5 ; Kauffman *et al.*, 1978, p. 34, pl. 15, fig. 5.

Inoceramus (Cremnoceramus) ernsti Heinz. Lôpez, 1990, p. 189-193, pl. 5, figs. 6a, b ; Lôpez, 1992, p. 2-245—2-248, pl. 1, figs. 4, 5a, b.

Cremnoceramus ernsti (Heinz). Walaszczyk, 1992, p. 55, 56, pl. 32, figs. 1-3.

Tethyoceramus (Protoceramus) ernsti (Heinz). Heinz, 1934, p. 250, pl. 19, fig. 1.

Compare.

Inoceramus cf. *ernsti* Heinz. Pergament, 1971, p. 119, 120, pl. 33, fig. 2, pl. 34, fig. 3.

Lectotype.—The specimen hand-drawn by Woods (1912a, p. 325, fig. 85) was designated as the lectotype by Tröger (1967, p. 128). The same specimen was photographed by Walaszczyk (1992, pl. 32, figs. 2a, b).

Material.—JG.H3017 from loc.Ob0020, JG.H3059 from loc. Ob0013, JG.H3061 from loc.Ob0011, JG.H3203 from loc. Ob2100 in Obira area, WE.P1312 and 1331 from loc.Ik8617a in Ikushunbetsu area.

Description.—Shell medium to large, slightly inequivalve, inequilateral, much higher than long. Valve considerably convex from anterior to posterior and also along growth axis which is straight or somewhat concave to anterior. Anterior wall angularly bent from disk and deeply concave to commissure plane, posterior and posterodorsal parts fairly steep without forming a clearly defined wing. Two or three blunt radial elevations developed, of which anterior one demarcates sharply anterior wall from disk, median one corresponds to growth axis and posterior one is indistinct or hardly perceptible. Umbo small and situated at anterior end, left one more projected over hinge line than the right and curved inwards. Anterodorsal margin long and straight, anterior through ventral ones broadly or moderately rounded and more or less acutely bent at ventral extremity where median radial elevation intersect. Posteroventral to posterior ones broadly arcuate and forming an obtuse angle with hinge line which is shorter than half of the shell length. Hinge plate fairly thick and ligament pits deep, rectangular and interspaces with round ridge.

Surface ornamented with concentric ribs and rings in combination, the former are round-topped, variable in height and irregular in breadth and broaden with growth, the latter are superimposed on ribs and interspaces.

Biometry.—Measurements are shown in Table 2.

Figure 8 gives individual relative growth of l vs. h of JG.H3017 in left and right valves. The l vs. h reduced major axes show negative allometry in both valves and b vs. h positive diphasic allometry with different critical points between two valves.

Ontogenetic changes in l/h, b/h and obliquity (δ) are shown in Figures 9A, B and C, respectively. The simple ratio l/h decreases gradually with growth, whereas that of b/h increases gradually or abruptly in some specimens ; obliquity increases gradually in early stage of growth and becomes constant in later growth stage.

Profiles of well preserved specimens in two directions are illustrated in Figure 10. Geniculation is clearly shown in JG.H3017L and WE.P1321, and anterior wall is angularly bent from the main part of disk and distinctly concave to commissure plane in all specimens.

Remarks.—JG.H3017L and 3017R (Figures 6-1, 2) were obtained as separate valves in a single nodule. These probably belong to one and the same individual. These "are fairly well preserved with no secondary deformation but some eroded portions. The hinge structure is clearly observed in the right valve (Figure 6-2b). The ligamental groove is fairly broad with scooped pits and angular ridges. Geniculation at a growth stage of 26 mm in H and a radial elevation develop distinctly along growth axis. JG.H3203 is a huge individual, which was initially assigned to *I.* (*I.*) *hobetsensis nonsulcatus*, but is distinct from the typical form of that subspecies in a deeply concave anterior wall, fairly crowded ribs, blunt elevation along the growth axis and its higher stratigraphic occurrence in the upper Turonian.

Comparison and discussion.—*Inoceramus ernsti* was established by Heinz (1928b) on the basis of the specimen figured by Woods (1912a). According to Woods (1912a), the specimen drawn by himself was brought probably from the zone of *Holaster planus* of the Upper Chalk (upper Turonian), but its locality is unknown. Tröger (1967) designated Woods' specimen as the lectotype. It is characterized by the concave anterior wall as Woods (1912a) originally pointed out and vaulted shell with distinct geniculation, which is an important criterion of *I.* (*Cremnoceramus*). Tröger (1967) described precisely the specific characters and examined the species biometrically on the basis of more than twenty specimens from the lower middle Coniacian (="oberen Oberturon bis unteren Coniac" before Seibertz, 1979) of the Sachsen (Saxony), Böhmen (Bohemia) and Brandenburg regions.

Specific characters described by Tröger (1967) agree with those of the present specimens, especially in showing two radial elevations, one of which clearly demarcates the concave anterior wall from the convex disk as drawn by himself (Tröger, 1967, pl. 14, fig. 3) while the other runs along the growth axis.

From the above comparison, the specimens available are identical with *I.* (*Cr.*) *ernsti* Heinz.

The specimens of *I.* (*Cr.*) *ernsti* from the lower Coniacian of the Babadag Basin of Romania figured by Szász (1985, pl. 29, figs. 3a, b) and also from the lower Coniacian of the Navarro-Cantabrian Basin of Spain figured by Lôpez (1990, pl. 5, figs. 6a, b ; 1992, pl. 1, figs. 5a, b) closely resemble each other, and both specimens show a somewhat larger l/h in comparison with the Japanese ones.

The specimen from the uppermost Turonian of northwestern Kamchatka, figured by Pergament (1971, pl. 33, fig. 2, pl. 34, fig. 3) somewhat resembles the specimens of Japan in its biconvex shell and concave anterior wall but has much coarser concentric ribs. Although the lateral view of the

Figure 6. *Inoceramus (Cremnoceramus) ernsti* Heinz. JG.H3017L and 3017R from loc.Ob0020, ×0.86. **1a, b.** Left valve. **2a-d.** Right valve, 2b shows hinge structure (coll. T. Shimanuki, 1989).
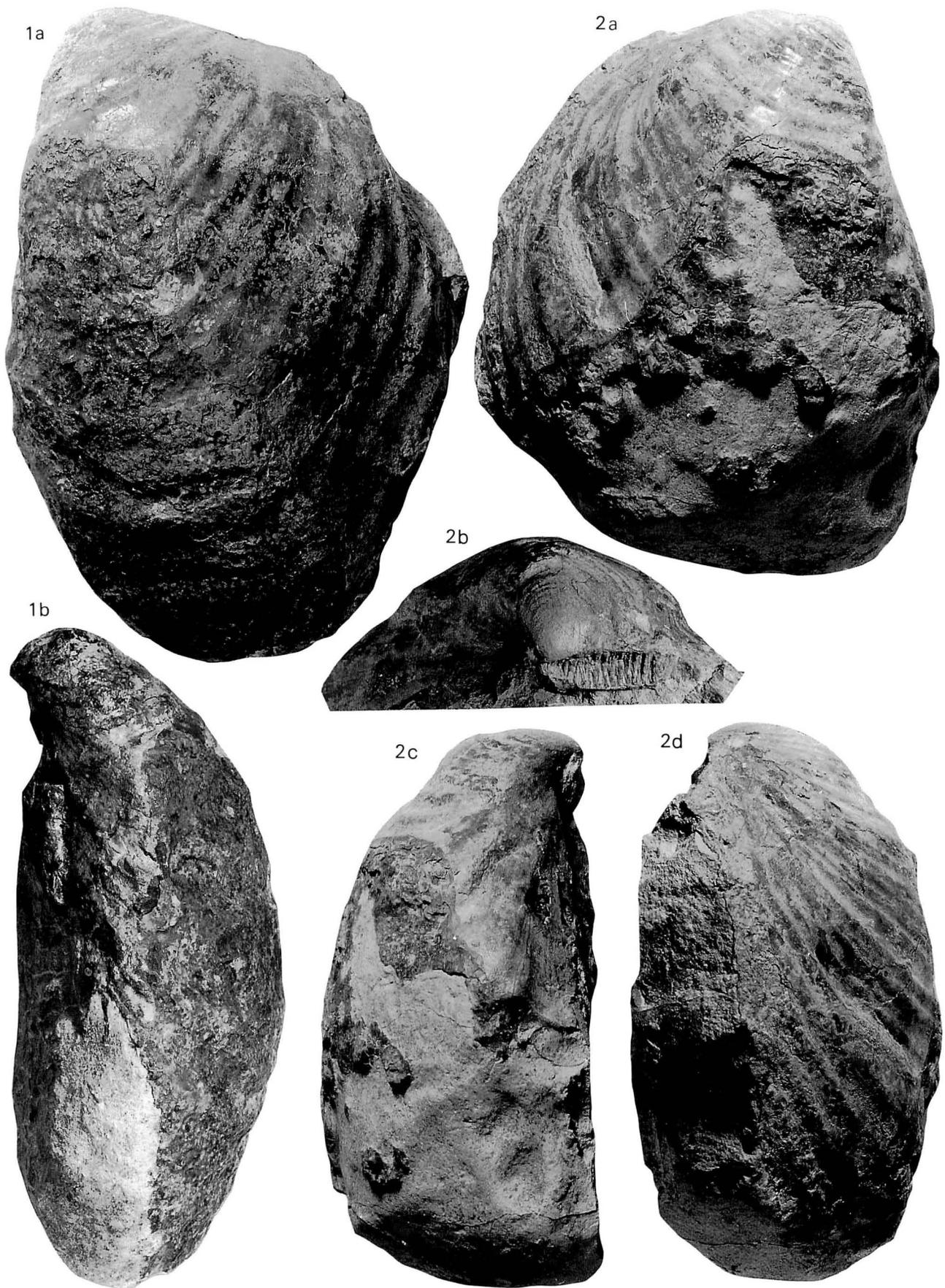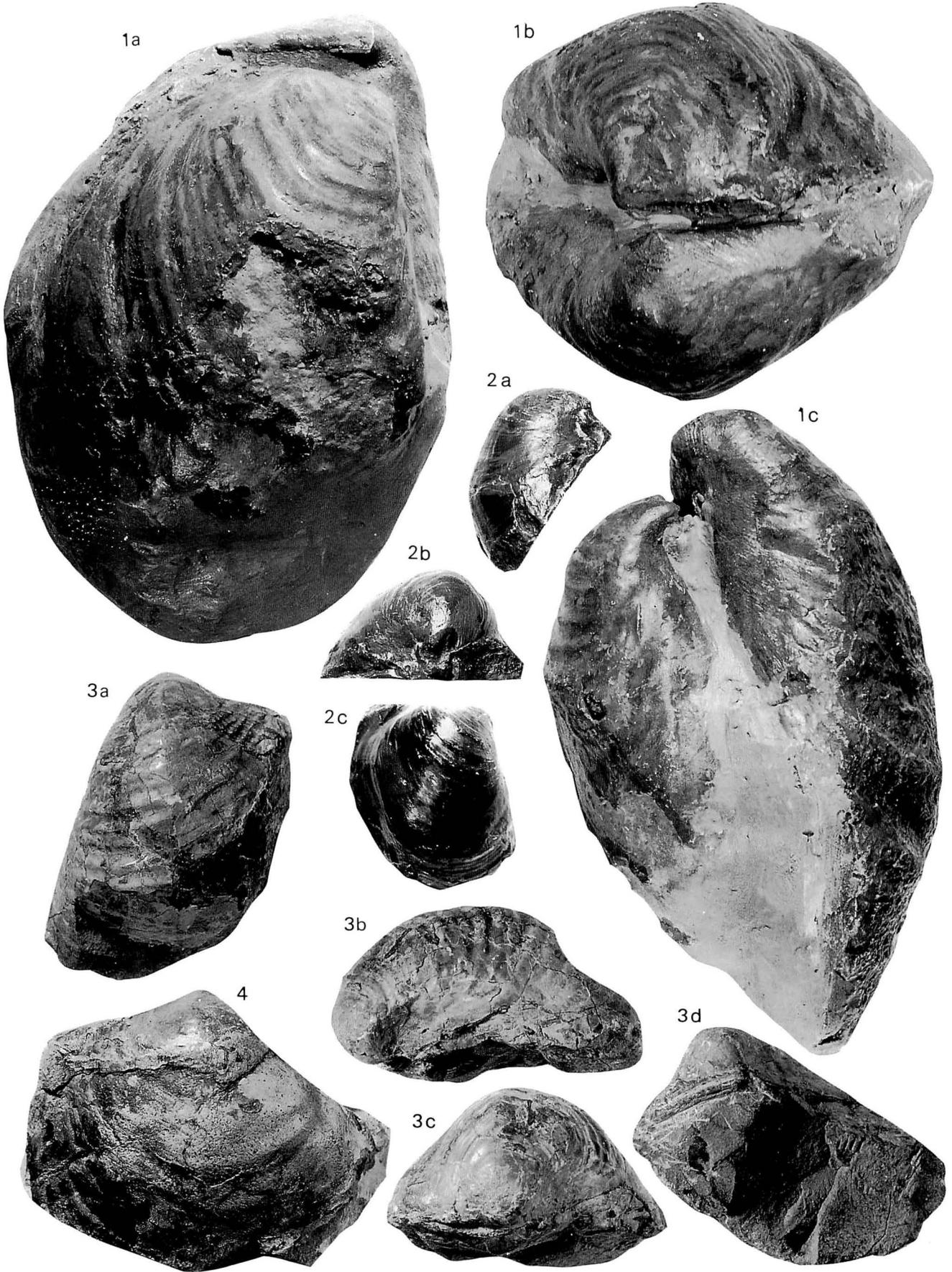
Table 2. Measurements of *Inoceramus (Cremnoceramus) ernsti* Heinz from Hokkaido. Linear dimension in mm.

specimen	valve	h	l	b	s	H	L	α	γ	δ	$\delta_{H=60mm}$
JG. H3017	L.	140.0	109.2	46.2	38.4	141.0	102.5	120°	140°	87°	83°
	R.	109.0	95.9	33.8	35.9	111.6	90.0	121°	138°	81°	78°
JG. H3059	L.	52.1	45.3	25.5	19.8	57.6	36.4	136°	90°	86°	—
WE. P1321	R.	34.7	30.1	19.1	15.0	35.4	29.5	117°	128°	80°	—

specimen	valve	l/h	l/h_{H=60mm}	b/h	b/h_{H=60mm}	L/H	s/l	remarks
JG. H3017	L.	0.78	0.93	0.33	0.26	0.73	0.35	
	R.	0.88	0.89	0.31	0.28	0.81	0.37	
JG. H3059	L.	0.87	—	0.49	—	0.63	0.34	secondarily deformed less than 60 mm in H
WE. P1321	R.	0.86	—	0.55	—	0.83	0.50	less than 60 mm in H
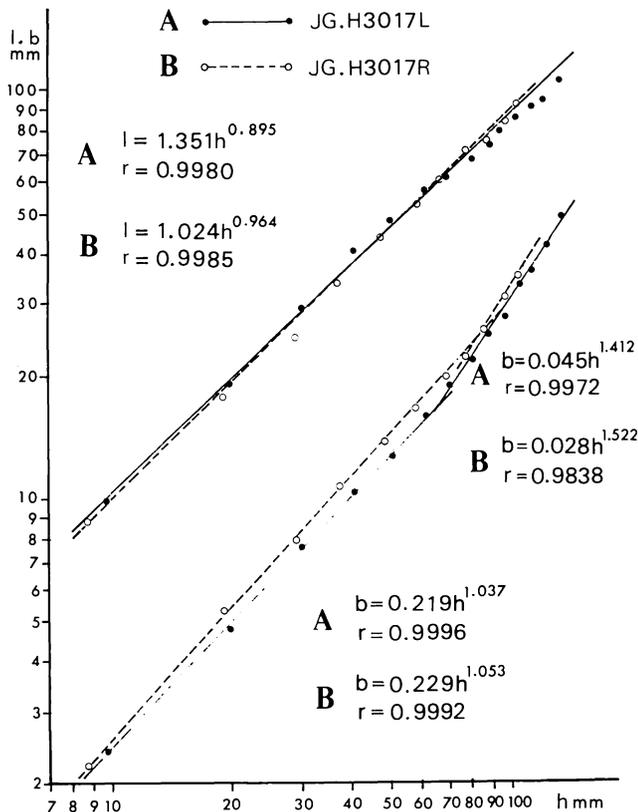
Figure 8. Diagram showing individual relative growth between l and h, and b and h of *Inoceramus (Cr.) ernsti* (specimen JG.H3017).

specimen is not shown, his specimen may be rather comparable with *I. (I.) iburiensis* Nagao and Matsumoto, 1939.

Phylogeny.—The lectotype of *I. (Cr.) ernsti* was originally regarded as a variety of *I. lamarcki* Parkinson which belongs undoubtedly to *I. (Inoceramus)*. Herm *et al.* (1979) pointed out the ambiguity of whether *I. rotundatus* Fiege and the group of "*I.*" *waltersdorfensis* Andert are assigned to *I. (Inoceramus)* or to *I. (Cremnoceramus)*, which suggests a close phylogenetic relationship between *I. (Inoceramus)* and *I. (Cremnoceramus)*. The development of blunt radial elevations in some specimens of *I. (Cr.) ernsti* may foretell the characters of *I. (Cordiceramus)* in the upper Coniacian and subsequent stages. In other words, it may be a "transient" linking *I. (Cremnoceramus)* and *I. (Cordiceramus)*. *I. (Co.) kawashitai* Noda, 1986, from the upper Coniacian of some areas of Hokkaido and Kyushu is certainly a descendant of *I. (Cr.) ernsti*. On the other hand, Tröger (1969, p. 74) located *I. (Cr.) ernsti* as a linking species between *I. (I.) lamarcki stümckei* Heinz, 1926, from the middle Turonian and *I. (Volviceramus) koeneni* Müller, 1887, from the middle Coniacian (so-called lower Coniacian before Seibertz, 1979). I agree with Tröger's scheme (1969, p. 74, fig. 8) for the reason mentioned previously in the phylogeny of *I. (Volviceramus) koeneni* (Noda, 1996).

The above discussion materializes a notion that *I. (Cr.) ernsti* is important as a common ancestor of *I. (Co.) kawashitai* and *I. (V.) koeneni*.

Occurrence.—*Loc. Ob0013.* See Noda, 1996, p. 569, for the locality of *I. (V.) koeneni*.

Loc. Ob0011. The opposite bank of loc. Ob0012 [see p. 576, for the locality of *I. (Cr.) deformis*] and the same layer as loc. Ob0012 which is stratigraphically about 20 m above loc. Ob0013.

Loc. Ob0020. (=NH54 of Tanaka, 1963). Topographic map

Figure 7. **1a-c.** *Inoceramus (Cremnoceramus) ernsti* Heinz. JG.H3063, ×0.86. Reconstructed plaster cast from JG. H3017L and 3017R. **2a-c.** *Inoceramus (Cremnoceramus) ernsti* Heinz. WE.P1321 from loc.Ik8617a. Natural size (coll. A. Asai). **3a-d.** *Inoceramus (Cremnoceramus) ernsti* Heinz. JG.H3059 from loc.Ob0013, natural size (coll. T. Shimanuki and M. Noda, 1991). **4.** *Inoceramus (Cremnoceramus) deformis* Meek. JG.H3058, same locality. Natural size (coll. T. Shimanuki and M. Noda, 1991).
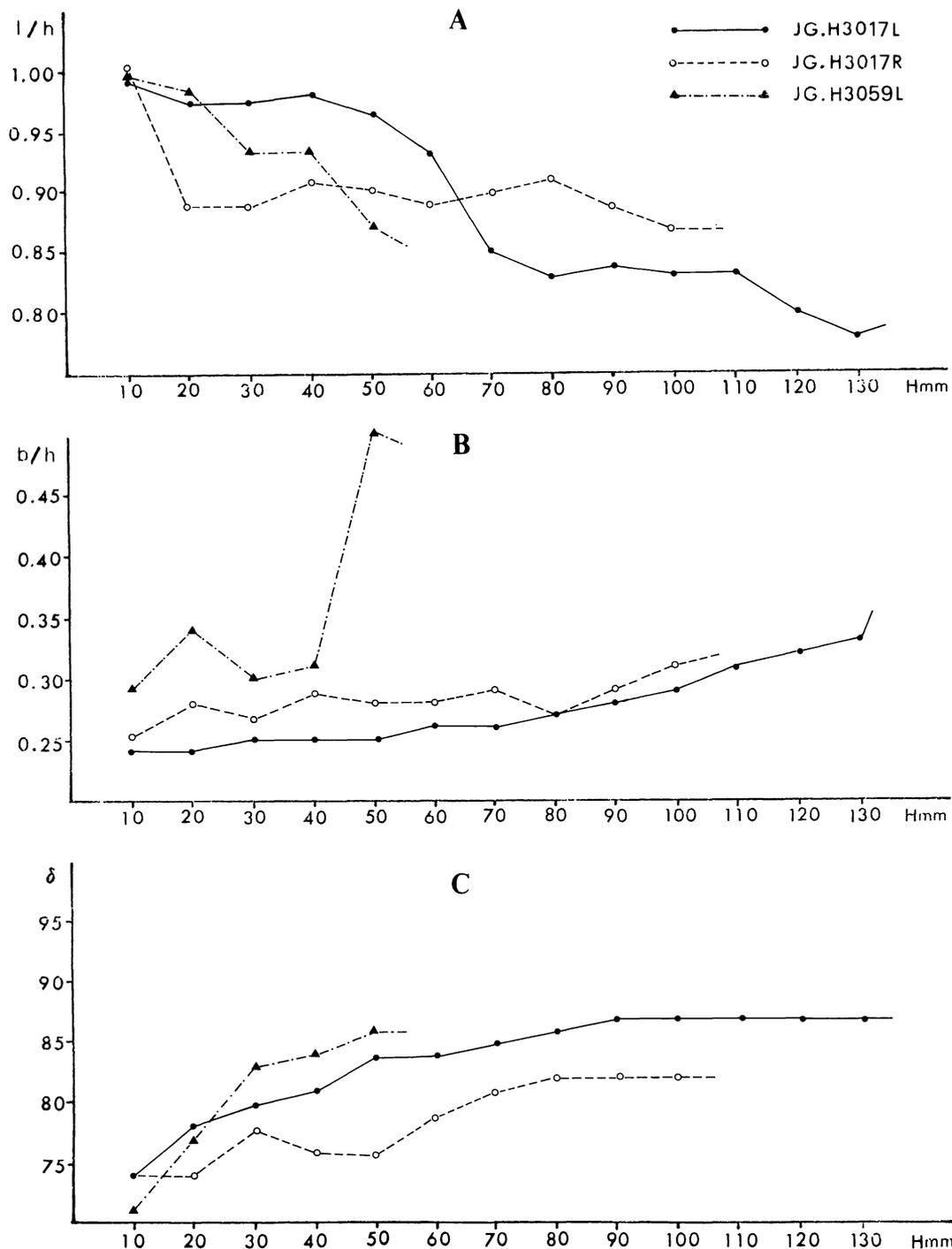
**Figure 9.** Diagram showing ontogenetic changes in selected characters of *Inoceramus* (*Cr.*) *ernsti*. A : l/h, B : b/h, C : obliquity.

"Takishita", Scale 1 : 25000. The right bank of the River Obirashibe, about 50 m below the confluence of the Jugosen-zawa, below the surface of the lake at full water seasons. Silty sandstone bed of Unit Ub. Associated with *I.* (*I.*) *uwajimensis* and *I.* (*Pl.*) *troegeri*.

Loc.Ob2100. Topographic map, ditto. A cliff of the River Kamikinenbetsu at the confluence with the Shigeruno-sawa. Sandy siltstone bed of Unit Mo (Tanaka, 1963). Frequently associated with huge individuals of *I.* (*I.*) *iburiensis.*
Loc.Ik8617a. For the locality map, see Noda (1996, fig. 9).

A   **B**

JG.H3059L   20mm   JG.H3059L
p   a   u   v

JG.H3017R   20mm   JG.H3017R
a   p   v   u

JG.H3017L   20 mm   JG.H3017L
p   a   u   v

WE.P1321R   20mm   WE.P1321R
a   p   v   u

JG.H3203L

40mm

p   a

JG.H3203L

u   v
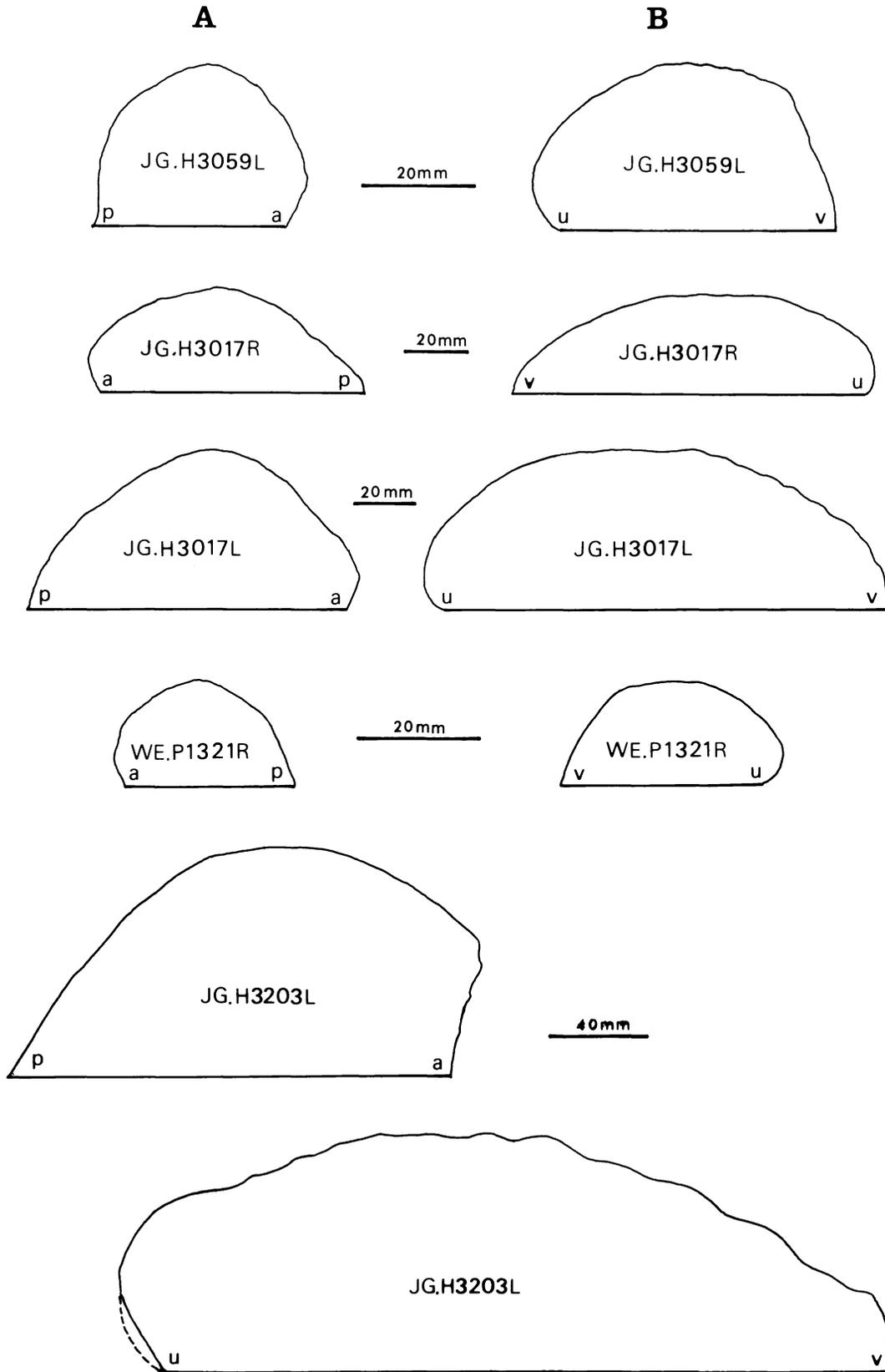
**Figure 10.** Profiles of selected specimens of *Inoceramus* (*Cr.*) *ernsti* in two directions.   A : cross section at the highest point of shell convexity.   B : vertical section along the growth axis.
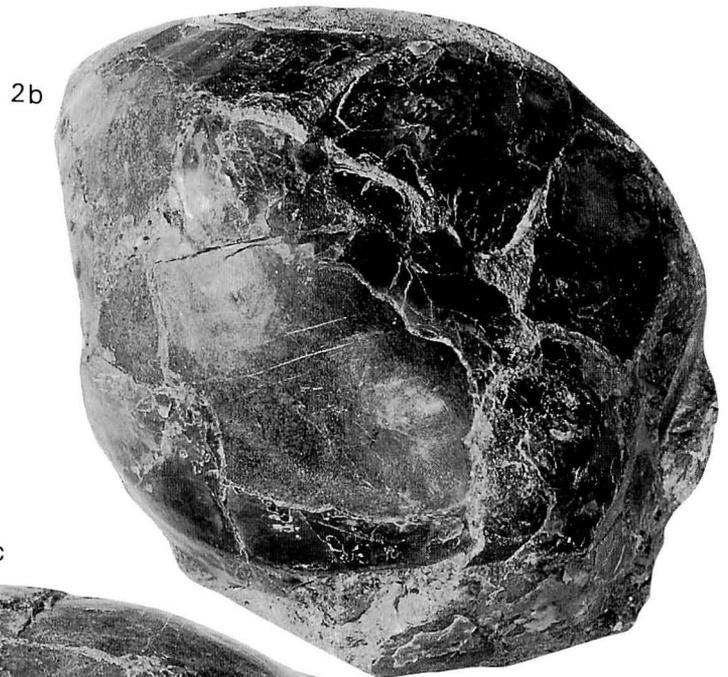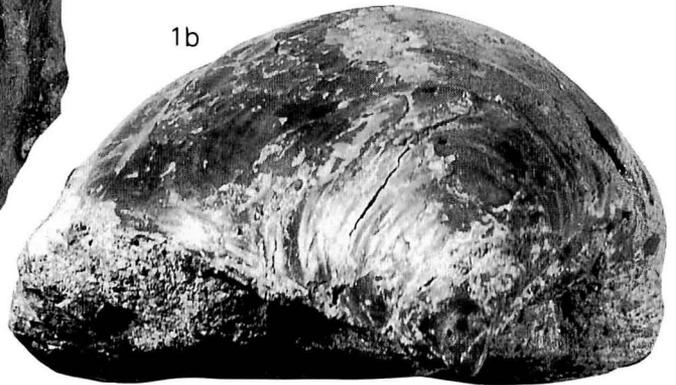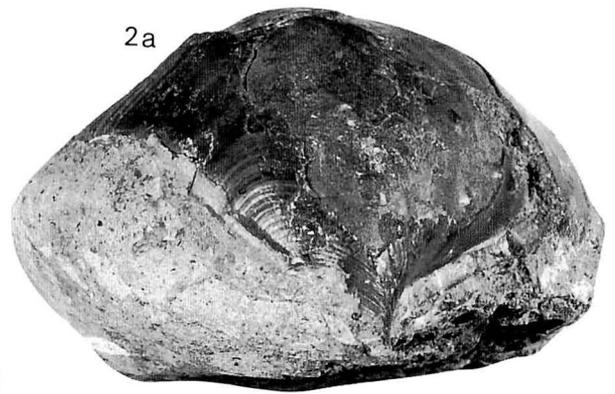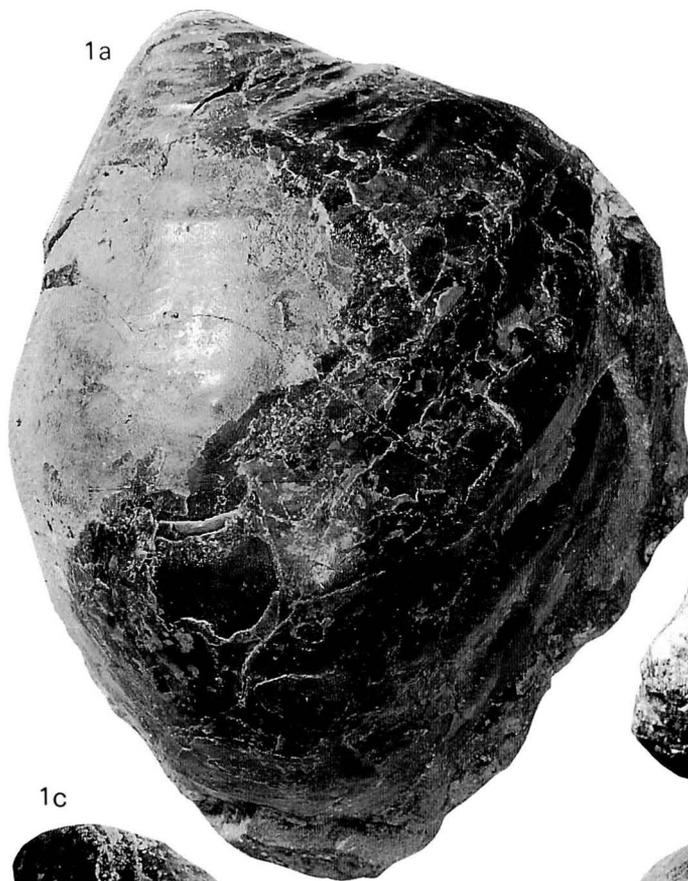
Topographic map "Katsurazawako", Scale 1 : 25,000.   A cliff on a forestry road along the Okuhidarimata-zawa (so-called Okusamata-zawa), about 450 m west of the fork along the left branch.   Fine sandy siltstone bed of IIIb member (Matsumoto, 1965) of the Upper Yezo Group.   Associated with *I. (I.) uwajimensis.*

Range.—The specimens examined occurred in the upper Turonian to the lower middle Coniacian.   This is in good agreement with its range in Europe.

Inoceramus (Cremnoceramus) lueckendorfensis
Tröger, 1967

Figures 11-1a—c, 2a—c

Inoceramus inconstans Woods.   Dobrov and Pavlova, 1959, p. 137, pl. 5, figs. 1a, b.
Inoceramus inconstans lueckendorfensis Tröger, 1967, p. 102-105, pl. 11, figs. 1a-c ; Tarkowski, 1991, p. 109, pl. 13, fig. 8.
Inoceramus "inconstans" lueckendorfensis Tröger. Tröger, 1981a, p. 102, 106, 107, pl. 1, figs. 8-11.
Inoceramus (Cremnoceramus) inconstans lueckendorfensis Tröger.   Tröger, 1989, p. 917, 918, list.

Holotype.—Arbeitanr. 92F (Tröger, 1967, pl. 11, fig. 1) by original designation.
Material.—JG.H3097 and 3098 from loc.Ob0003f.
Description.—Shell large-sized, subequivalve and inequilateral, highly convex from anterior to posterior and also along growth axis with geniculation.   Anterior part steep or perpendicular to commissure plane and concave near umbo.   Posterior part sloping steeply and posterodorsal one almost perpendicular to hinge line.   Small posterior wing developed.   Umbo small, situated at anterior end, slightly projected beyond hinge line and twisted forwards.   A blunt elevation developed along growth axis.   Anterodorsal margin long and straight ; anterior one circularly rounded up to midventer where narrowly or subangularly bent and continuing to broadly arcuate posterior margin ; posterodorsal margin long and straight, forming an obtuse angle with hinge line which is more than half of the shell length.

Surface ornamented with concentric ribs and rings in combination, of which the former are considerably variable in shape and intensity, that is, sharp-topped or round-topped,
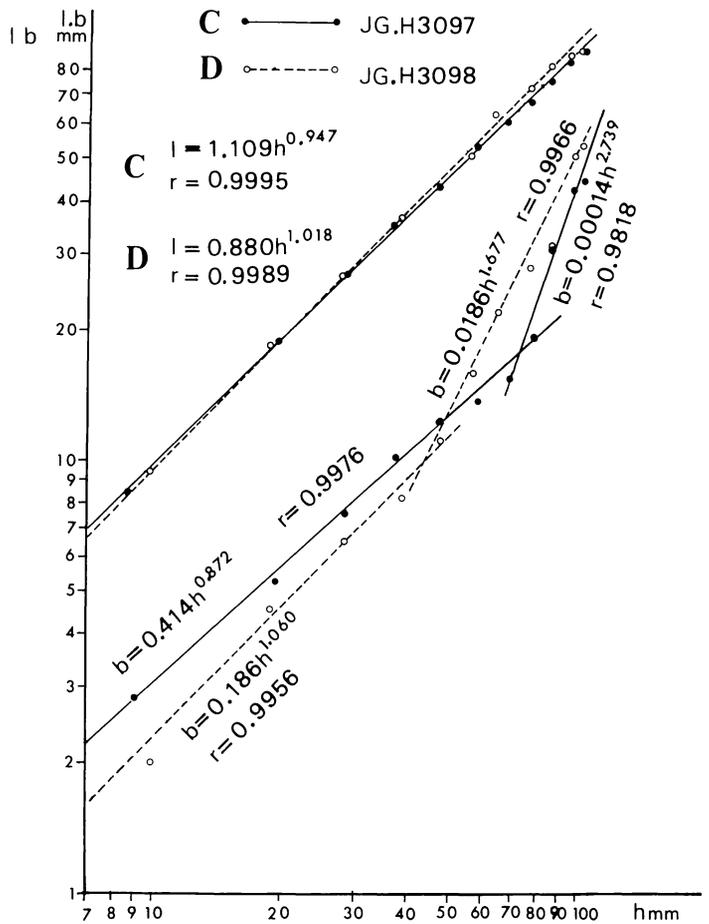
Figure 12.   Diagram showing individual relative growth between I and h, and b and h for selected specimens of *Inoceramus (Cr.) lueckendorfensis.*

irregular in size, interspacing and intensity, while the latter are superimposed on ribs and interspaces and regular in breadth and intensity.

Biometry.—Measurements of two specimens are shown in Table 3.   Figure 12 shows individual relative growth of JG. H3097 and 3098.   The reduced major axes of I vs. h show

Table 3.   Measurements of *Inoceramus (Cremnoceramus) lueckendorensis* Tröger from Hokkaido. Linear dimension in mm.

specimen	valve	h	l	b	s	H	L	α	γ	δ	$\delta_{H=60mm}$
JG. H3097	L.	105.7	89.2	45.4	45.0	107.6	87.5	118°	120°	77°	72°
JG. H3098	L.	102.8	89.1	42.0	37.8	106.1	86.4	118°	—	73°	66°

specimen	valve	l/h	l/h$_{H=60mm}$	b/h	b/h$_{H=60mm}$	L/H	s/l
JG. H3097	L.	0.84	0.90	0.43	0.24	0.81	0.50
JG. H3098	L.	0.87	0.93	0.41	0.29	0.81	0.42

Figure 11.   *Inoceramus (Cremnoceramus) lueckendorfensis* Tröger.   All figures natural size.   **1a-c.** JG.H3097 from loc. Ob0003f.   **2a-c.** JG.H3098, same locality (coll. T. Shimanuki, T. Matsumoto and M. Noda, 1993).
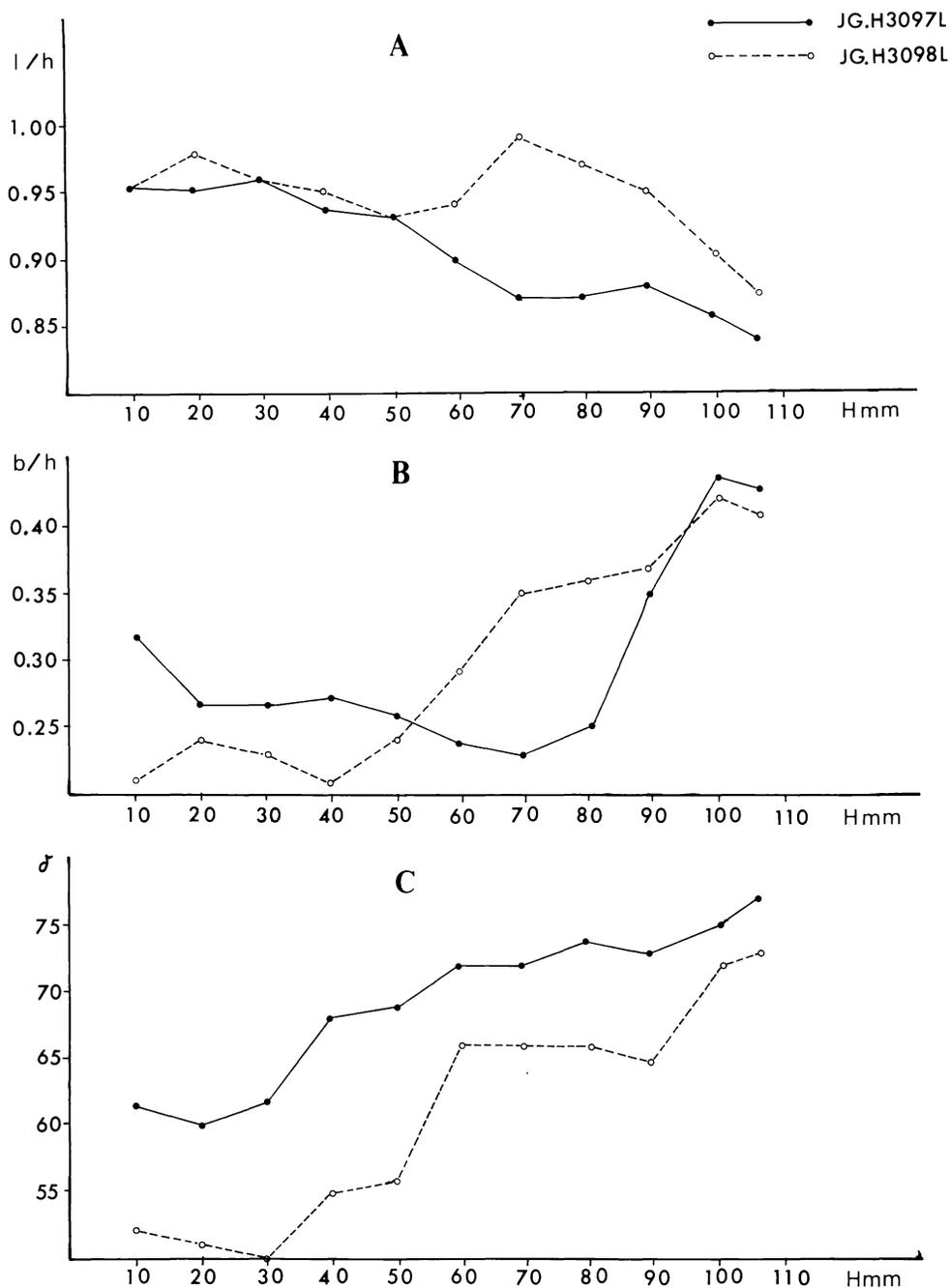
Figure 13. Diagram showing ontogenetic changes in selected characters of *Inoceramus* (*Cr.*) *lueckendorfensis*.
A : l/h, B : b/h, C : obliquity.

negative allometry for JG.H3097 and isometry for JG.H3098, and those of b vs. h show a negative allometry in young stage of JG.H3097 and isometry in the same stage of JG. H3098, while both turn to positive allometry in later stages. Critical points are different between the two specimens : 70 mm in H for JG.H3097, and 40 mm in H for JG.H3098.

Ontogenetic changes in l/h, b/h and obliquity (gun) are shown in Figure 13A, B and C, respectively. As is clear from

Figure 13A, the simple ratio l/h decreases gradually with growth, whereas, as shown in Figure 13B, the simple ratio b/h increases abruptly at a certain stage of growth which varies from individual to individual. As a matter of course, convexity abruptly changes at the critical point of individual relative growth b vs. h in each specimen.

Profiles of the specimens in two directions are illustrated in Figure 14. In the cross section, somewhat angular eleva-
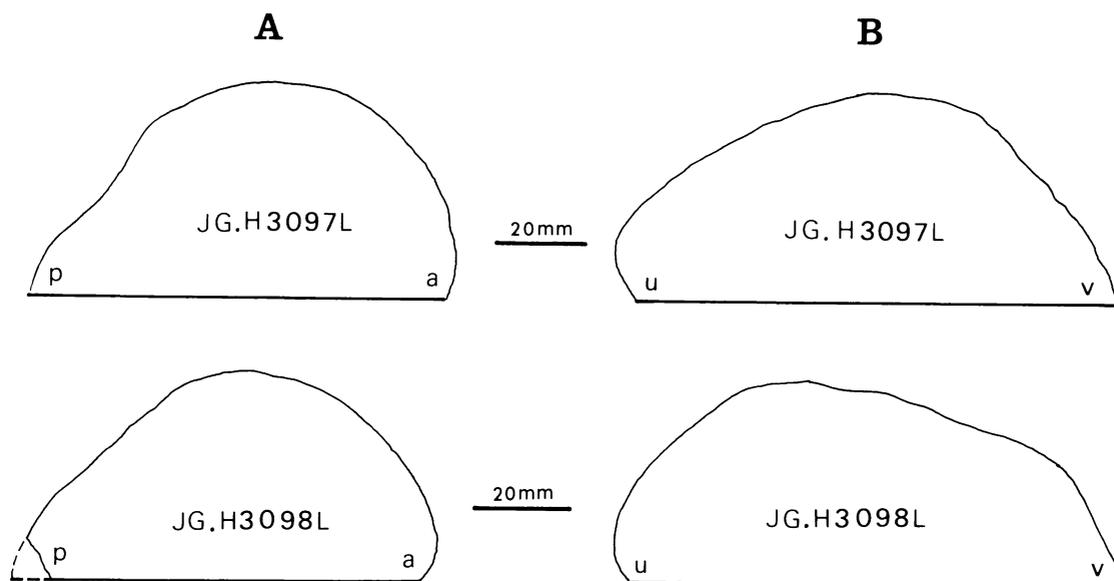
Figure 14. Profiles of available specimens of *Inoceramus* (*Cr.*) *lueckendorfensis* in two directions. A : cross section at the highest point of shell convexity, B : vertical section along the growth axis.

tions are perceptible on the flank and in the vertical section, geniculation in various stages of growth is clearly perceptible.

Remarks.—JG.H3097 and 3098 are fairly well preserved, with the original outline being a pentagonal margin in general aspect and the shell convexity, but no precise surface ornamentation is known because the outer shell layer is lost.

Comparison and discussion.—The pentagonal margin, vaulted shell with geniculation, development of radial elevation along the growth axis and the presence of a blunt depression on the posterior flank are common in the present specimens and the holotype of *I.* (*Cr.*) *lueckendorfensis* Tröger. Moreover, profiles in two directions of the specimens agree well with those of the holotype (Tröger, 1967, p. 104, fig. 27 above; pl. 11, figs. 1a and c). The original description and figures of Tröger (1967) show that *I.* (*Cr.*) *lueckendorfensis* exhibits a considerable extent of variation in outline, shell convexity and surface ornamentation. The above comparison leads to the conclusion that the present specimens surely fall within the range of variation of *I.* (*Cr.*) *lueckendorfensis.* Tröger (personal letter, May 10, 1993) suggested to me that the Japanese specimens accord well with the type specimens in outline but are distinct in surface ornamentation.

The present species was originally erected as a subspecies of *I. inconstans* by Tröger (1967). Subsequently he (1981a) listed it as *I.* "*inconstans*" *lueckendorfensis* without any comment. I think that *I. inconstans* Woods, 1912a is a heterogeneous species, about which specific definitions among researchers can be expected to vary. Tröger (personal communication, 1988) treated his specimen No. p-6 as an independent species, *I. lueckendorfensis,* thus *I.* (*Cr.*) *lueckendorfensis* (personal letter of May 10, 1993). I agree with him in this treatment.

Phylogeny.—The specimen (JG.H3077 from loc.Ik2799) of

I. (*Cr.*) *rotundatus* resembles the specimens No. p-6 of Warsaw University from the lower Coniacian of Kolonkh and RT1062 from the upper lower Coniacian of the Opole Trough, Poland, figured by Tarkowski (1991, pl. 13, fig. 8). On the route along the Ponbetsu-gono-sawa, loc.Ik2799 is located somewhat above the horizon of loc.Ik2798 (=Ik2726, see Matsumoto and Noda, 1985), which immediately overlies the Tu/Co boundary containing *I.* (*Cr.*) *rotundatus.* The morphological similarity and stratigraphic relation may imply a phylogenetic relationship between the two species.

Besides, the holotype of *I.* (*Co.*) *cordiformis purus* Seitz, 1961 from the upper Santonian of the Lüneburg area, Germany, is similar to the holotype of *I.* (*Cr.*) *lueckendorfensis* in the pentagonal outline, vaulted shell, sharply demarcated and broad anterior wall and the development of radial elevations. The former is, however, discriminated from the latter in the stronger radial elevations, irregular concentric ribs and age of occurrence. The above fact may suggest some relationship between *I.* (*Cremnoceramus*) and *I.* (*Cordiceramus*).

Occurrence.—Loc.Ob0003f. See Noda (1992, p. 1235).

Range.—The specimens handled were obtained from a limited horizon of the lower lower Coniacian of the Obira area, Hokkaido, but its stratigraphic range is yet to be clarified. Tröger (1981b, 1989) located it in the lower lower Coniacian. The range of the species in Japan is in good agreement with that of Germany. Tarkowski (1991) recorded it from the lower Coniacian of the Opole area, Poland, and from the upper Turonian to Coniacian of the Caucasus.

Conclusions

1. The examined specimens from the upper Turonian to lower middle Coniacian of Hokkaido are all identical or comparable with some species hitherto described, that is, *I.*

(*I.*) *lusatiae* Andert, *I.* (*V.*) *koeneni* Müller, *I.* (*Cr.*) *deformis* Meek, *I.* (*Cr.*) *ernsti* Heinz and *I.* (*Cr.*) *lueckendorfensis* Tröger. They are well known abroad but this is their first recorded in Japan.

2. Some specimens with intermediate or transitional characters are important for delineating the phylogenetic relationships among the following subgenera: *I.* (*Inoceramus*), *I.* (*Cremnoceramus*), *I.* (*Cordiceramus*) and *I.* (*Volviceramus*). The discussion of each species leads to an argument in favor of Tröger's scheme (1969) and implies, in addition, that *I.* (*Cordiceramus*) may have been derived from *I.* (*Cr.*) *ernsti*, which is assumed to be the common ancestor of *I.* (*Cordiceramus*) and *I.* (*Volviceramus*).

3. With respect to taxonomic ranks, *Inoceramus, Cremnoceramus* and *Volviceramus* are each regarded herein as a subgenus of *Inoceramus*. Generally, it may be more reasonable that those species groups which comprise some transitional species with wide individual variation are treated as subgenera than full genera.

4. The species concerned are important for international correlations and elucidating paleogeography in early Coniacian time.

Acknowledgments

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Asahikawa 旭川, Ashiyachi-zawa 葦谷地沢, Banno-sawa 盤の沢, Bungo 豊後, Chiba 千葉, Fukagochi 深河内, Hatsudenshono-sawa 発電所の沢, Hidarimata-zawa 左股沢, Ikushunbetsu 幾春別, Inari-zawa 稲荷沢, Iwamizawa 岩見沢, Kamiichino-sawa 上一の沢, Kamikinenbetsu 上記念別, Katsurazawako 桂沢湖, Kikumen-zawa 菊面沢, Kumaoi 熊追, Kumaoi-zawa 熊追沢, Kurisawa 栗沢, Mikasa 三笠, Nishikatsurazawa 西桂沢, Obira 小平, Obirashibe 小平蘂, Obirashibeko 小平蘂湖, Oita 大分, Onogawa 大野川, Okuhidarimata-zawa (Okusamata-zawa) 奥左股沢, Ponbetsugono-sawa 奔別五の沢, Sapporo 札幌, Shigeruno-sawa シゲルの沢, Takimi-Ohashi 滝見大橋, Takishita 滝下, Tano 田野, Tappu 達布, Uwajima 宇和島, Waseda 早稲田, Yezo 蝦夷, Yoshiashi-zawa 芳葦沢, Yubarigoe-zawa 夕張越沢

1021 Latest Permian ammonoid *Paratirolites* from the Ofunato district, Southern Kitakami Massif, Northeast Japan

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Abstract. The latest Permian ammonoids, *Paratirolites compressus* sp. nov. and *P.* sp., are described from the Permian strata in the Ofunato district of the Southern Kitakami Massif, Northeast Japan. This is the first record of Late Permian fossils from the Ofunato district.

Key words : *Paratirolites*, uppermost Permian, Kitakami Massif

Introduction

Y. Onuki's collection of Kitakami fossils stored in the Institute of Geology and Paleontology, Tohoku University, includes one ammonoid and one nautiloid (?) collected by T. Sugiyama. The attached labels indicate their occurrences somewhere near Maeda (Figure 1), Ikawa- cho, Ofunato City, but no formation name. The ammonoid is labeled as *Gonioclymenia*, which is one of the typical genera of latest Devonian clymeniids.

On the other hand, Sugiyama (1942) reported the occurrence of *Clymenia* (=*Clymenia* spp. of Sugiyama, 1944 ?) in the Devonian "Omori Series" (=upper Nakazato Series) in the Ofunato district of the Southern Kitakami Massif and correlated the series to the Famennian. These clymeniids are important for geochronologic consideration of the "Omori Series", because the series is now generally correlated with the Middle Devonian. They have hitherto, however, been neither described nor figured. Ammonoid fossils are rather rare in Paleozoic strata of the Kitakami Massif, but the Maeda specimen may not be one of those listed by Sugiyama (1942), because the clymeniids (?) of the "Omori Series" were collected from a locality at Choanji or Omori, Hikoroichi- cho, Ofunato City (Sugiyama, 1944), both far from Maeda (Figure 1). Moreover, reexamination proves that the Maeda specimen is not a clymeniid. It has, in fact, a typical ceratitic suture (Figure 3c) and is considered to be a Late Permian ammonoid, *Paratirolites*. This paper describes it as *Paratirolites compressus* sp. nov. and discusses its stratigraphic significance. *Paratirolites* sp. recently collected by the author near Maeda is also described.

Geologic settings

On the geologic map of Yabe and Sugiyama (1937), the strata distributed near Maeda are assigned to the Upper Carboniferous- Middle Permian Maiya Group, which lies in fault contact with the Devonian Nakazato Group on the northwest. Onuki (1956, fig. 2) treated them as Permian (possibly Lower to Middle Permian) and Minato *et al.* (1979, fig. 2k-1) as the Middle Permian Kanokuran Series, although no formation name had been given. Near Maeda, the Permian strata strike NNW-SSE to NW- SE and dip 40 to 80°W. Observation in the field shows that they are composed mainly of black to dark gray shale, with subordinate amounts of sandy shale, sandstone and conglomerate. The gray shales, which are similar in lithology to that containing the present ammonoid, crop out in the cuttings along the railroad of Iwate Kaihatsu Tetsudo just north of Maeda (Figure 2, Loc. A). They yield some brachiopods, pelecypods, bryozoans and crinoid stems. Although no additional ammonoids have been collected from there and the age of *Paratirolites* little differs from the previous geochronology, as mentioned later, Sugiyama's specimen of *Paratirolites* is considered to have been collected from Loc. A in Figure 2 or its environs. I also collected the same fossils as from Loc. A and an ammonoid *Paratirolites* sp. from sandy shales intercalated in black shales at Loc. B, a road cut on the Sanriku Highway (under construction), about 200 m east of Loc. A.

Stratigraphic significance of *Paratirolites*

Species of *Paratirolites* are index fossils of the uppermost Permian. They are known extensively : Dorashamian strata of Transcaucasia (Ruzhentsev and Sarycheva, 1965 ; Teichert *et al.,* 1973, and others) and Central Iran (Bando, 1979), Changxingian formations of South China (Zhao *et al.,* 1978 ; Liang, 1983, and others), undeterminate horizon of Madagascar (Tozer, 1969) and latest Permian *Palaeofusulina*-bearing bed of Thailand (Ishibashi and Chonglakmani, 1990). One of them was also reported, though its generic position is somewhat questionable, from the Senmatsu Formation in the
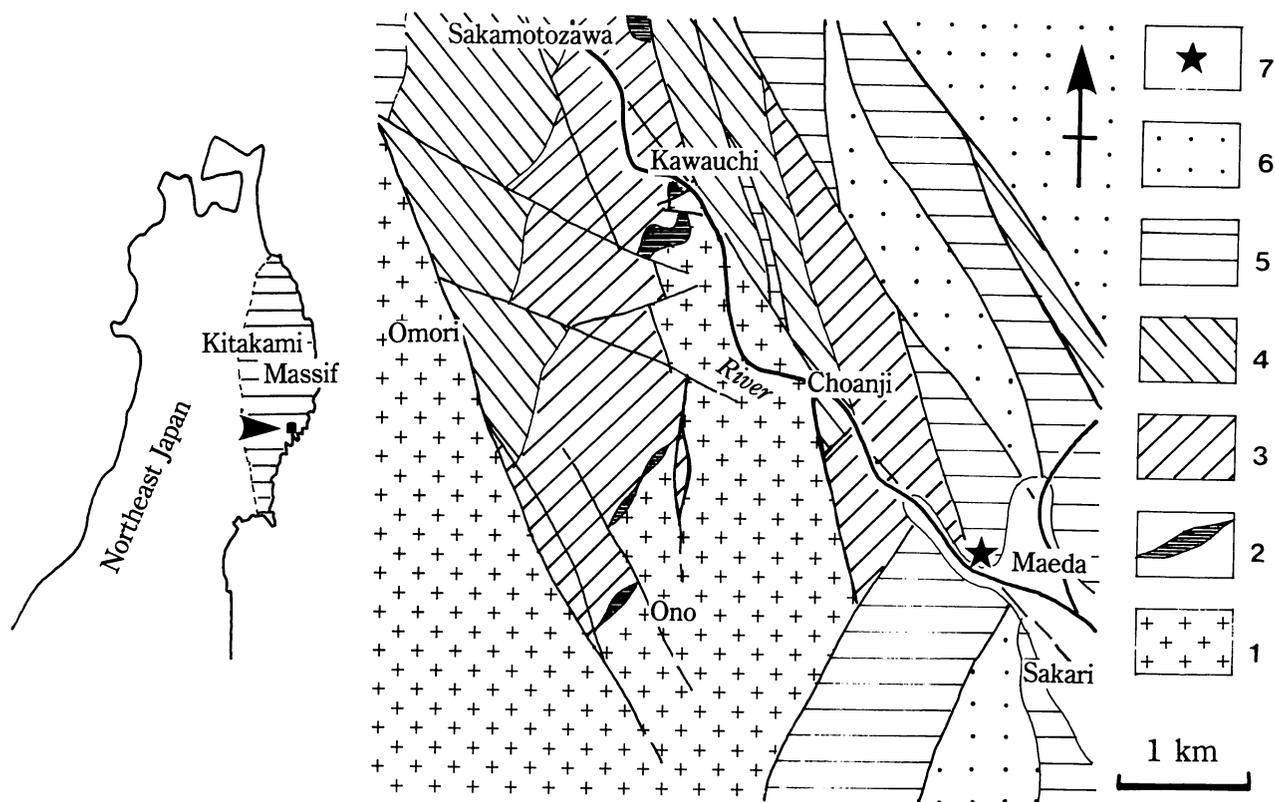
Figure 1. Simplified geologic map of the northern Ofunato district (compiled from various sources), with supposed ammonoid locality. 1. Pre-Silurian Hikami Granites, 2. Silurian, 3. Devonian, 4. Carboniferous, 5. Permian, 6. Lower Cretaceous, 7. ammonoid locality.

Okago district of the Southern Kitakami Massif (Ehiro and Bando, 1985).

Upper Permian formations are widely distributed in the southern part of the Southern Kitakami Massif and ones correlative with the Changxingian (Dorashamian) are disclosed in the northern Kesennuma (Tazawa, 1975 ; Ishii *et al.,* 1975), Utatsu (Murata and Shimoyama, 1979), and probably Okago (Ehiro and Bando, 1985) districts. To date, no reliable Upper Permian fossil has been found from the Ofunato district. The present ammonoid *Paratirolites* is the first record of an Upper (uppermost) Permian fossil from there and the shales distributed near Maeda are the uppermost Permian, not the Lower or Middle Permian as previously thought. The naming of this *Paratirolites*-bearing strata near Maeda is left pending, until the stratigraphy of the strata is further studied in detail.

Description of species

Family Dzhulfitidae Shevyrev, 1965
Genus *Paratirolites* Stoyanow, 1910
[Type species : *Paratirolites kittli* Stoyanow, 1910]

Remarks.—Shevyrev (in Ruzhentsev and Sarycheva, 1965) established the family Dzhulfitidae to contain three genera :

Dzhulfites Shevyrev, *Abichites* Shevyrev and *Paratirolites* Stoyanow. All these three genera have evolute whorls with lateral ribs and ventrolateral nodes, and a subquadrate to subtrapezoidal cross section. They also have a unique suture with low saddles separating two denticulate lateral lobes. Teichert and Kummel (in Teichert *et al.,* 1973) placed the genera *Dzhulfites* and *Abichites* in *Paratirolites* based on their morphological similarities. According to Tozer (1979), the species of the genus *Schizoloboceras* described by Zhao *et al.* (1978) from the Changxingian beds of South China may also be included in the genus *Paratirolites*.

Paratirolites compressus sp. nov.

Figures 3a–c

Material.—A fragmental specimen, IGPS coll. cat. no. 103144 (Holotype), collected by Toshio Sugiyama from the unnamed strata distributed near Maeda, Ikawa-cho, Ofunato City, Iwate Prefecture.

Diagnosis.—*Paratirolites* with compressed shell form and a large umbilicus.

Description.—The specimen consists of parts of two volutions : a phragmocone and a body whorl. It is moderately large and is considered to attain a diameter of at least 75 mm. The conch is evolute and thinly discoidal in outline,

Figure 2. Location map of Permian fossil localities (Locs. A and B) near Maeda, Ofunato City. Base map adopted from Quadrangle "Sakari", 1 : 25,000 scale topographic map of Japan, Geographical Survey Institute.

with a wide umbilicus. The ratio of the umbilical diameter to shell diameter is estimated to be about 0.48 in the mature stage. The specimen has a compressed shell form, though deformed obliquely. The flanks are nearly flat and very slightly converge toward the umbilicus, with the maximum width at the ventral shoulder. The ratio of width to height at the last whorl (living chamber) ranges from 0.3 to 0.4. The venter is slightly convex. The cross section of the conch is subquadrate, with acutely rounded to edged umbilical and ventral shoulders. The sides of the whorl are ornamented by radial ribs. They are rather short, high and widely spaced, with maximum height near the center of the side, on the phragmocone. On the body whorl they are rather closely spaced, extend from the umbilical to ventral shoulder, becoming wider toward the venter, and are nodose at the ventral margin.

The suture is ceratitic, consisting of a large and rounded ventrolateral saddle, a considerably low lateral saddle separating two strongly denticulated lateral lobes, and a high and rounded second lateral saddle. The ventral part of the suture is not observed.

Comparison.—Among the species of the genus *Paratirolites, P. mojsisovicsi* (Stoyanow) has rather compressed shell form, the ratio of width to height ranges from 0.6 to 0.8 (for example : Shevyrev in Ruzhentsev and Sarycheva, 1965, p. 178, pl. 23, figs. 2-3 described as *Paratirolites dieneri,* p. 179,

pl. 24, figs. 2-3 described as *Abichites stoyanowi,* p. 180, pl. 23, fig. 4 described as *A. mojsisovicsi,* p. 181, pl. 24, fig. 4 described as *A. abichi* ; Teichert and Kummel in Teichert *et al,* 1973, p. 414, pl. 6, figs. 8-9, pl. 7, figs. 1-2, 6, 7 ; Bando, 1979, p. 135, pl. 5, figs. 2, 6, pl. 6, fig. 1, pl. 8, figs. 1, 3) and somewhat resembles the present species. But the Kitakami species is more compressed than *P. mojsisovicsi.* The present species is also distinguished from the latter and the other species in having a wider umbilicus.

Etymology.—The specific name is derived from its compressed shell form.

Paratirolites sp.

Figures 3d-e

Material.—IGPS coll. cat. no. 103276, collected by M. Ehiro from the unnamed strata distributed near Maeda, Ikawa-cho, Ofunato City, Iwate Prefecture.

Descriptive remarks.—An outer mould and a small fragmental inner mould of a moderately large specimen were examined. It attains a diameter of 75 mm. The conch is evolute and has a wide umbilicus. The ratio of the umbilical diameter to shell diameter is about 0.4 in the inner volution, but attains 0.47 in the mature stage. The flanks are flat and the venter is slightly convex. The conch is subquadrate in cross section, with acutely rounded umbilical and ventral shoulders. The ratio of width to height at the last whorl is 0. 6 to 0.7, although it is smaller in the inner mould. The side of the whorl is ornamented by fine radial ribs. They are widely spaced on the inner whorls, but closely spaced in the mature stage.

In having an evolute and compressed shell form with subquadrate conch section and radial ribs, the present specimen is considered to belong to the genus *Paratirolites* and to be similar to *P. mojsisovicsi* (Stoyanow) (for example : Shevyrev in Ruzhentsev and Sarycheva, 1965, p. 178, pl. 23, figs. 2-3 described as *Paratirolites dieneri,* p. 179, pl. 24, figs. 2-3 described as *Abichites stoyanowi,* p. 180, pl. 23, fig. 4 described as *A. mojsisovicsi,* p. 181, pl. 24, fig. 4 described as *A. abichi* ; Teichert and Kummel in Teichert *et al.,* 1973, p. 414, pl. 6, figs. 8-9, pl. 7, figs. 1-2, 6, 7 ; Bando, 1979, p. 135, pl. 5, figs. 2, 6, pl. 6, fig. 1, pl. 8, figs. 1, 3) and *P. compressum* sp. nov. It is, however, difficult to identify it at the specific level, owing to the rather poor state of the preservation. Moreover, the generic position is somewhat questionable, because the ventrolateral nodes, characteristic for the genus *Paratirolites,* seem to be obscure or missing in the present species and the suture is not known.

Acknowledgments
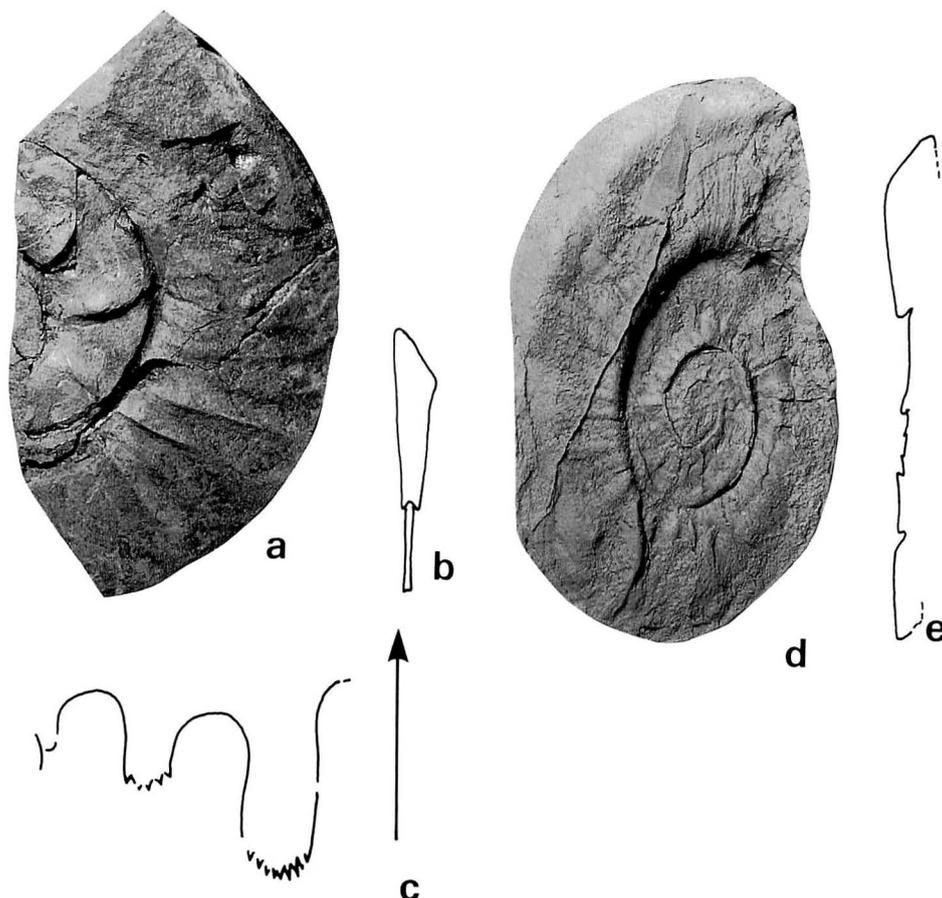
Figure 3. *Paratirolites* from Maeda, Ofunato district. **a–c**: *Paratirolites compressus* sp. nov., IGPS coll. cat. no. 103144, lateral view (a, ×1), cross section (b, ×1) and suture line (c, ×4). **d–e**: *Paratirolites* sp., IGPS coll. cat. no. 103276, lateral view of the rubber cast of the outer mould (d, ×1) and cross section (e, ×1).

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Family Dermochelyidae (Superfamily Chelonioidea) from the Upper Cretaceous of North Japan

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Abstract. *Mesodermochelys undulatus,* a new genus and species, is described as the best Mesozoic representative of the Dermochelyidae (order Testudines, superfamily Chelonioidea). This new taxon is described from 15 specimens which include cranial fragments, lower jaw, axial and appendicular skeleton, and a nearly complete shell. These specimens were collected from the Lower Maastrichtian, Upper Cretaceous of Hobetsu-cho, Central Hokkaido, North Japan. *Mesodermochelys* shares with Cenozoic dermochelyids such derived characters as the reduced *processus trochlearis oticum* formed by prootic, the anterior process of surangular, and the elongate anterior projection of lateral process of humerus. The scute sulci of *Mesodermochelys* are nearly absent, only remaining in the neural region of the carapace. The bony shell of *Mesodermochelys* is well developed as a primitive condition. Some characters such as the unique configuration of the lower triturating surface with isolated simphyseal and lingual ridges, the undulating medial margin of broad peripherals, the narrow neurals, and the elongate iliac blade with outward curvature are considered as autapomorphic conditions of *Mesodermochelys.* Frequent occurrence of this primitive dermochelyid in the Upper Cretaceous of Japan suggests endemic distribution among Mesozoic chelonioid species.

Key words : *Mesodermochelys,* Dermochelyidae, Testudines, Reptilia, Upper Cretaceous, North Japan

Introduction

The living leatherback turtle *Dermochelys coriacea* is the most aberrant and unusual of turtles ; the bony plates of the typical turtle shell are nearly completely lost and jellyfish are a major component of its diet (Volker, 1913 ; Hendrickson, 1980). Because of its bizarre morphology and early ideas that it might be the most primitive of living turtles, the living leatherback has been the subject of more anatomical description than any other single species of turtles (Gaffney, 1984). Most of the fossil dermochelyids from the Tertiary have been identified as extinct genera, *Eosphargis* or *Psephophorus* in most cases, but no sea turtle from the Mesozoic has been assigned to the Dermochelyidae with certainty (Gaffney and Meylan, 1988). *Allopleuron,* a chelonioid from the Upper Cretaceous of Western Europe, is adopted as an ancestral dermochelyid solely based on shell similarity (Weems, 1988) ; however, some Cretaceous sea turtles such as *Corsochelys* (originally described as an "advanced cheloniid" by Zangerl, 1960) and an unnamed Japanese chelonioid are currently hypothesized as being very primitive dermochelyids (Hirayama, 1992, 1995 and in press ; Hirayama and Chitoku, 1994). A portion of this Japanese Cretaceous sea turtle was originally identified as an indeterminable chelonioid which might be close to both dermochelyid and

protostegid in a preliminary report (Hirayama and Suzuki, 1985).

Here we present a detailed description of this new taxon of sea turtle from the Upper Cretaceous of North Japan, and discuss its significance to the phylogeny and evolution of the Dermochelyidae.

Geological setting

All material described here was contained in sandy calcareous concretions which came from surface outcrop of the lower sandy siltstone formation of the Hakobuchi Group exposed at Hobetsu-cho, Hokkaido, North Japan (Hirayama and Suzuki, 1985 ; Chitoku, 1990 ; Hirayama and Chitoku, 1994). The Hakobuchi Group as found in Central Hokkaido is characterized by coarse-grained sediments consisting mainly of sandstones. It ranges from the Campanian to Maastrichtian (Upper Cretaceous) (Matsumoto, 1942, 1943, 1954 ; Toshimitsu *et al.,* 1995). In Hobetsu-cho, the Hakobuchi Group is exposed from the Inasato district to the Tomiuchi district (Figure 1 ; Tanaka, 1960 ; Takahashi and Wada, 1985, 1987). The middle portion of the lower sandy siltstone formation consists of dark gray sandy siltstone, bearing marine invertebrates such as *Inoceramus (Cataceramus) shikotanensis, Pachydiscus (Neodesmoceras)*
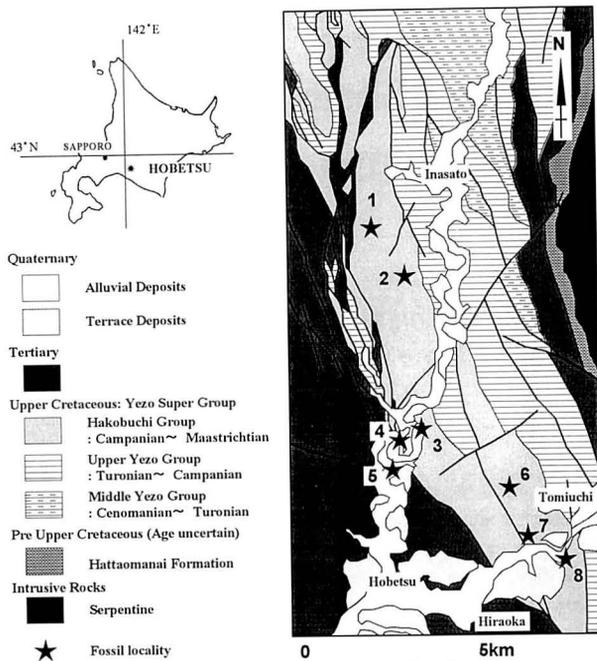
Figure 1. Geological map of Hobetsu-cho, showing localities of *Mesodermochelys undulatus* gen. et sp. nov. (after Takahashi and Wada, 1985). See text for the locality of each specimen.

japonicus and *Neophylloceras hetonaiensis* which indicate an early lower Maastrichtian age. In addition to turtles, a marine reptile, *Mosasaurus hobetsuensis,* was reported from this horizon along the Pankerusanosawa River of Hobetsu (Suzuki, 1985). Obata *et al.* (1972) mentioned a piece of bone presumed to be of a plesiosaur from the same locality, which in fact belongs to an indeterminable turtle (pers. comm. M. Manabe ; pers. obs. Hirayama).

The fossil turtle localities are scattered along the valley of the major rivers of Hobetsu-cho, although 8 of the 15 specimens were concentrated within the basin of the Pankerusanosawa River (Figure 1 ; localities 6 and 7).

Material and methods

All material described below is housed in the Hobetsu Museum at Hobetsu-cho, Hokkaido, Japan (Institutional Abbreviation : HMG). The specimens consist of disarticulated, scattered, uncrushed (except HMG 363 and 365, the largest individuals) skeletons, although in many instances some portions of the bone have been eroded (Figure 2).

Specimens were prepared by using both dilute acetic acid and mechanical methods.

Phylogenetic analysis of 135 characters for 18 eucryptodires, including 13 chelonioids, was conducted using PAUP program (version 3.0) of Swofford (1989). A list of the 135 osteological characters utilized in the analysis, along with their character states, is provided in Appendices I and II. The data on chelonioids discussed below are largely based

on Hirayama (1995). In those instances where the characters are drawn from sources other than Hirayama (1995), the reference is shown in Appendix II. All characters were coded as reversible, and multistate characters coded as unordered to avoid a *priori* assumptions of transformation vectors.

Outgroup polarity among centrocryptodires (eucryptodires exclusive of plesiochelyids ; Gaffney and Meylan, 1988) was determined using characters of the plesiochelyids. We agree with the opinion that the plesiochelyids are the most primitive among eucryptodires (Gaffney and Meylan, 1988 ; Gaffney *et al.,* 1991), rather than the former view that the plesiochelyids were the sister group of the remaining chelonioids (Gaffney, 1976). Information on eucryptodires exclusive of chelonioids is derived from the following references : Plesiochelyidae, Bräm (1965), Gaffney (1975a, 1976), Rieppel (1980) ; *Meiolania,* Anderson (1925), Gaffney (1983, 1985a, b, 1990) ; Chelydridae and *Platysternon,* Boulenger (1889), Gaffney (1975b, 1979) and observations on the private collection of Hirayama ; Testudinoidea, Hirayama (1985) ; Trionychoidea, Meylan and Gaffney (1989).

We adopt the higher categorical rank among turtles as proposed by Gaffney (1984), and Gaffney and Meylan (1988).

Character state changes have been optimized on the resulting trees using PAUP's DELTRAN option. This optimization was selected because we feel it to be slightly more conservative in terms of assigning synapomorphies to clades in a data matrix with a substantial amount of missing data (as adopted by Gaudin, 1995).

Systematic paleontology

Order Testudines Linnaeus, 1766
Gigaorder Casichelydia Gaffney, 1975
Megaorder Cryptodira Gray, 1825
Parvorder Eucryptodira Gaffney, 1975
Suborder Polycryptodira Gaffney, 1984
Superfamily Chelonioidea Aggasiz,1857
Family Dermochelyidae Gray, 1825

Type.—*Dermochelys coriacea* (Linnaeus, 1766)
Known distribution of the family.—Santonian to Maastrichtian of the northwestern Pacific Ocean, Early Campanian of the Gulf Coast, Late Paleocene to Pliocene of the Atlantic Sea and Pacific Ocean, and Recent of worldwide tropical to subtropical sea.
Revised diagnosis.—Large chelonioids with shell length exceeding 1.3 m ; *processus trochlearis oticum* formed by prootic reduced ; ossification of *rostrum basisphenoidale* much reduced or lost ; surangular with anterior projection onto dentary ; lateral process of humerus antero-posteriorly elongate, forming prominent anterior projection ; pisiform as large as ulnare ; fontanel between hyo-hypoplastra as large as or larger than plastron ; scute sulci of shell rudimentary even in primitive forms.

Mesodermochelys gen. nov.

Type Species.—*Mesodermochelys undulatus* sp. nov.
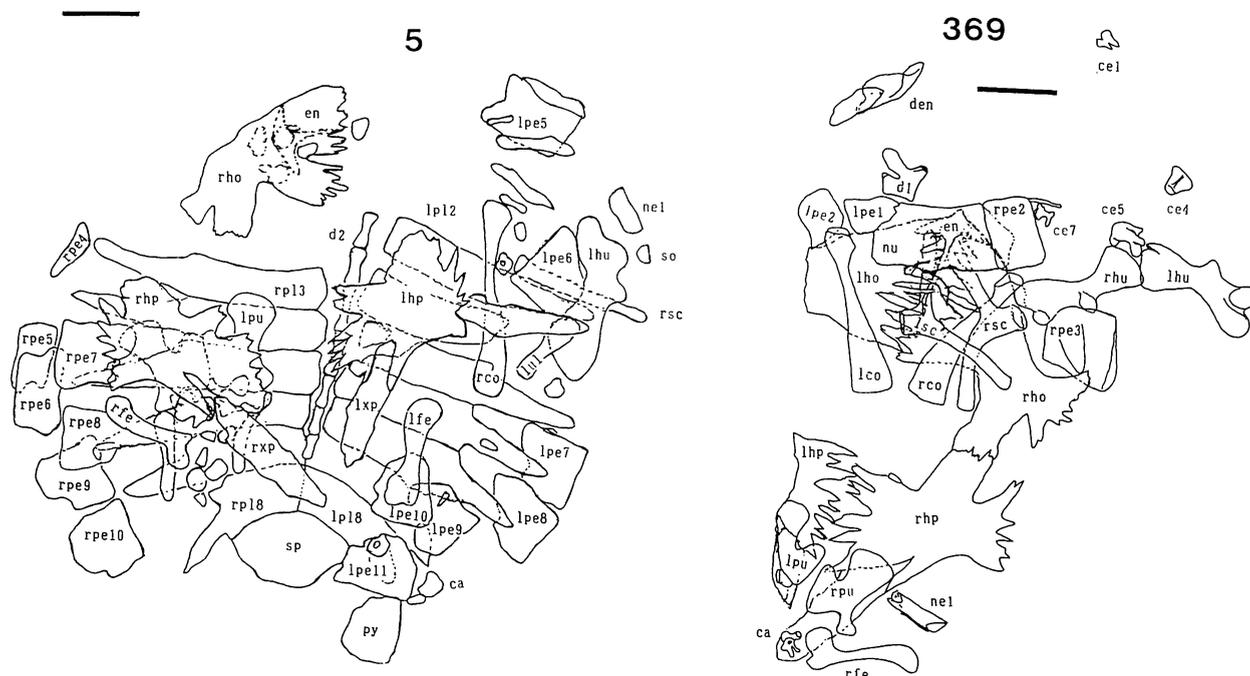
Figure 2. *Mesodermochelys undulatus* gen. et sp. nov., HMG 5 (holotype) and 369. Scale=10 cm. r : right, l : left. ca : caudal vertebra, ce1-ce8 : first to eighth cervical vertebrae, co : coracoid, d1 and d2 : first and second thoracic vertebrae, den : dentary, en : entoplastron, ep : epiplastron, fe : femur, ho : hyoplastron, hp : hypoplastron, hu : humerus, il : ilium, is : ischium, ne1 : first neural, nu : nuchal, pe1-pe11 : first to 11th peripherals, pl2-pl8 : second to eighth pleurals, pu : pubis, py : pygal, sc : scapula, so : supraoccipital, sp : suprapygal, ul : ulna, xp : xiphiplastron.

Known distribution.—Upper Cretaceous of northwestern Pacific Ocean.

Etymology.—Mesozoic relative of *Dermochelys*.

Diagnosis.—Dermochelyid with moderately developed triturating surface; lingual ridge of dentary weak, much lower than labial one, but reduced anteriorly; symphyseal ridge of dentary high, exposed from lateral view above labial ridge; lateral process of humerus with primitively more proximal location, without distal expansion anterior to ectepicondylar foramen; iliac blade elongate, with prominent outward curvature; shell length up to 1.5 m; shell ossification primitively well developed; scute sulci remain only on 3rd and 5th neurals and proximal portion of adjacent pleurals; neural plates narrowing posteriorly, 7th neural is reduced, 8th neural absent, 7th and 8th pleurals meet medially; peripherals broad and robust, with undulated medial border much expanded between costal ribs; T-shaped entoplastron with large lateral wings and rod-like posterior projection.

Mesodermochelys undulatus sp. nov.

Figures 2-17

Holotype.—HMG 5, supraoccipital, 4th cervical to posterior extremity of caudal vertebrae, and appendicular skeleton including partial manus and pes, carapace lacking anterior

portion, and nearly complete plastron.

Type Locality.—Shirafunenosawa River, Inasato, Hobetsu, Hokkaido, Japan (locality 1 in Figure 1).

Type Horizon.—Lower sandy Siltstone formation (lower Maastrichtian), Hakobuchi Group.

Distribution.—Same as genus.

Collectors.—M. Ishizaki and S. Araki, September, 1980.

Etymology.—From the Latin for the undulating medial border of the peripheral plates.

Diagnosis.—As for genus.

Referred specimens.—HMG 6, partial carapace and appendicular skeleton. Locality-Ohmagarinosawa River, Hiraoka, Hobetsu (locality 8 in Figure 1). Collector-M. Susumago, May, 1977.

HMG 8-thoracic and sacral vertebrae, hind limbs, posterior portion of shell. Locality-Pankerusanosawa River, Hiraoka, Hobetsu (locality 7 in Figure 1). Collector-S. Suzuki, October 6, 1981.

HMG 363-prootic, caudal vertebrae, hind limbs and peripherals. Locality-Same as the above. Collector-T. Chitoku, August 21, 1985.

HMG 365-pectoral girdles and anterior portion of plastron. Locality-Same as the above. Collector-T. Chitoku, September 12, 1987.

HMG 369-lower jaw, hyoids, almost complete cervicals, first thoracic and caudal vertebrae, appendicular skeletons, anterior portion of carapace, and good plastron. Locality-

Same as the above. Collector-S. Toshimitsu, September 6, 1989.

HMG 9-coracoid and anterior portion of carapace. Locality-Pankerusanosawa River, Tomiuchi, Hobetsu (locality 7 in Figure 1). Collector-S. Suzuki, October 4, 1981.

HMG 368-sixth peripheral. Locality-Same as the above. Collectors-T. Chitoku and H. Takahashi, June 11, 1989.

HMG 1053-pelvic girdle, partial carapace. Locality-Same as the above. Collector-T. Chitoku, September 8, 1992.

HMG 7-sacral and caudal vertebrae, hind limbs, and posterior portion of shell. Locality-Hobetsu River, Mobetsu, Hobetsu (locality 4 in Figure 1). Collector-S. Araki, September 4, 1980.

HMG 362-pubis and eighth pleural. Locality-Mobetsu, Hobetsu (locality 5 of Figure 1). Collector-S. Araki (date unknown).

HMG 342-cervical and first thoracic vertebrae, scapula, anterior portion of carapace, and partial plastron. Locality-Hobetsu River, Kiusu, Hobetsu (locality 3 in Figure 1). Collector-S. Suzuki, September 16, 1984.

HMG 1062-dentary. Locality-Sososhisawa, Inasato, Hobetsu (locality 1 in Figure 1). Collector-K. Chiyokawa, November 2, 1994.

HMG 1063-1st and 2nd sacral and caudal vertebrae, pelvic girdle, right femur. Locality-Same as the above. Collec-

tor-T. Furuno, November 2, 1994.

HMG 1064-left pubis, peripherals, and xiphiplastra. Locality-Same as the above. Collector-T. Furuno, November 2, 1994.

Description and comparisons
Skull (Figure 3)

The only cranial elements of *Mesodermochelys* are two fragments.

The posterior portion of the supraoccipital (Figures 3-A, B) is preserved in the holotype (HMG 5). It includes a very short *crista supraoccipitalis,* which projects little beyond the overlapping area of the parietals. This condition of the *crista supraoccipitalis* is quite similar to that of living *Dermochelys* among chelonioids (Gaffney, 1979). The vertical sheet of bone gradually narrows ventrally, without any swelling, as in *Dermochelys.*

The left prootic (Figures 3-C, D) was recovered with HMG 363. Its configuration suggests a very weak *processus trochlearis oticum* as shown by its smooth dorsal surface which lacks the rugosity seen in *Dermochelys* (Gaffney, 1979). Both the *canalis semicircularis horizontalis* and the *canalis semicircularis anterior* are confluent with the *cavum labyrinthicum* as in *Dermochelys* (Nick, 1912).

canalis semicircularis

anterior

canalis semicircularis

horizontalis
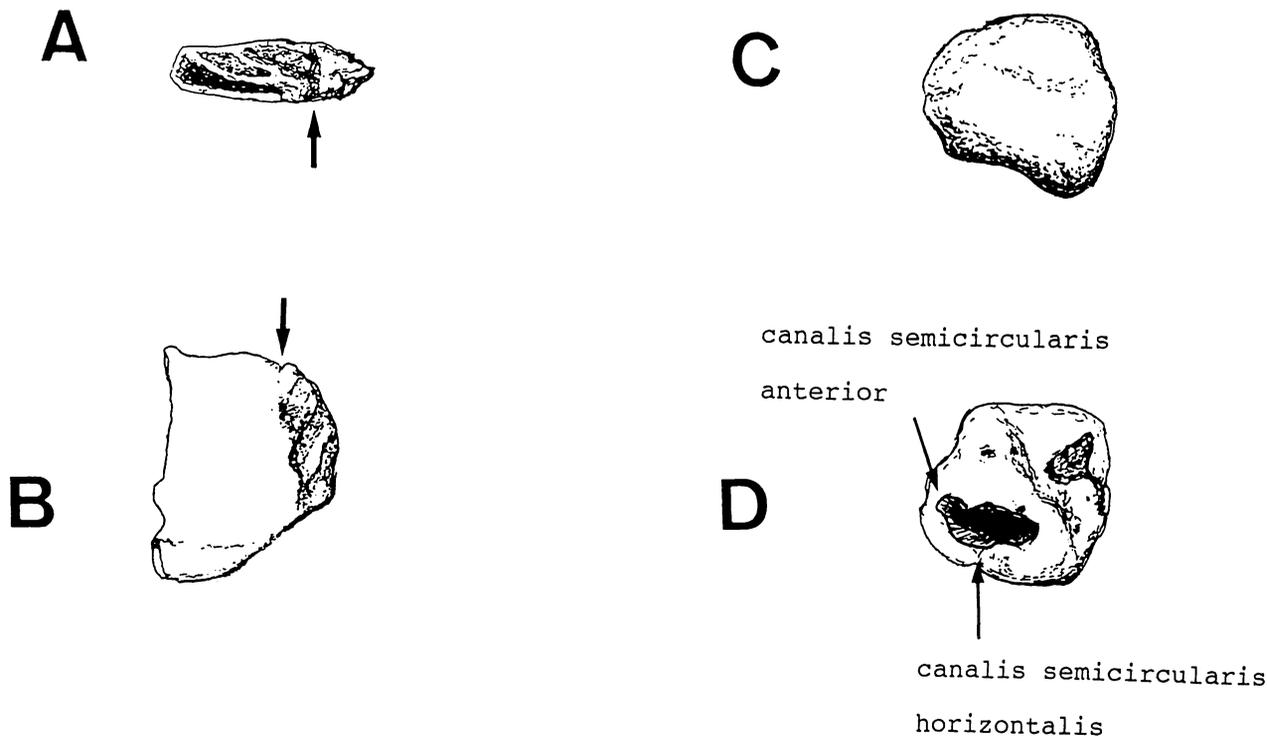
Figure 3. Cranial elements of *Mesodermochelys undulatus* gen. et sp. nov. A, B. Posterior portion of supraoccipital, HMG 5 (holotype), A : dorsal view, B : left lateral view. Arrow showing posterior limit of suture with parietal. C, D. Left prootic, HMG 363, C : anterodorsal view, D : ventral view. Scale=5 cm.
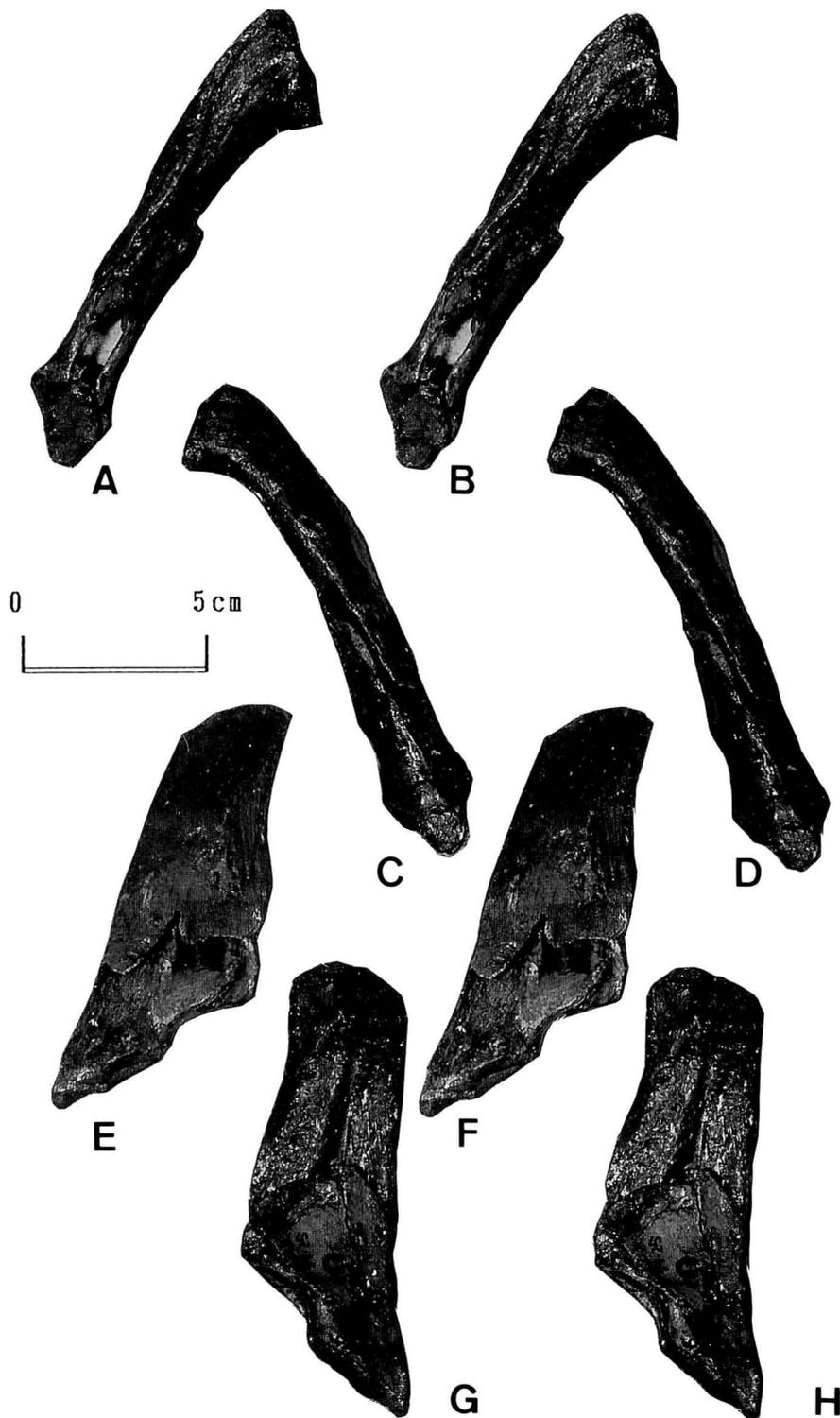
Figure 4. Stereophotographs of left half of lower jaw of *Mesodermochelys undulatus* gen. et sp. nov., HMG 369. **A, B.** Dorsal view. **C, D.** Ventral view. **E, F.** Lateral view. **G, H.** Medial view.

Lower jaw (Figures 4, 5)

The lower jaw is preserved in HMG 369 and 1062. HMG 1062 consists of an isolated dentary, lacking its posterior portion. HMG 369 (Figure 4) is a nearly complete left half of the lower jaw, lacking only a small symphyseal portion of the dentary. HMG 1062 shows a unique configuration of the lower triturating surface among turtles; the symphyseal ridge is very high. It is visible in lateral view above the labial ridges (Figure 5-B). The lingual ridges are very low, becoming reduced anteriorly such that there is no connection between symphyseal and lingual ridges (Figure 5-A). The lingual ridge of HMG 369 is identical to that of HMG 1062. The lateral surface of the dentary is ornamented with numerous longitudinal ridges, suggesting the presence of relatively thick rhamphotheca. The triturating surface of the dentary is moderately developed in *Mesodermochelys* just like living *Eretmochelys* (Cheloniidae) which has a secondary palate and *Protostega* (Protostegidae) which has only a primary palate. It is much broader than the dentary in *Toxochelys* (primitive Cheloniidae) or *Dermochelys,* both of which have only a primary palate. Thus, it is not possible to determine if *Mesodermochelys* had a secondary palate based solely on the development of the lower jaw.
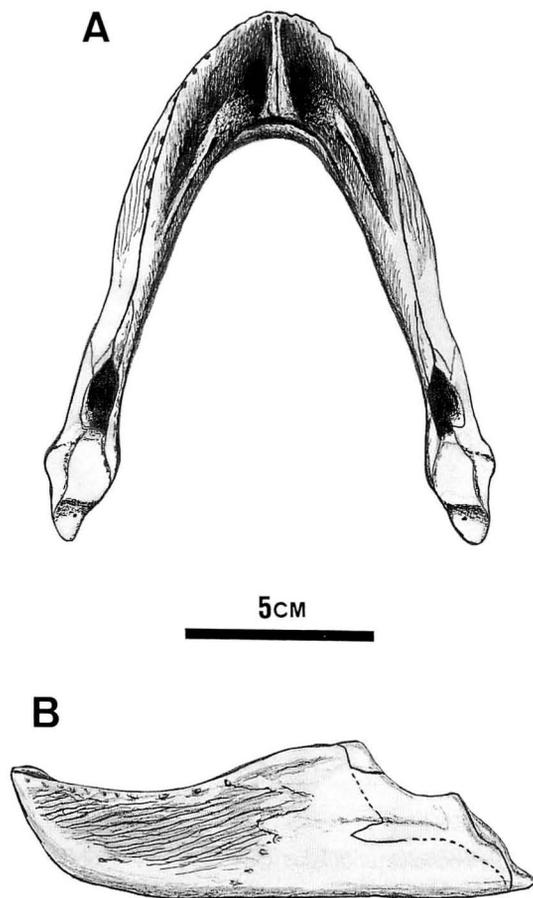
The angular is a long and slender sheet of bone as in other turtles. The surangular has a short anterior process onto the dentary, which is not seen in any other Mesozoic turtles. This surangular process of *Mesodermochelys,* however, is much smaller than in living cheloniids (exclusive of *Natator depressus,* which lacks the surangular process; Hirayama, 1995) and *Dermochelys* (Gaffney, 1979). The coronoid has the *processus coronoideus* narrowly exposed from lateral view. It is barely higher than the dentary. The articular has a definite retroarticular process, on which the *foramen chorda tympani* is visible at the base. The prearticular is a large sheet, covering the posterior half of the *fossa meckelii.* Hyoid : In HMG 369 both right and left cornu branchiale are preserved. Each is 95 mm in length. Their configuration and size relative to the lower jaw are identical to living chelonioids.

Cervical vertebrae (Figures 6, 7)

The cervical vertebrae are preserved in the holotype (HMG 5), HMG 342 and 369, being the most complete in HMG 369. Only the atlas intercentrum and the third vertebra are not preserved in any other specimens. In all of the cervicals the transverse process is single, and there is no trace of any cervical rib as is the case in other polycryptodires (Gaffney and Meylan, 1988). The cervical vertebrae are proportionally high and short as in *Dermochelys, Corsochelys* and protostegids, and the central articular surface is as high as wide or higher than wide even in the 5th to 8th cervicals unlike cheloniids (Zangerl, 1960 ; Zangerl and Sloan, 1960 ; Hirayama, 1995). The neural spine of the 8th cervical is particularly high, with a prominent dorsal articular facet that articulates with the ventral knob of the nuchal plate as in other chelonioids. The 8th cervical centrum is longer than the 7th as in protostegids and *Dermochelys,* not shorter than the 7th as in the other polycryptodires including cheloniids (Volker, 1913 ; Williams, 1950 ; Zangerl, 1953 ; Zangerl and Sloan, 1960).

The centra of the cervicals of *Mesodermochelys* all have fully formed articulations, with cervicals two (and three) opisthocoelous, cervical four biconvex, and cervicals five to eight procoelous. Therefore, the formula of the cervical central articulation is shown as (2 (3 (4) 5) 6) 7) 8). This pattern is common in the centrocryptodires including *Meiolania* (Gaffney, 1985 ; Gaffney and Meylan, 1988). There is no indication of double or platycoelous articulations between centra as seen in most living chelonioids (Williams, 1950 ; Hirayama, 1995)

Thoracic vertebrae and ribs

The thoracic vertebrae, exclusive of the first one, are preserved in the holotype. The thoracic centra are rather slender in both lateral and ventral aspects. The openings for the spinal nerves are long semilunar embayments extending about 60% of the centrum length as in cheloniids and

A

5CM

B

Figure 5. Composite reconstruction of lower jaw of *Mesodermochelys undulatus* gen. et sp. nov., based on HMG 369 and 1062. **A**. Dorsal view. **B**. Left lateral view.
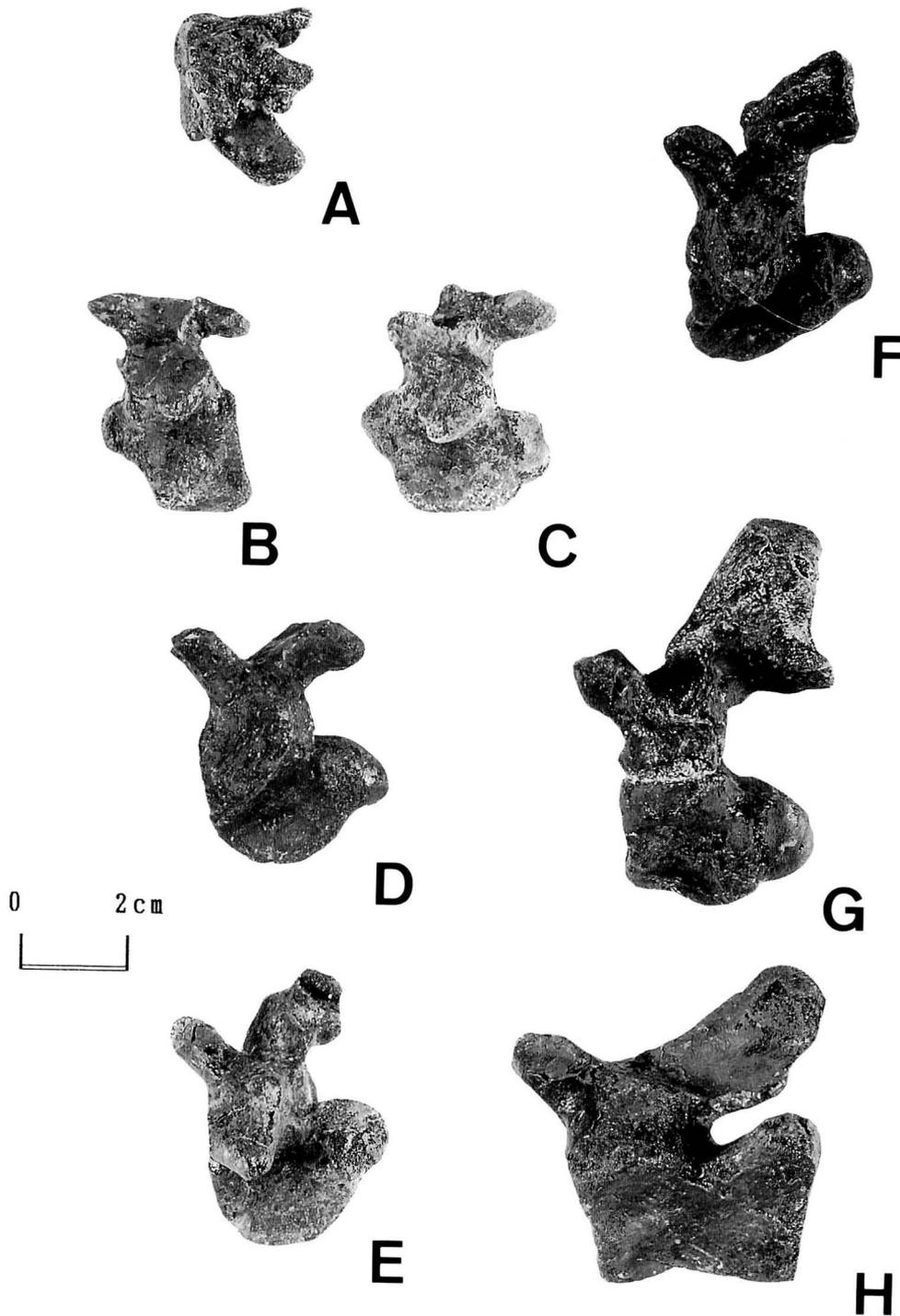
Figure 6. Cervical (A to G) and first thoracic (H) vertebrae of *Mesodermochelys undulatus* gen. et sp. nov., HMG 369, left lateral view. Third cervical is missing.

Dermochelys. They are not as extensive as in advanced protostegids such as *Archelon* (Baird, 1978). The first thoracic is preserved only in HMG 342 and 369 (Figure 8-H). The first thoracic vertebra has its anterior articulation with a nearly vertical plane to the axis of centrum, facing anteriorly as in *Dermochelys* and protostegids (including *Desmatochelys*), rather than ventrally or anteroventrally as in cheloniids, including *Toxochelys* and *Allopleuron* (Hirayama,
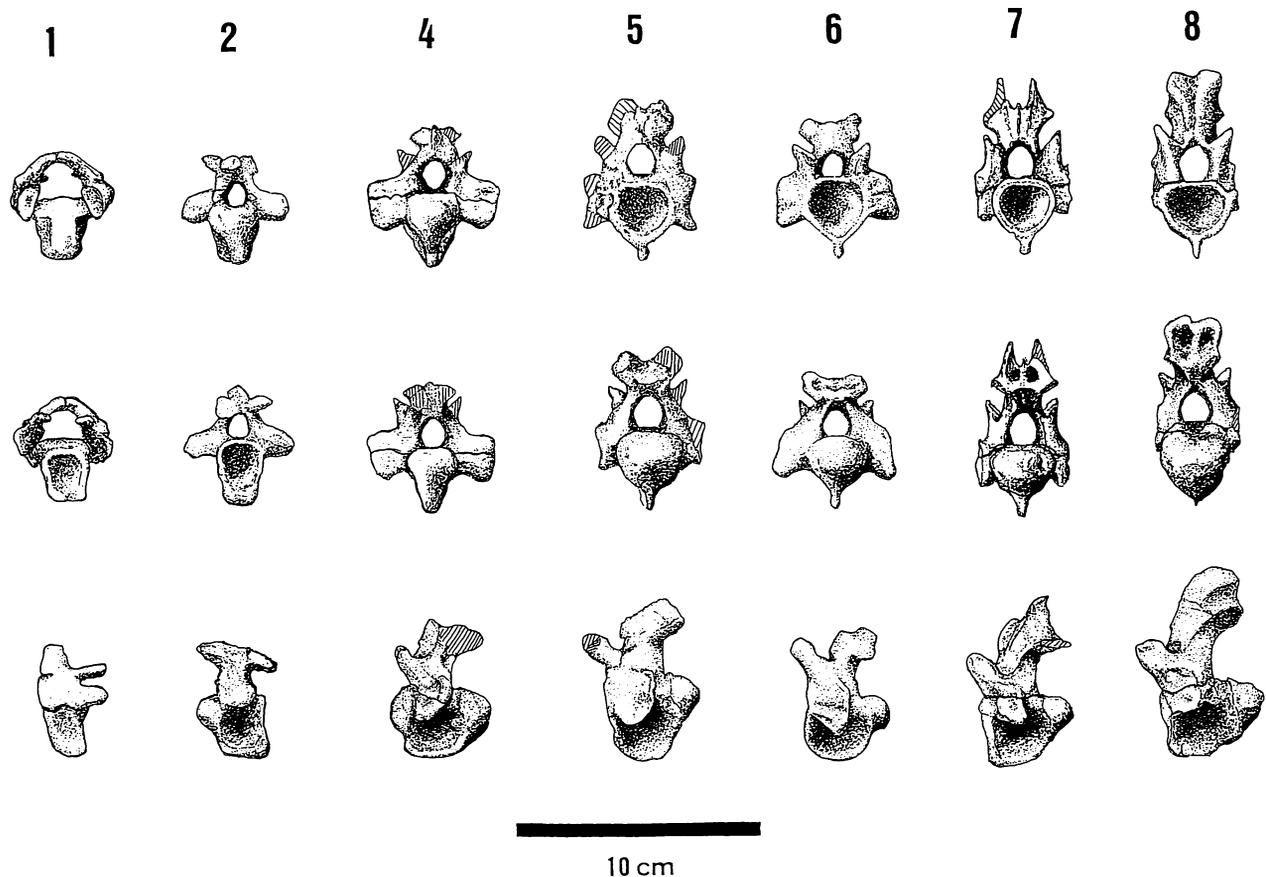
Figure 7. Cervical vertebrae of *Mesodermochelys undulatus* gen. et sp. nov. First, second and sixth cervicals, HMG 369. Fourth, fifth, seventh and eighth cervicals, HMG 5 (holotype). Third cevical is missing. Upper row, anterior view. Middle row, posterior view. Lower row, left lateral view.

1995), and most other polycryptodires (Gaffney *et al.,* 1991).

The isolated first thoracic ribs were recovered from HMG 342 and 369 (65 mm in length). These are relatively short bones as in cheloniids and *Dermochelys* (Zangerl, 1953). Their distal end does not extend beyond the nuchal width unlike plesiochelyids in which it extends beyond the nuchal (Rieppel, 1980).

Both the ninth and tenth thoracic ribs are well preserved in the holotype. They both show fusion to the overlying pleurals as in most turtles.

Sacral vertebrae and ribs (Figures 8-A, D, E)

Both first and second sacral vertebrae and their attached ribs are preserved in the holotype. The second sacral and right rib are preserved in HMG 7. The first and second sacral vertebrae are also known from HMG 1063. The sacral vertebrae are roughly platycoelous, rather than procoelous. These vertebrae and ribs are relatively stout bones in comparison with those of living chelonioids.

Caudal vertebrae and ribs (Figures 8-B, C, F-P, 9)

The caudal vertebrae are preserved in the holotype, HMG

7, 363, 369 and 1063. All caudals are procoelous, showing no trace of chevron bones ventrally. In the holotype, ten disarticulated caudals, which appear to represent the first to seventh and the last three, are present. The first caudal of the holotype has small ribs. By comparison with this series for the holotype, the position of the caudals in the other spcimens could be determined with some certainty. Three caudals of HMG 7 are presumed to be the second, third and sixth, the two from HMG 363 are likely the fourth and ? tenth, the one from HMG 369 is the fourth, and the two of HMG (94-206-B) are the first and second. The tail of the male is much larger and longer, often twice or more than the female in most living turtles including chelonioids (Ernst and Barbour, 1989 ; Hirayama, pers. obs.). Thus, a careful comparison of the relative size of these caudals with those of living forms might reveal sexual dimorphism in *Mesodermochelys*.

Pectoral girdle (Figure 10)

The scapulae have been recovered from five specimens, the holotype, HMG 6, 342, 365 and 369. The pectoral girdle shows the characteristic triradiate structure of turtles. The scapular angle formed by the scapular prong and the acromion is wide, reaching up to 110 degrees. The cor-
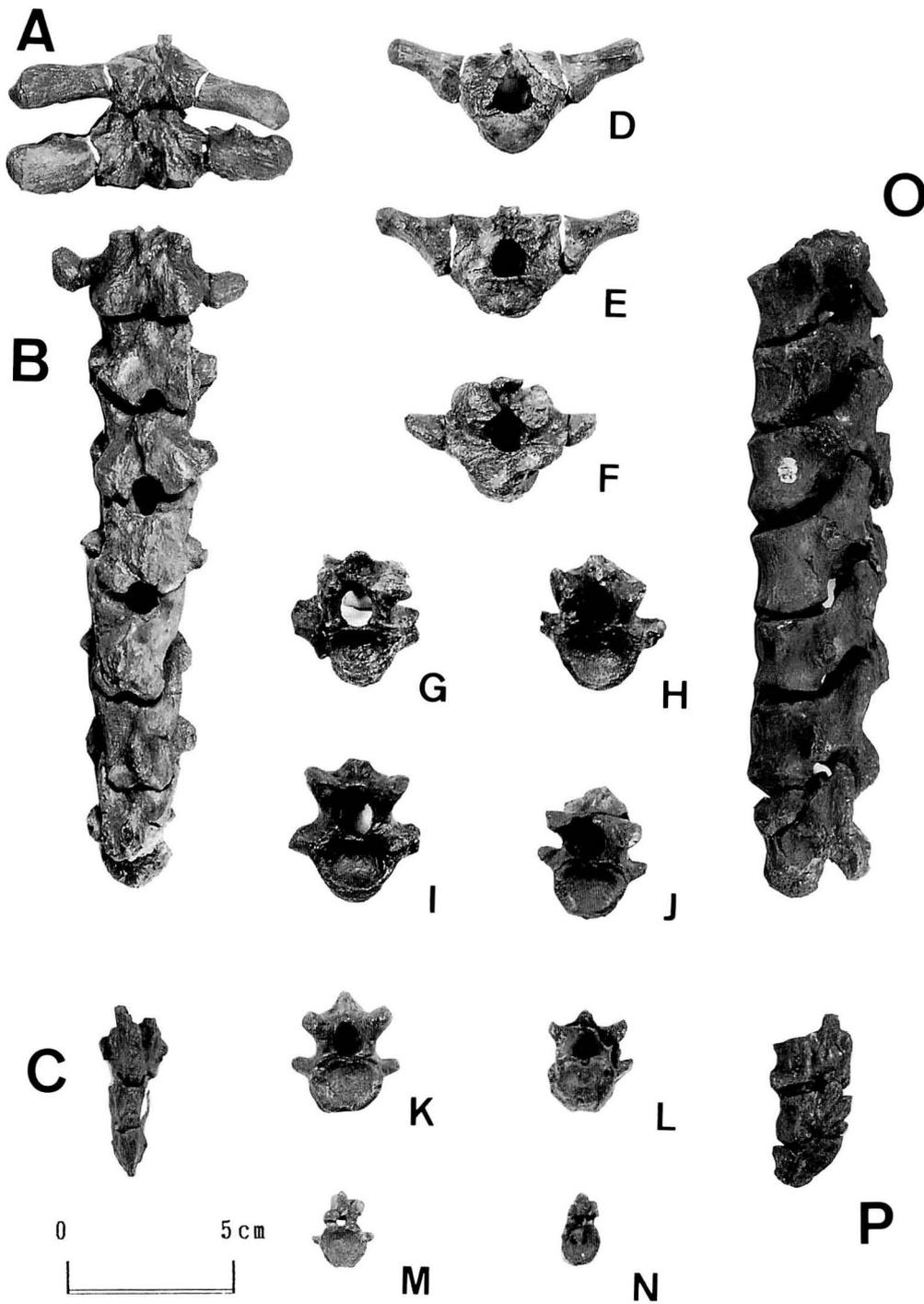
Figure 8. Sacral and caudal vertebrae of *Mesodermochelys undulatus* gen. et sp. nov., HMG 5 (holotype).   **A, D, E.** First and second sacrals with ribs, A : dorsal view, D (first), E (second) : anterior view.   **B, O.** First to seventh caudals in articulation, dorsal and left lateral views.   **C, P.** Last three caudals in articulation, dorsal and left lateral views.   **F to L** : Anterior views of first to seventh caudals.   **M, N** : Anterior views of two of the last three caudals (last two caudals fused together).
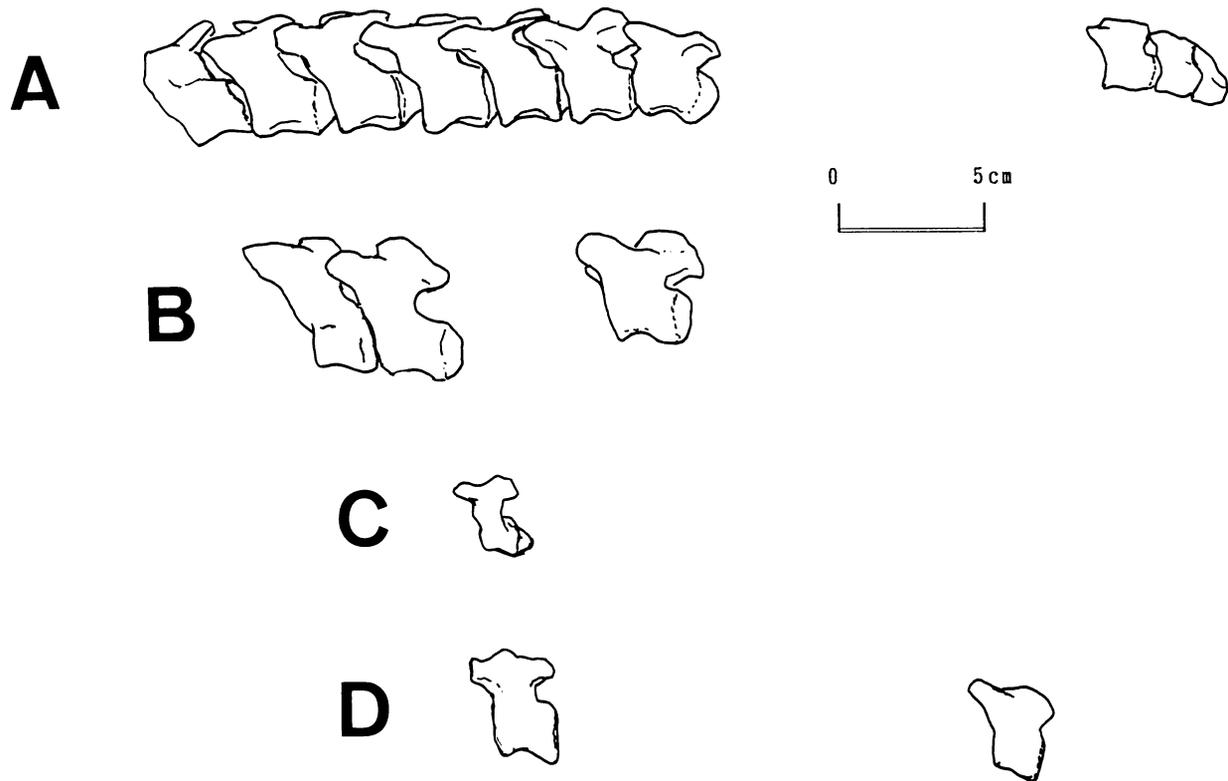
Figure 9. Caudal vertebrae of *Mesodermochelys undulatus* gen. et sp. nov., in left lateral view. **A.** (HMG 5 : holotype), first to seventh, and last three caudals. **B.** (HMG 7), second, third and sixth caudals. **C.** (HMG 369), fourth ? caudal. **D.** (HMG 363), fourth and tenth ? caudals.

acoids are preserved in four specimens, including the holotype, HMG 9, 365 and 369. The coracoid is proportionally narrow and elongate, 248 mm long (right side) in the holotype and 228 mm long (left side) in HMG369, much longer than the humerus. The coracoid of HMG 365 as preserved is 380 mm long (left side), and was probably twice the size of the holotype coracoid. A median keel for the *M. supracoideus* is distinct in the holotype, whereas this keel is not so prominent in the other specimens. The general morphology of the pectoral girdle in *Mesodermochelys* is identical with those of the pelagic chelonioids such as the dermochelyids including *Corsochelys,* the protostegids, and some cheloniids such as *Allopleuron.*

Pelvic girdle (Figure 11)

The elements of the pelvic girdle is preserved in nine individuals, the holotype, HMG 6, 7, 8, 362, 363, 369, 1063, and 1064. Of them the pelvic girdle is completely preserved only in the holotype. The *thyroid fenestra,* or the *obturator foramen,* is small and completely subdivided by the medial pubo-ischium contact as in protostegids and dermochelyids, and unlike those of cheloniids which have a large, confluent fenestra (Hirayama, 1995).

The ilia are preserved in HMG 7, 8 and 1053. The ilium of *Mesodermochelys* is quite peculiar among chelonioids. The iliac blade is quite elongate, somewhat like in the trionychids. It is also laterally curved as in the testudinoids, particularly the living batagurids (Hirayama, pers. obs.). The pubis of *Mesodermochelys* is identical to those of dermochelyids and protostegids in the possession of the huge lateral process (=pectineal process), which is much extended anteriorly beyond the medial border of this bone. This is not the case in cheloniids which have a much smaller lateral process (Hirayama, 1995). The ischium has a rudimentary lateral process (=metischial process) as in dermochelyids, advanced protostegids (e.g., Protostega) and living chelonioids exclusive of *Natator* (Zangerl *et al.,* 1988)

Forelimb (Figures 12, 13)

Only in the holotype and HMG 369 is a part of the forelimb preserved. The humerus (left) is 195 mm long in the holotype and 172 mm long in HMG 369 (right). It is much longer than the femur as described below. In HMG 369, the ossification of the distal end is incomplete, indicating the possible immaturity of this specimen. Hirayama (1992) fully discussed the humeral morphology of sea turtles including the holotype of *Mesodermochelys,* and recognized "toxo-chelyid", "cheloniid", "protostegid" and "dermochelyid" grades among chelonioids. Thus, we follow this "grade-system" here.
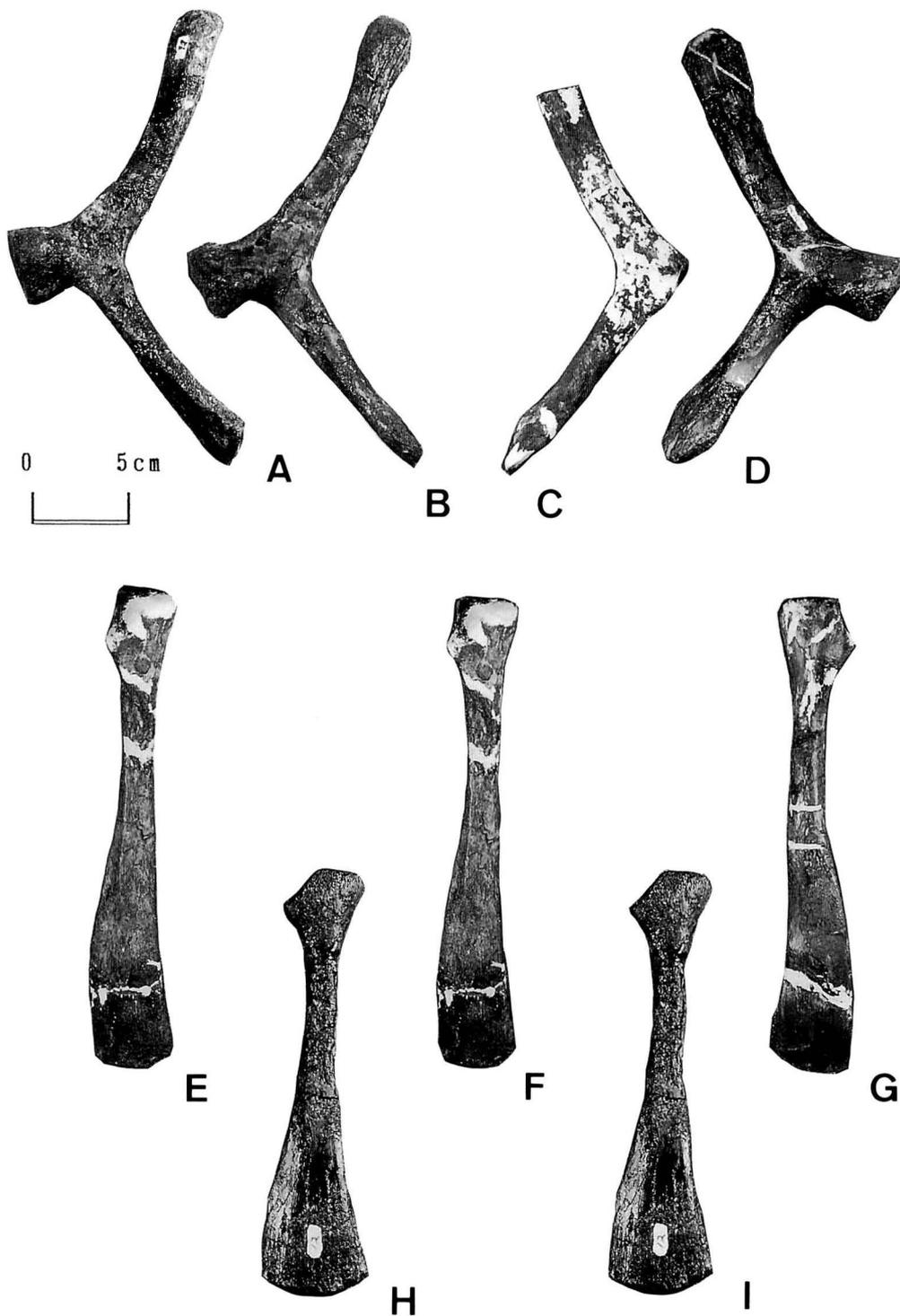
Figure 10. Pectoral girdle of *Mesodermochelys undulatus* gen. et sp. nov. **A.** Right scapula, HMG 369, anterior view. **B.** Left scapula, HMG 369, posterior view. **C.** Right scapula of HMG 5 (holotype), posterior view. **D.** Right scapula, HMG 342, posterior view. **E-G**: right coracoid, holotype, dorsal (stereopair) and ventral views. **H, I.** Right coracoid, HMG 369, dorsal view (stereopair).
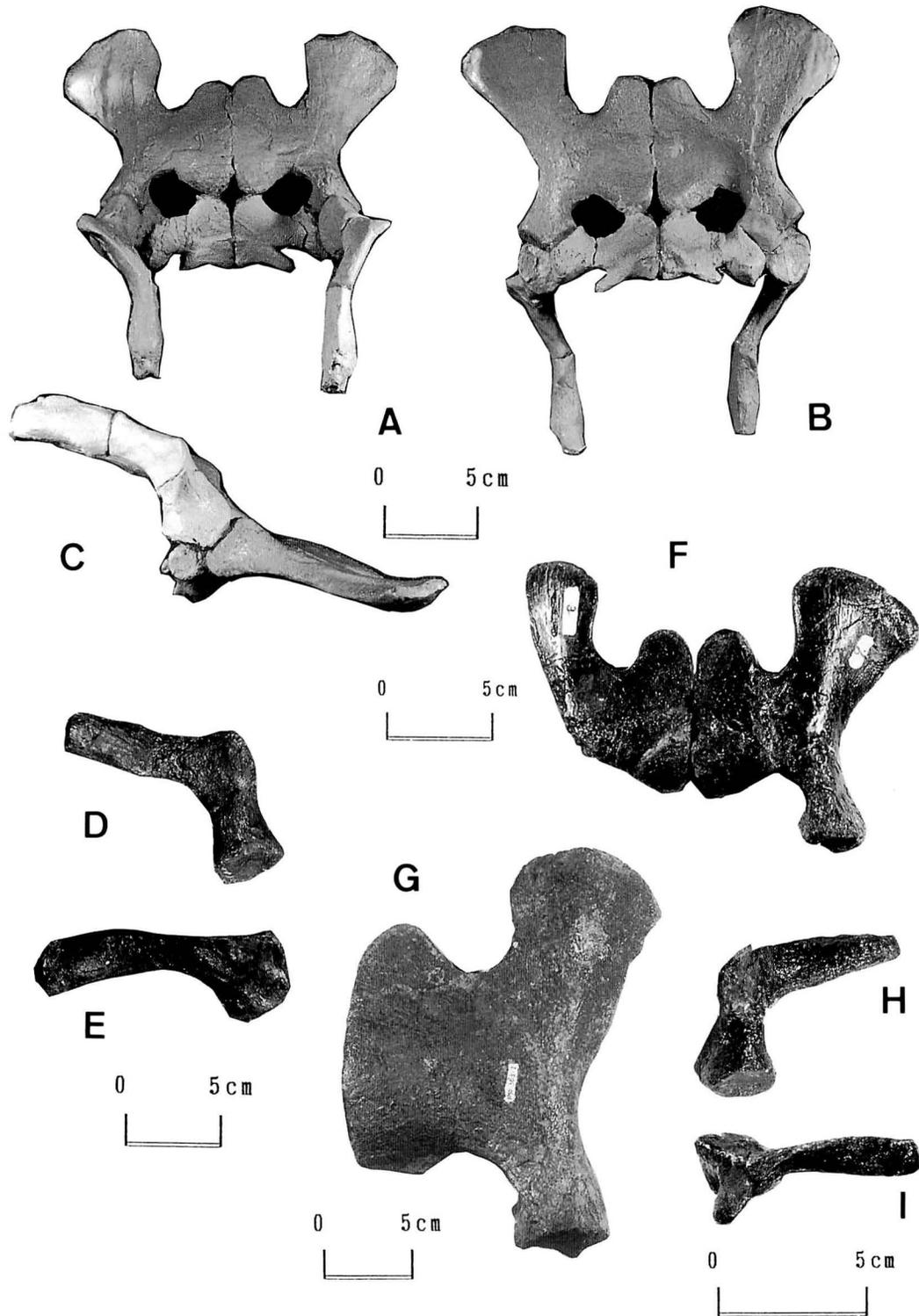
Figure 11. Pelvic girdle of *Mesodermochelys undulatus* gen. et sp. nov. **A–C.** Pelvic girdle in articulation (cast), HMG 5 (holotype), dorsal, ventral and right lateral views. **D, E.** Right ilium, HMG 7, lateral and dorsal view. **F.** Pubes, HMG 369, dorsal view. **G.** Right pubis, HMG 363, dorsal view. **H, I.** Left ilium, HMG 8, lateral and dorsal views.
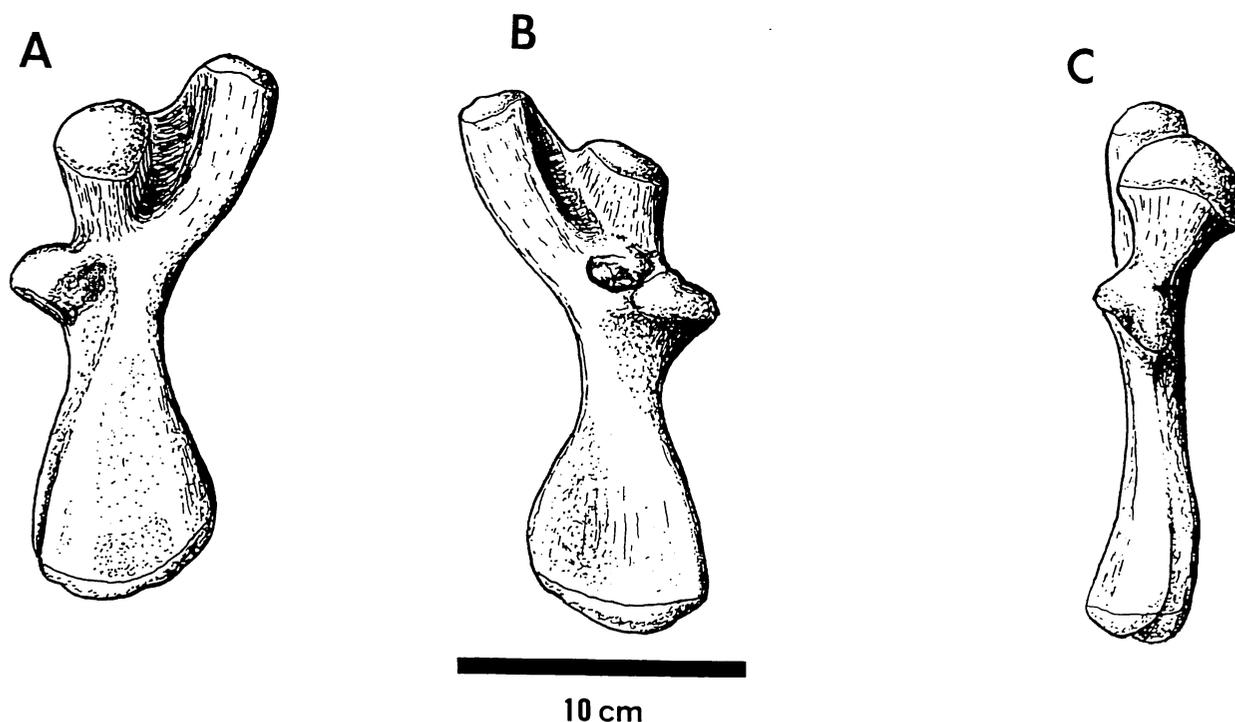
Figure 12. Left humerus of *Mesodermochelys undulatus* gen. et sp. nov., HMG 5 (holotype). **A-C.** Dorsal, ventral and anterior views (slightly modified from Hirayama, 1992).

The humerus has a nearly straight shaft extending toward large *caput humeri* and high medial process. The greatly expanded muscle scars for *M. coracobrachialis brevis, latissimus dorsi* and *teres major,* and the lateral process are located more distally and ventrally than in primitive cheloniids of the "toxochelyid grade" such as *Ioxochelys* or *Osteopygis.* The lateral process of the humerus of *Mesodermochelys* is characterized by its long anterior projection where the *M. deltoideus* inserts as in dermochelyids or *Syllomus,* a Neogene cheloniid. The lateral process of *Mesodermochelys,* however, is elongate and nearly straight relative to the shaft as in other dermochelyids. It lacks the V-shaped structure of advanced cheloniids such as *Syllomus* or the medial concavity of protostegids. The lateral process in *Mesodermochelys* is located at a more proximal position than in Cenozoic dermochelyids, and its shaft is greatly constricted as in *Toxochelys,* primitive protostegids (e.g., *Desmatochelys*) and *Corsochelys.* It is neither as wide nor as flat as in Cenozoic dermochelyids or advanced protostegids (e.g., *Archelon*). In summary, the humeral morphology of *Mesodermochelys* could be interpreted as a primitive "dermochelyid grade", intermediate between the Cenozoic dermochelyids with an advanced "dermochelyid grade" and the primitive chelonioids such as *Toxochelys* (Hirayama, 1992).

The left ulna is present in the holotype. It does not have a distal area with distinct rugosities for articulation with the radius as in all of the cheloniids (Hirayama, 1995; e.g., *Toxochelys* and *Allopleuron*).

The manus is preserved in the holotype and HMG 369. Two carpal elements, the ulnare and pisiform, two metacarpals of the second and fifth digits, and the first distal phalanx,

all of the left side, were recovered with the holotype. The ulnare is roughly rectangular, a rather thick and massive bone, with a clear articular facet along each border, like in modern cheloniids rather than *Dermochelys.* The pisiform is similar to the ulnare, just slightly smaller than the latter, though it is relatively much larger than in any cheloniid. One metacarpal, presumed as the third, is preserved in HMG 369. The articular surface of this element is flattened, and hence inmovable as in most chelonioids. Among chelonioids only some primitive cheloniids such as *Toxochelys* and one undescribed protostegid primitively retain the movable articulation at the first and second digits (Hirayama, 1995, in press).

Hind limb (Figure 14)

Parts of the hind limb, including the femur, were recovered from the holotype, HMG 6, 7, 8, 363, 369 and 1063. The right femur is 145 mm long in the holotype and 136 mm long in HMG 369, much shorter than the humerus as in most chelonioids. The major and minor trochanters of the femur are connected by a bony ridge with a straight proximal border as in *Dermochelys,* protostegids including *Desmatochelys,* and living cheloniids (exclusive of *Natator* ; Zangerl *et al.,* 1988). The major trochanter of the femur is not higher than the minor one as seen in advanced cheloniids including *Allopleuron* and most Cenozoic forms. The tibia is preserved in HMG 7, 363, and 369, and the fibula is preserved only in HMG 363. These are rather stout bones as in cheloniids. There is no trace of tendon pit on tibia.

Elements of the right pes preserved with the holotype
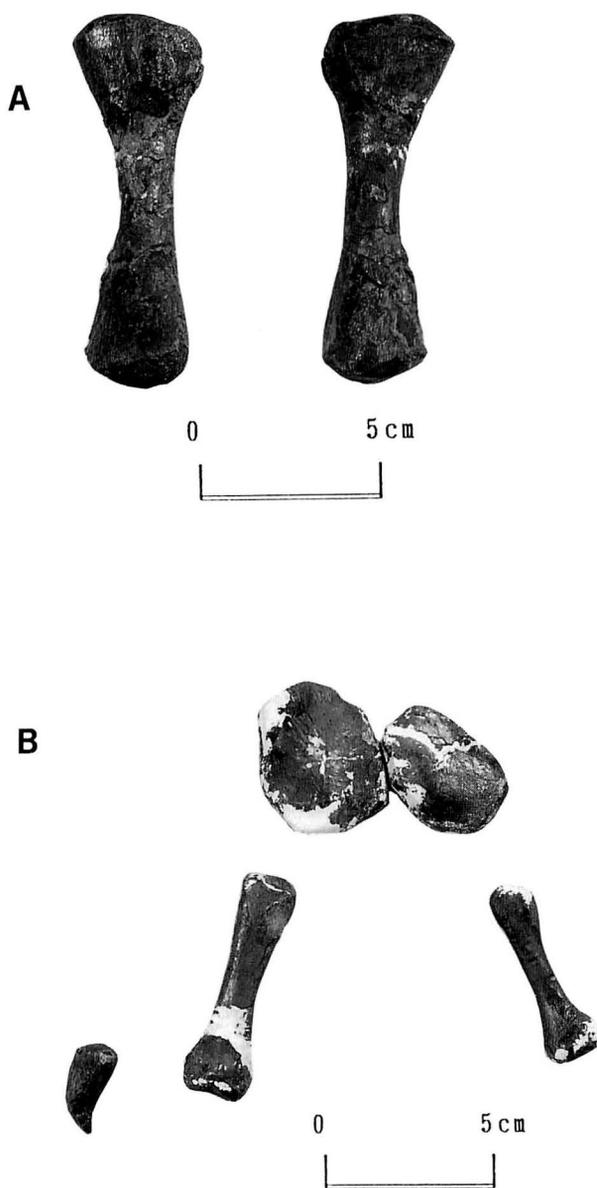
Figure 13. Left ulna and manus of *Mesodermochelys undulatus* gen. et sp. nov., HMG 5 (holotype). **A.** Ulna, dorsal and ventral views. **B.** Manus, with ulnare, piciform, ungual I, metacarpals II and V preserved.

include the astragalus, calcaneum, third metatarsal, and two phalanges of the first digit. Movable articulations are absent in these bonse (as in the menues). The pes is presumed to be about 60% of the legth of the menues, as in living cheloniids.

Shell (Figures 15, 16, 17)

The shell is partially preserved in all specimens exclusive of HMG 1062. The best shell is that of the holotype, although its anterior portion of the carapace is missing. The

anterior portion of the carapace including the nuchal bone is known from HMG 342 and 369. The plastron of HMG 369 is also essentially complete. Thus, a composite reconstruction of the entire shell is made with certainty.

The shell scute sulci are very poorly developed in *Mesodermochelys.* Prominent scute sulci are observed only on the third and fifth neural plates, then become reduced and disappear at the proximal portion of the third and fifth pleurals. Rudimentary furrows, possibly scute sulci, are preserved at the lateral edge of the sixth to ninth peripherals. Thus, it is highly probable that *Mesodermochelys* had shell scutes covering only the neural (and possibly marginal) region of the carapace in life. This condition is reminiscent of the juvenile of living *Carettochelys insculupta* (Carettochelyidae ; Trionychoidea ; Zangerl, 1959).

The reconstructed carapace of *Mesodermochelys* is rather more circular than oval ; its width is only 10% smaller than its median length. The nuchal plate has a prominent ventral knob to which the neural spine of the eighth cervical articulates as in many chelonioids including *Dermochelys.* The neural plates are rather rectangular as in the protostegids, *Corsochelys* and *Eosphargis,* and unlike the cheloniids which have hexagonal neurals (Hirayama, in press). The neurals of *Mesodermochelys,* however, are extremely narrow and reduced particularly in the posterior part. The pentagonal seventh neural is reduced posteriorly, and the eighth is absent resulting in the seventh and eighth pleurals meeting medially as in *Cuora* (Bataguridae) and the pelomedusids (Pleurodira). The suprapygal is single as in protostegids, and not subdivided as in most cryptodires including *Corsochelys, Eosphargis,* and cheloniids. Contrary to the reduced neural area, the peripheral plates are robust and broad in *Mesodermochelys.* The medial portion of the peripherals extends medially between the costal rib ends so that the medial border of the peripheral series is strongly undulating and results in a restriction of the pleuro-peripheral fontanelles. These fontanelles are more restricted than in *Corsochelys* in which ossification of the pleurals is comparable to that in *Mesodermochelys.*

The plastron is best preserved in the holotype and HMG 369. The plastron shows no trace of scute sulci, as is the condition found in protostegids, *Corsochelys* and *Dermochelys.* The maximum thickness of the hyo-hypoplastra is about 10 mm in the holotype and HMG 369. It is characterized by a high plastral index (the ratio of the minimum length of the hyo-hypoplastral bridge to half the width of the plastron), about 110 in the holotype and 120 in HMG 369, and shows a large fontanelle between the hyo-hypoplastra. Thus, its general appearance is most similar to that of *Corsochelys* (Zangerl, 1960). The epiplastra are preserved in the holotype, HMG 363 and 369, showing a notable difference among *Mesodermochelys.* The epiplastron is rather narrow and slender in the holotype and HMG 369 as in *Toxochelys,* whereas this is a much wider element in HMG 363, the largest specimen. The entoplastron is preserved in the holotype, HMG 363 and 369. The bone is T-shaped, with large lateral wings and a long posterior process, which is rod-like without a horizontal sheet. This is unlike other chelonioids but more similar to *Chelydra* and *Macroclemys*
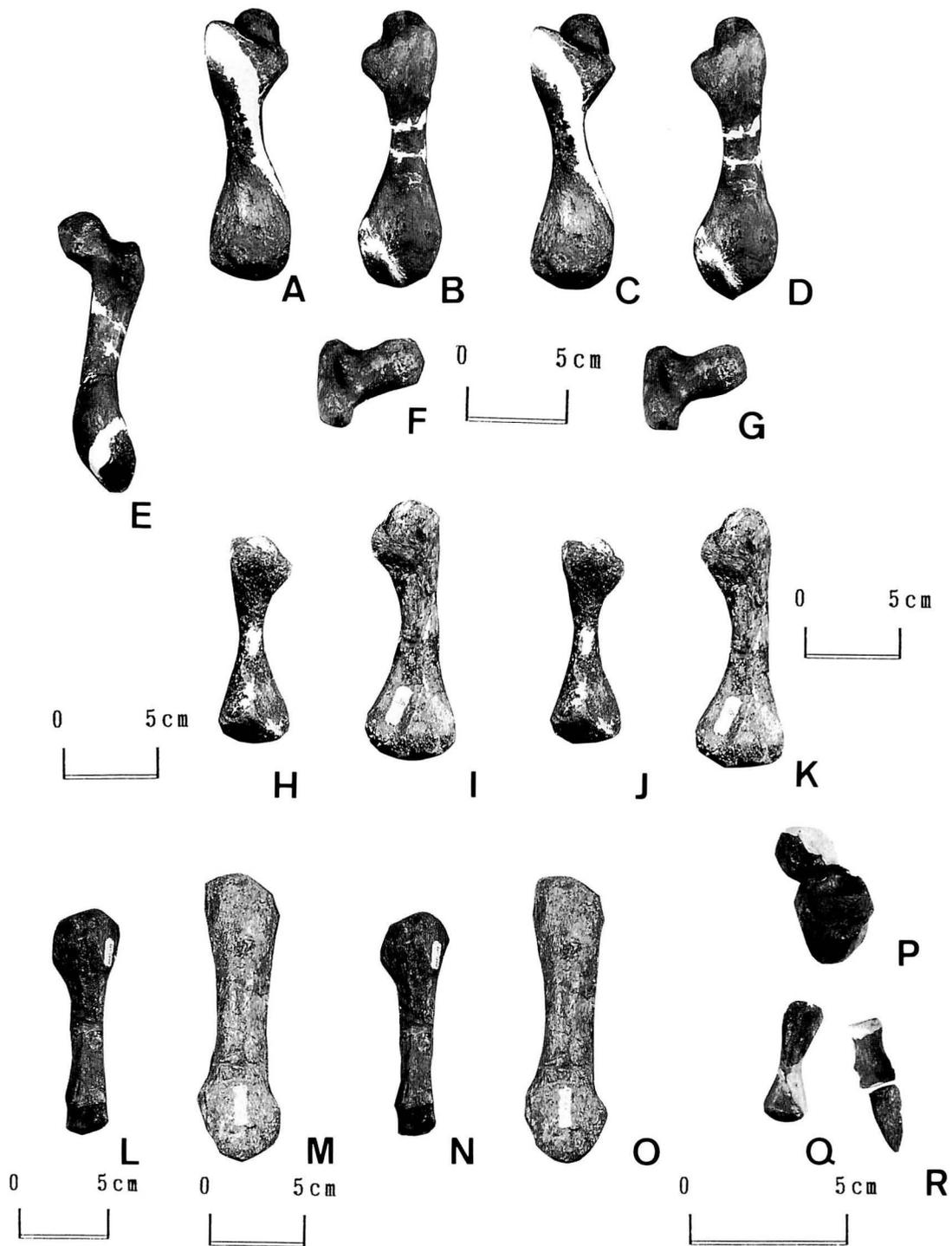
Figure 14.   Hind limb of *Mesodermochelys undulatus* gen. et sp. nov.   **A–G.** Femora of HMG 5 (holotype), A, C : left side, ventral view (stereopair), B, D : right side, ventral view (stereopair), E : right side, anterior view, F, G : right side, proximal view.   **H, J.** Left femur, HMG 8, ventral view (stereopair).   **I, K.** Right femur, HMG 369, ventral view (stereopair).   **L, N.** Left tibia, HMG 7, anterior view (stereopair).   **M, O.** Right fibula, HMG 363, anterior view (stereopair).   **P.** Right astragalus and calcaneum, holotype, dorsal view.   **Q.** Right metatarsal II, holotype, dorsal view.   **R.** Right phalanx and ungual of phalanges I, holotype, dorsal view.
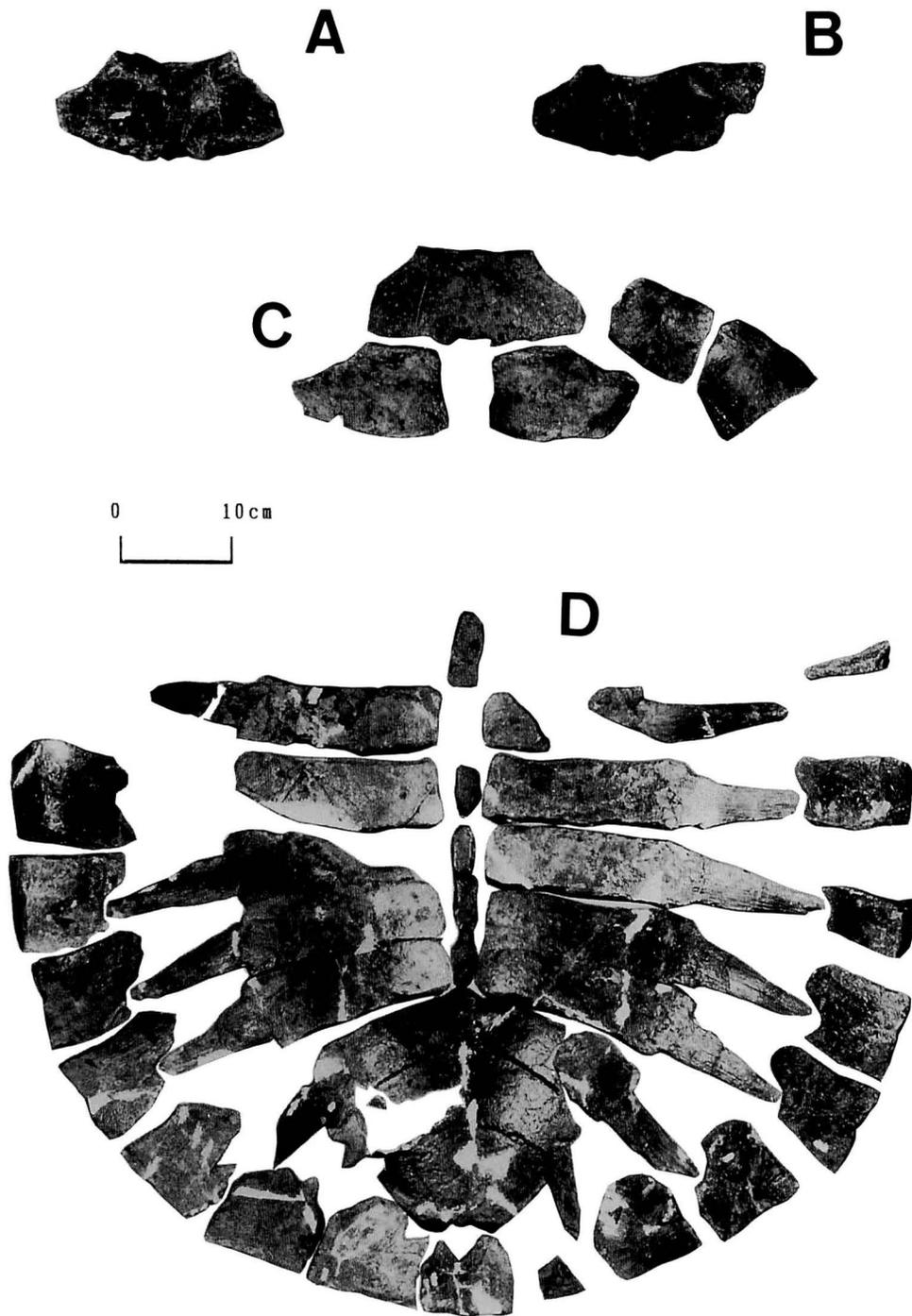
Figure 15. Carapace of *Mesodermochelys undulatus* gen. et sp. nov. **A.** Nuchal, HMG 342, ventral view. **B.** Nuchal with left first peripheral attached, HMG 369, ventral view. **C.** Nuchal, right first and second peripherals, first pleurals, HMG 342, dorsal view. **D.** Carapace, HMG 5 (Holotype), dorsal view.

(Chelydridae). Each lateral wing of the entoplastron has a facet for the epiplastron, whereas there is no facet for the hyoplastron. The medial processes of the hyo-hypoplastra are not as long as in *Corsochelys,* possibly not interdigitating with corresponding processes across the midline. The lateral processes of the hyo-hypoplastra are also rather short, not showing any contact with the peripherals as is the case in most chelonioids. The xiphiplastra are nearly straight,
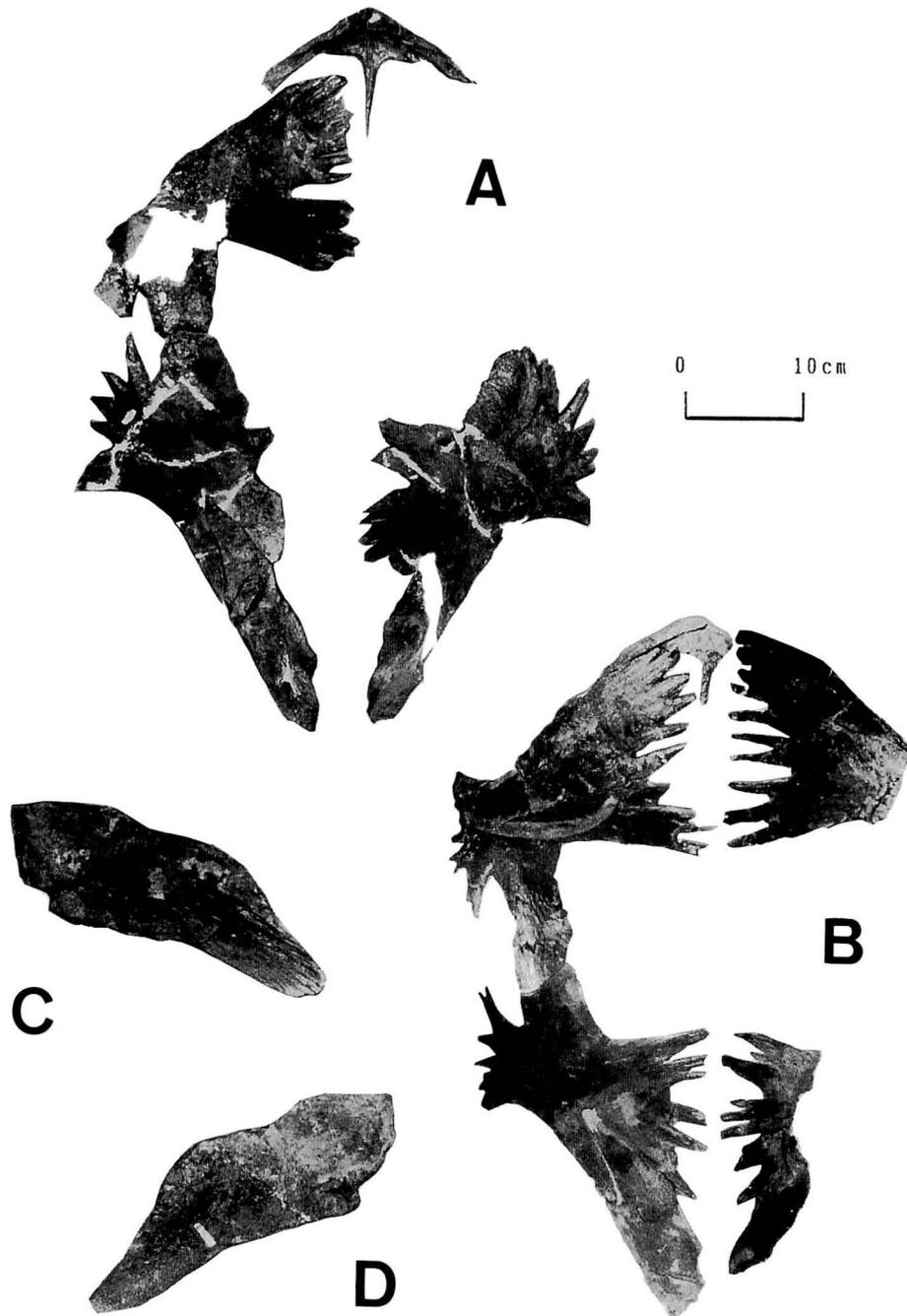
Figure 16. Plastron of *Mesodermochelys undulatus* gen. et sp. nov. **A.** HMG 5 (holotype), ventral view. **B.** HMG 369, ventral view. **C, D.** Left epiplastron, HMG 365, dorsal and ventral views.

blade-shaped bones, rather tightly sutured to the hypoplastra in the holotype and HMG 369. There is no trace of a medial meeting between the xiphiplastra.

Phylogenetc analysis

Results.—A single tree of 252 steps (Figure 18) and a consistency index of 0.587 was obtained by branch-and-

bound search options of PAUP (version 3.0 ; Swofford, 1989). This result supports the monophyly of most higher categorical ranks among eucryptodires, proposed by Gaffney and Meylan (1988), but not the procoelocryptodires (chelonioids, trionychoids and testudinoids). The inclusion of additional fossil taxa such as *Ordosemys, Sinemys,* and *Macrobaena* from Asia into the data matrix may be ready to alter the relationships and character transformations among eu-

Ren Hirayama and Tsutomu Chitoku
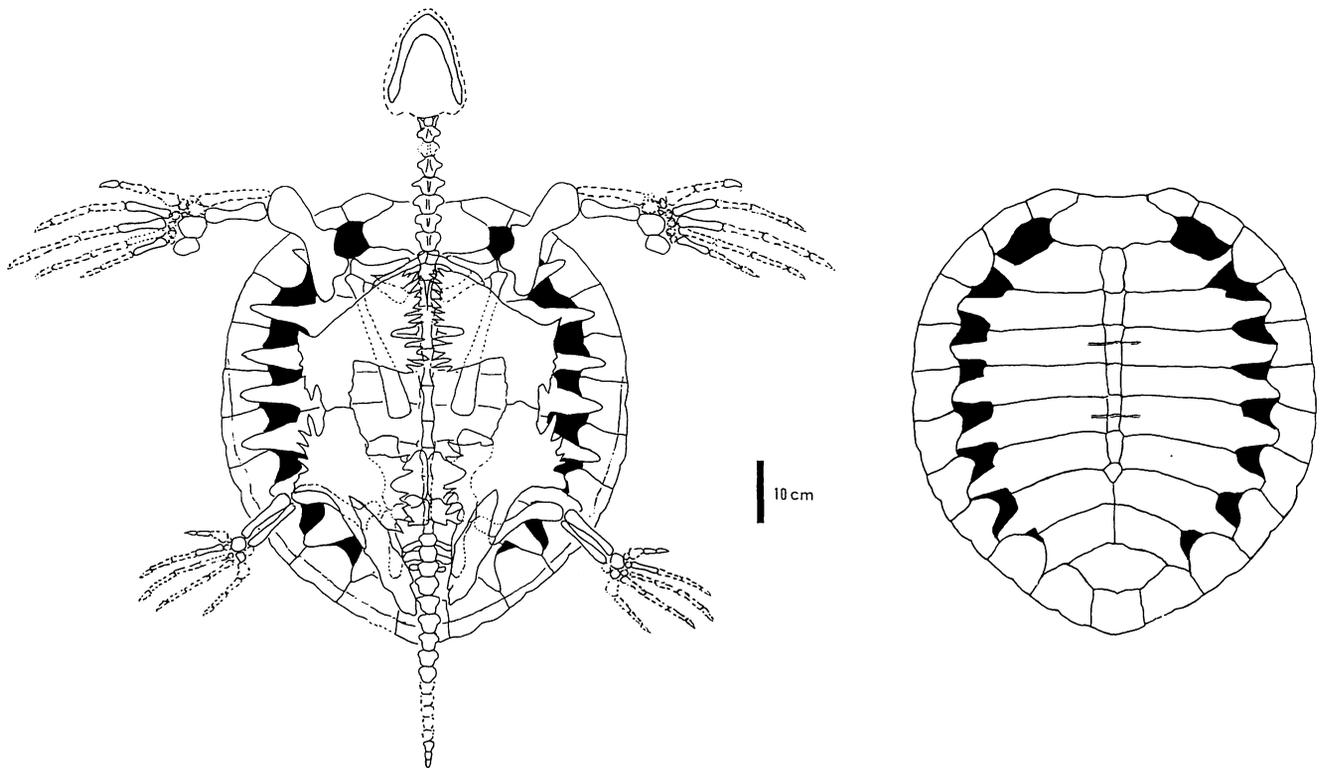
Figure 17. Composite reconstruction of *Mesodermochelys undulatus* gen. et sp. nov. largely based on HMG 5 (holotype), 342 and 369. Skeleton in ventral view, carapace in dorsal view.

cryptodires (Brinkman and Gaffney, pers. commun.; Hirayama, in preparation).

The monophyly of chelonioids is supported by 16 characters, of which 14 are unequivocal. Four are related to the formation of paddles, seven are related to reduced shell ossification. The monophyly of each family among chelonioids of Hirayama (1995) is supported; Cheloniidae (including *Toxochelys* and *Ctenochelys*) was united by 14 (8 unequivocal) characters, Protostegidae by 13 (11 unequivocal) characters, and Dermochelyidae by 5 (4 unequivocal) characters. Both *Mesodermochelys* and *Corsochelys* were placed as very primitive members of the family Dermochelyidae, as hypothesized by previous works of Hirayama (1992, 1995, in press).

Discussion.—The goal of this analysis is to assess the phylogenetic position of *Mesodermochelys* among chelonioids. Due largely to missing data and differences of

preservation (Appendix I), the phylogeny of the family Dermochelyidae is rather poorly resolved in comparison to those of the protostegids and cheloniids. In the case of Mesozoic dermochelyids, there is a significant gap in the data set because of the poor preservation of cranial materials. Most of the skull of *Mesodermochelys* is unknown, whereas the anterior portion of the skull and the lower jaw is missing in *Corsochelys*. Thus, the large *foramen caroticum laterale* and the short subdivided *rostrum basisphenoidale* are equivocal in *Mesodermochelys*, whereas the anterior process of the surangular is equivocal in *Corsochelys*. Nonetheless, two characters, the poor development of the *processus trochlearis oticum* formed by prootic and the rudimentary scute sulci on the carapace, could be explained as an unequivocal synapomorphy uniting them with Cenozoic dermochelyids. Large size with maximum shell length exceeding over 1.3 m seems also to be shared by all known dermochelyids (Hi-

Figure 18. Hypothesized phylogeny of the Chelonioidea based on PAUP analysis of 13 extinct and extant taxa and their 5 outgroups in the Eucryptodira. Distribution of apomorphies at each Node is shown by numbers which correspond to characters listed in Appendix II and scored in Appendix I as follows. Parallelisms are marked with (″), and character reversals are marked with (*). Node A1 : Centrocryptodira (61, 64, 65-1, 81*, 120, 121*), A2 : Polycryptodira (3, 4, 54, 58, 59, 60, 72, 76-2), B1 : (7″, 8-2″, 34″,43-0*, 62″, 63″, 66″, 67″, 68, 71″), B2 : Chelomacryptodira (32″, 74″, 125*), C1 : Chelonioidea (14, 37, 50″,74″, 85, 86, 95, 96, 112, 119, 122, 127, 128, 129, 132), C2 : (11″, 12″, 16″, 24″, 77-2″, 79″, 80, 87″, 97″, 109-2, 133″), C3 : Cheloniidae (6, 15, 19, 38″, 40, 62″, 63″, 71″, 77-1, 81″, 93, 103″, 108, 123-2), C4 : (8*, 16″, 27, 41, 44″), C5 : (2″, 18*, 24″, 46″, 67″), C6 : (6*, 66″, 70″, 77-2″, 87″, 88, 97″, 99″, 123-1*), C7 : (17″, 54*, 79″, 133″), C8 : Protostegidae (22, 23, 28, 29, 30, 36″, 39*, 44″, 72*, 89, 90, 94, 112-2″), C9 : Dermochelyidae (31, 45, 46″, 101-1″, 125-2″), C10 : (35, 56″, 82″, 91, 98″, 103″), C11 : (5″, 8*, 10″, 20, 26″, 42, 49″, 92, 101-2″, 112-3, 125-3), C12 : (50*, 86-2, 113).

Plesiochelyidae

Meiolania

Chelydroidea

B 1

Testudinoidea

B 2

Trionychoidea

A 1

Toxochelys

C 3

Ctenochelys

A 2

Osteopygis

C 4

Allopleuron

C 5   C 7

Family

Cheloniidae

Chelonia mydas

C 1   C 6

Puppigerus

Desmatochelys

C 8   Family
Protostegidae

Protostega gigas

Superfamily

Chelonioidea

Corsochelys

C 2

Mesodermochelys

C 9

Family

C 10

Eosphargis

Dermochelyidae

C 11

Psephophorus

C 12

Dermochelys

rayama, 1995) *Mesodermochelys* appears to be more advanced than *Corsochelys* in the possession of relatively large paddles involving a humerus with an elongate projection of the lateral process and the short *crista supraoccipitalis*.

The pronounced reduction of shell ossification and the scute loss are also seen in *Allopleuron* (Cheloniidae) and advanced protostegids (*Protostega* and *Archelon*). These are explained as a result of extreme convergence among chelonioids as proposed by Hirayama (1995, in press). With *Allopleuron* forced into the basal position for both protostegids and dermochelyids as hypothesized by Hirayama (1992), we require 4 more derived characters shared by those chelonioids than by others and the tree length increases from 252 steps to 259 steps, the remaining cheloniids then collapse into a paraphyletic group constituting primitive grades among chelonioids as shown by Gaffney and Meylan (1988) or Hirayama (1992). Furthermore, to force *Allopleuron* into the basal position for Cenozoic dermochelyids as hypothesized by Weems (1988) we require 21 more derived characters shared by them of which at least 8 are not shared by *Corsochelys* and *Mesodermochelys* and the tree length increases to 293 steps. The cheloniid affinity of *Allopleuron*, however, is supported by overwhelming characters, although *Mesodermochelys* remains within the dermochelyids as a monophyletic group, in every case.

Conclusions

The phylogeny of the family Dermochelyidae is rather poorly supported due to missing data and variation in preservation. However, two Mesozoic dermochelyids, *Mesodermochelys* and *Corsochelys,* demonstrate that the significantly reduced shell ossification seen in Cenozoic dermochelyids including *Eosphargis* was preceded by shell scute loss and the development of the characteristic dermochelyid humerus. *Mesodermochelys* is considered to be more closely related to Cenozoic dermochelyids than *Corsochelys* in its possession of relatively large paddles and a humerus with an elongate projection of the lateral process and a short *crista supraoccipitalis.*

The pronounced reduction of shell ossification and the scute loss is also seen in *Allopleuron* (Cheloniidae) and advanced protostegids (*Protostega* and *Archelon*). These are explained as a result of extreme convergence among chelonioids.

Hirayama (1994, in press), and Hirayama and Chitoku (1994) demonstrate the peculiarity of the Japanese chelonioid fauna during the Upper Cretaceous. Primitive dermochelyids such as *Mesodermochelys* are the most abundant chelonioids from the Santonian to Maastrichtian of Japan, whereas the cheloniids, which dominate the Cretaceous of North America and Western Europe, are virtually unknown from Japan. Upper Cretaceous dermochelyids are extremely rare outside Japan. *Corsochelys haliniches*, known only from the holotype, is the only Mesozoic dermochelyid known with certainty from outside Japan. Thus, Hirayama (in press) suggests that endemic speciation may have occurred among the chelonioids during the Cretaceous, resolving into a pattern of diversity unlike that for living sea turtles, of which

most genera including *Dermochelys,* are cosmopolitan. We suppose the western part of the Pacific Ocean around Japan might be the center of diversification of Cretaceous dermochelyids at least since the Santonian. This might be the reason why Mesozoic dermochelyids are so rare outside Japan. Nonetheless, *Mesodermochelys* should be a side branch of dermochelyid phylogeny, not directly ancestral to any later taxon. It possesses peculiar autapomorphic characters such as the unique configuration of the lower triturating surface, unique iliac blade, and peripherals with an undulating medial border. This is also the case in *Corsochelys* which has several autapomorphic characters such as the amphicoelous cervicals (explained as character reversal). Thus, it seems highly probable that we will discover another dermochelyid of Cretaceous age that is more closely related to the Cenozoic forms.

Acknowledgments

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APPENDIX I. Data Matrix

The symbol "?" represents missing or equivocal data. The following symbols are used to represent character states in polymorphic taxa: a=(0, 1), b=(1, 2), c=(02), d=(012), e=(1, 3).

	5	10	15	20	25	30	35	40	45	50	55	60	65	70
Plesiocelyidae	010a0	0a100	aa000	00000	0a00a	00000	00000	1aaa0	00a00	0000a	00000	000?0	00000	00000
Meiolania	01001	00300	00000	00000	00000	00000	02110	10010	00100	00000	00100	00000	10011	00000
Chelydroidea	1a111	a1c00	00aoa	00000	00000	00000	02010	10110	00000	00010	00010	00111	1111b	111a0
Testudinoidea	0011a	a1200	aa00a	aaa00	a000a	00a00	0b010	10a10	00000	00a0a	aaaa0	a0111	111b2	111a0
Trionychoidea	aa11a	01200	00a0a	0000a	00000	00000	01010	10a10	00000	a0aaa	0a0a0	00111	111de	11100
Toxochelys	00010	10100	00011	00010	00000	00000	00000	11111	00100	0000a	00010	00111	11111	10000
Ctenochelys	00110	10000	00011	11010	00000	01000	00000	11111	10110	00001	00010	00111	11111	00000
Osteopygis	01110	10000	00011	10110	10010	01000	00000	11111	10110	10100	00011	00111	111?1	?10?0
Allopleuron	00110	01201	11011	11110	00000	01000	00000	11111	10110	00001	00000	00111	11111	11001
Puppigerus	01110	00000	00011	10110	10010	01000	00000	11111	10110	10101	00010	00111	11111	11001
Chelonia mydas	01110	00000	00011	11110	00010	01000	00000	11111	10110	11001	11100	10111	11111	11001
Desmatochelys	01000	011?0	11010	10000	01110	00111	00000	01000	00110	00001	00010	00111	10021	00000
Protostega gigas	10111	00010	11110	1??00	01110	10111	00000	01000	00110	00000	00010	00111	100?1	00000
Corsochelys	00??0	?1200	11???	?????	???10	00000	10000	11110	00101	10???	?????	???11	0000?	?0000
Mesodermochelys	0????	?????	?????	?????	?????	????0	1???1	?????	?????	??001	10000	10111	10011	00000
Eosphargis	00111	00001	11010	10001	00010	10000	10001	????0	01???	??011	10000	???11	??0??	?0??0
Psephophorus	00111	00001	??010	10001	00010	1000?	?0001	????0	01???	??010	00010	?????	?????	?????
Dermochelys	00111	00001	11010	10001	00010	10000	10001	01000	01101	11010	00010	11111	10011	00001

	75	80	85	90	95	100	105	110	115	120	125	130	135
Plesiochelyidae	000?0	00000	10000	00000	00000	00000	00000	00000	0a000	00001	2000a	10000	00001
Meiolania	00?01	00000	00000	00000	00000	00000	00000	00??0	?0000	00000	00102	0??00	0?001
Chelydroidea	1aa01	10000	a0000	00000	00000	00000	00000	000c0	0a000	a0000	0ab01	1aaa0	0a001
Testudinoidea	11010	20000	0a00a	00000	00000	00a00	00000	a0a0a	a0000	a0001	b0000	10000	00001
Trionychoidea	11110	20000	a0000	a0000	00000	00000	a0000	0000a	a0000	0000a	00d00	1aa00	0aa01
Toxochelys	1??10	21000	10001	10000	00101	10000	00111	00100	01000	000a0	01201	11110	01001
Ctenochelys	11010	21000	10001	10000	00101	10000	00110	11110	01000	10010	01201	11110	01001
Osteopygis	?????	??000	10000	00000	00101	10000	00000	00100	00000	00010	01201	11100	01001
Allopleuron	11010	22010	10001	11100	00101	11011	21000	10110	02000	00110	01102	11110	01101
Puppigerus	11010	22000	11001	11100	00101	11011	00100	11010	22000	11001	11100	00101	11011
Chelonia mydas	11010	22010	11001	11100	00101	11110	00100	11010	22000	11001	11100	00101	11011
Desmatochelys	00???	?2011	00001	11011	00011	11000	00000	00020	?2000	00010	01002	11110	011?1
Protostega gigas	00010	22111	01011	11011	00011	11100	20100	10120	12000	01010	01011	11111	01111
Corsochelys	?????	?201?	??0?1	11?00	00001	1???0	10000	00020	01000	00110	01002	11?10	011?1
Mesodermochelys	01010	22011	01101	11000	100?1	11100	10100	00021	11001	00010	01002	11110	01101
Eosphargis	?????	?2011	01001	11000	11001	11100	21100	00020	03000	00010	01003	11110	01101
Psephophorus	?????	?????	????1	21000	11??1	11???	20100	?????	??1??	?????	?????	?????	?????
Dermochelys	01010	22111	01001	21000	11001	11101	20100	00002	03110	00010	01003	11110	11101

APPENDIX II. Characters and character states
* : character first identified here.

Skull

1. Megacephalic : (0)=no, (1)=yes. Cranial length reaching up to one third or more of shell length (Boulenger, 1889 ; Hirayama, in press).
2. Cranial scute sulci on dermal roofing elements : (0)=present, (1)=absent.
3. Nasal bone : (0)=present, (1)=lost.
4. Medial meeting of prefrontals : (0)=absent, (1)=present.
5. Prefrontal-postorbital contact : (0)=absent, (1)=present.
6. Orientation of orbital opening : (0)=lateral, (1)=dorso lateral (Fastovsky, 1985).
7. Parietal-squamosal contact : (0)=present, (1)=absent.
8. Posterior temporal emargination : (0)=*foramen stapedio temporale* concealed from dorsal, (1)=*foramen stapedio temporale* exposed from dorsal, (2)=entire of *processus trochlearis oticum* exposed from dorsal (Gaffney, 1979).
9. Jugal-quadrate contact : (0)=absent, (1)=present.
10. Jugal-squamosal contact : (0)=absent, (1)=present.
11. Medial process of jugal : (0)=present, (1)=lost.
12. Jugal-pterygoid contact : (0)=present, (1)=lost
13. Hooked premaxillae : (0)=absent, (1)=present.
14. Foramen *praepalatinum* : (0)=present, (1)=lost.
15. Upper triturating surface involving palatines : (0)=no, (1)=yes.
16. Upper triturating surface involving vomer : (0)=no, (1)=yes.
17. Vomerine trough on upper triturating surface : (0)=absent, (1)=present (Kesteven, 1910).
18. Vomerine pillar concealed by upper triturating surface : (0)=absent, (1)=present (Zangerl, 1971).
19. *Apertura narium interna* entirely formed by vomer and palatines, excluding premaxillae : (0)=no, (1)=yes.
20. Pit between premaxillae and vomer : (0)=absent, (1)=present (Gaffney and Meylan, 1988).
21. *Meatus choanae* at level of medial process of jugal : (0)=absent, (1)=present (Zangerl, 1971).
22. High lingual ridge of maxilla exposed from lateral* : (0)=absent, (1)=present.
23. Vomer-pterygoid contact lost, palatines medially meeting : (0)=no, (1)=yes.
24. *Foramen palatinum posterius* enclosed : (0)=present, (1)=lost.
25. *Foramen palatinum posterius* open posterolaterally : (0)=absent, (1)=present.
26. *Processus pterygoideus externus* : (0)=present, (1)=lost.
27. Median ventral ridge of pterygoids* : (0)=absent, (1)=present.

28. Pterygoid extending onto mandibular articulating surface of quadrate : (0)=no, (1)=yes.
29. Pterygoid narrow, C-shaped : (0)=no, (1)=yes.
30. Large *processus pterygoideus trochlearis oticum* involving deep notch of quadrate : (0)=no, (1)=yes.
31. *Processus pterygoideus trochlearis oticum* involving prominent shelf of prooitc : (0)=yes, (1)=no (Gaffney, 1979).
32. *Incisura collumerae auris* closed : (0)=no, (1)=yes (Gaffney, 1979).
33. Eustachian tube enclosed within elongate *incisura collumerae auris auris* : (0)=no, (1)=yes (Gaffney, 1979).
34. *Cavum tympani* with posterior ventral ridge* : (0)=absent, (1)=present.
35. *Crista supraoccipitalis* little projecting beyond parietal : (0)=no, (1)=yes.
36. *Canalis caroticus internus* excluding basisphenoid : (0)=no, (1)=yes (Gaffney, 1979).
37. *Foramen anterius canalis carotici interni* lie close together : (0)=no, (1)=yes.
38. *Foramen basisphenoidale* : (0)=present, (1)=absent (Meylan and Gaffney, 1989).
39. *Foramen canalis carotici interni posterius* separated from *foramen basisphenoidale,* enclosed within pterygoid : (0)=no, (1)=yes.
40. Ventral surface of basisphenoid with V-shaped crest emarginated from posterior : (0)=absent, (1)=present.
41. V-shaped basisphenoid with basipterygoid projection : (0)=absent, (1)=present (Kesteven, 1910).
42. Large basisphenoid, lying beneath the siginificant portion of pterygoids : (0)=no, (1)=yes.
43. High *dorsum sellae,* not concealing posterior portion of *sella turcia* : (0)=no, (1)=yes.
44. Single rod-like ossification of *rostrum basisphenoidale* : (0)=absent, (1)=present.
45. Ossification of *rostrum basisphenoidale* reduced : (0)=no, (1)=yes (ossification lost in *Dermochelys*).
46. *Foramen caroticum laterale* much larger than *foramen anterius canalis carotici interni* : (0) no ; (1) yes.
47. *Foramen caroticum laterale* confluent with *canalis cavernosum* : (0)=no, (1)=yes.

Lower Jaw

48. Lower triturating surface of dentary enlarged, with symphysis extending along more than one third of entire jaw length : (0)=no, (1)=yes (Zangerl, 1971).
49. Hooked dentary : (0)=absent, (1)=present.
50. Symphyseal ridge of dentary : (0)=absent, (1)=present (Gaffney, 1979).
51. High symphyseal ridge of dentary exposed from lateral beyond labial ridge* : (0)=absent, (1)=

present.

52. Denticulated lingual ridge of dentary: (0)= absent, (1)=present.
53. Lingual ridge of dentary higher than labial ridge* : (0)=no, (1)=yes.
54. Lingual ridge of dentary: (0)=present, (1)= reduced and lost (Gaffney, 1979).
55. *Foramen dentofaciale majus* anterior to lower jaw symphysis: (0)=no, (1)=yes (Zangerl, 1971).
56. Surangular process extending anteriorly onto dentary: (0)=absent, (1)=present.
57. Coronoid and articular ossification: (0)=present, (1)=lost.
58. Splenial: (0)=present, (1)=lost (Gaffney, 1979).

Axial Skeleton

59. Cervical rib: (0)=present, (1)=lost (Gaffney et al., 1991).
60. Transverse process of cervicals: (0)=double, (1)=single (Gaffney, 1985a).
61. Central articulation of cervicals formed: (0)=no, amphicoelous or platycoelous, (1)=yes, concavo-convex (Gaffney and Meylan, 1988).
62. Proportion of cervical central articulation: (0)=as high as wide thoroughout cervicals, (1)=much wider than high at posterior cervicals (Williams, 1950).
63. Posterior cervicals with thin ventral keel: (0)= absent, (1)=present (Meylan and Gaffney, 1989).
64. Biconvex centrum of anterior cervicals: (0)= absent, (1)=4th cervical, (2)=3rd or 2nd cervical (Williams, 1950).
65. 8th cervical: (0)=amphicoelous, (1)=procoelous, (2)=biconvex, (3)=opistocoelous (Williams, 1950 ; Meylan and Gaffney, 1989).
66. 8th cervical centrum much shorter than its neural arch and 7th centrum: (0)=no, 8th centrum as long as its neural arch and 7th centrum, (1)=yes (Zangerl, 1953).
67. Double cervical central articulation between 7th and 8th cervicals: (0)=absent, (1)=present.
68. Double cervical central articulation between 6th and 7th cervicals: (0)=absent, (1)=present (Williams, 1950).
69. Double cervical central articulation between 5th and 6th cervicals: (0)=absent, (1)=present (Williams, 1950).
70. Platycoelous cervical central articulation between 6th and 7th cervicals: (0)=absent, (1)=present.
71. Anterior central articulation of first thoracic vertebra: (0)=facing anteriorly, (1)=facing ventrally or anteroventrally.
72. First thoracic rib: (0)=distal ends extending beyond nuchal, (1)=distal ends limited within nuchal width (Rieppel, 1980 ; Gaffney and Meylan, 1988).
73. 10th thoracic rib: (0)=reaching 8th pleural, (1)= free from carapace (Meylan and Gaffney, 1989).
74. Chevrons: (0)=present, (1)=lost (Gaffney and

Meylan, 1988).
75. Opistocoelous caudal: (0)=absent, (1)=present.
76. Procoelous caudal: (0)=absent, (1)=present only within anterior portion, (2)=all caudals procoelous (Gaffney and Meylan, 1988).

Appendicular Skeleton

77. Coracoid: (0)=shorter than humerus, (1)=as long as humerus, (2)=much longer than humerus.
78. Elongate coracoid thickened, showing coulm-like appearance: (0)=no, flattened, (1)=yes.
79. Scapular angle formed by scapular prong and acromion: (0)=about 90°, (1)=exceeding over 110°.
80. Lateral process of pubis or pectineal process: (0)=restricted posteriorly to medial portion of pubis, (1)=enlarged, projecting anteriorly beyond medial portion of pubis.
81. *Thyroid fenestra*: (0)=small, subdivided, (1)= huge, confluent.
82. Lateral process of ischium or metischial process: (0)=prominent, as wide as whole iscium, (1)= reduced, often rudimentary.
83. Iliac blade: (0)=nearly straight, (1)=elongate, with medial curvature.
84. Large pelvic girdle, nearly touching coracoids: (0)=no, distant from coracoids, (1)=yes.
85. Humerus: (0)=shorter than femur, (1)=longer than femur.
86. Location of lateral process of humerus: (0)=at level of *caput humeri,* (1)=distal to caput humeri, (2)=at middle of humeral shaft (Walker, 1973).
87. Shoulder of *caput humeri* : (0)=present, (1)=lost (Hirayama, 1992).
88. Lateral process of humerus enlarged into V-shaped structure: (0)=no, (1)=yes.
89. Lateral process of humerus enlarged within the anterior portion of shaft, not well visible from ventral view: (0)=no, (1)=yes.
90. A median concavity of lateral process of humerus: (0)=absent, (1)=present.
91. Elongate lateral process of humerus, extending into prominent anterior projection: (0)=no, (1)= yes.
92. Ectepicondylar portion of humerus much enlarged anteriorly: (0)=no, (1)=yes.
93. Ulna-radius contact through prominent distal rugosities: (0)=absent, (1)=present.
94. Radius with middle portion bent toward anterior: (0)=no, nearly straight, (1)=yes.
95. Carpal and tarsal elements flattened, with restricted joint surfaces: (0)=no, (1)=yes.
96. Elongate 3rd to 5th digits of manus and pes, without movable articulation: (0)=no, all movable articulation retained, (1)=yes.
97. Movable articulation of first and second digits: (0)=retained, (1)=lost.
98. Femoral trochanters: (0)=separated by notch, (1)=connected by bony ridge.

99. Major trochanter of femur : (0)=as high as or slightly higher than minor trochanter, (1)=much higher than minor trochanter (Hirayama, 1992).
100. Pit on tibia for *M. pubi-tibialis* and *M. flexor tibialis internus* : (0)=absent, (1)=present (Zangerl, 1980).

Carapace

101. Scute sulci on carapace : (0)=present, (1)= remained only at neural and marginal area, (2)= entirely lost.
102. Nuchal with prominent anterior emargination : (0)=absent, (1)=present.
103. Nuchal with ventral knob to which the neural arch of 8th cervical attaching : (0)=absent, (1)=present.
104. Posterior nuchal fontanelles : (0)=absent, (1)= present.
105. Cervical scute : (0)=narrower than 1st vertebral scute, (1)=as broad as first vertebral, preventing contact between first vertebral and first marginal (Hirayama, in press).
106. Neurals thickened and keeled : (0)=no, (1)=yes.
107. Epineural elements between neurals : (0)= absent, (1)=present.
108. Number of neurals* : (0)=eight or less, (1)=nine by splitting of 8th or 7th neurals, (2)=more than ten.
109. Neural shape : (0)=mostly hexagonal, short-sided in anterior, (1)=mostly hexagonal, equally sided, (2)=mostly rectangular (Hirayama, in press).
110. Neural series : (0)=complete, (1)=reduced and lost at posterior portion, (2)=entirely lost.
111. Suprapygal* : (0)=subdivided into two or three, (1)=single.
112. pleural reduction : (0)=lost in adult, (1)=partially present, (2)=developed less than halfway to the edge of costal ribs, (3)=entirely lost (Hirayama, 1995).
113. Epithecal ossification of carapace : (0)=absent, (1)=present.
114. peripherals : (0)=present, (1)=lost.
115. prominent undulation along medial border of peripherals between costal ribs : (0)=absent, (1)= present.
116. peripherals with prominent lateral serration : (0)= absent, (1)=present (Zangerl, 1953).
117. 9th costal separated from 8th costal : (0)= absent, (1)=present (Zangerl, 1953).
118. Suprapygal-pygal contact : (0)=present, (1)=lost.

Plastron

119. Scute sulci on plastron : (0)=present, (1)=lost or rudimentary (Zangerl, 1953).
120. Axillary buttress : (0)=reaching only peripheral, or connected with carapace by ligament, (1)=reaching 1st pleural (Meylan and Gaffney, 1989).
121. Inguinal buttress : (0)=reaching only peripheral, or connected with carapace by ligament, (1)= reaching 5th pleural, (2)=reaching 5th and 6th pleural (Hirayama, 1985).
122. Medial connection of hyo-hypoplastra* : (0)= sutured, (1)=ligamentous.
123. plastral index (ratio between length and width of plastral bridge) : (0)=more than 100, (1)=between 100 and 60, (2)=less than 60 (Zangerl, 1953).
124. Star-shaped hyo-hypoplastra : (0)=absent, (1)= present.
125. Fontanelle between hyo-hypoplastra : (0)= absent, (1)=smaller than hyo-, or hypoplastron, (1)=as large as hyo, or hypoplastron, (2)=huge, remaining rudimentary hyo-hypoplastra.
126. Dorsal process of epiplastra : (0)=present, (1)= lost (Gaffney and Meylan, 1988).
127. Narrow, blade- like epiplastron : (0)=absent, (1)= present (Zangerl, 1953).
128. Narrow, elongate entoplastron : (0)=absent, (1)= present (Zangerl, 1953).
129. Entoplastron : (0)=connected with hyoplastra by suture, (1)=connected with hyoplastra by ligament (Zangerl, 1953).
130. Epi-entoplastra fused, T-shaped : (0)=no, epientoplastra separated, (1)=yes.
131. Entoplastron : (0)=present, (1)=lost.
132. Narrow, blade-like xiphiplastra : (0)=no, (1)=yes (Zangerl, 1953).
133. Medial contact between xiphiplastra : (0)=developed along its whole length, (1)=much reduced or lost (Zangerl, 1953).
134. Direction of xiphiplastron : (0)=nearly straight, extending posteriorly, (1)=curved toward medial (Zangerl, 1953).
135. Mesoplastron : (0)=present, (1)=lost (Gaffney and Meylan, 1988).

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Permian fusulinaceans from the Akuda and Horikoshitoge Formations, Hachiman town, Gifu Prefecture, Central Japan

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Abstract. Thirty-seven species belonging to 16 genera of fusulinaceans are discriminated from the Akuda and Horikoshitoge Formations, exposed in Hachiman town, Gifu Prefecture, Central Japan. Among them, the following six species are newly proposed: *Sphaerulina akudensis, Dunbarula uenoi, Schwagerina shukoae, S. kanumai, Pseudofusulina minoensis,* and *P. miyamensis.* This fusulinacean fauna is similar in composition to that described from the Nyukawa Group exposed about 60 km northeast of the present area, and indicates the Yakhtashian to Kubergandian of the standard stratigraphic scheme of the Tethyan Province.

Key words : Akuda Formation, fusulinaceans, Horikoshitoge Formation, Mino Terrane, Permian

Introduction

The study area is located in Hachiman town, Gujyo County, Gifu Prefecture, Central Japan. This area belongs to the northern part of the Mino Terrane of the Inner Zone of Southwest Japan, and is underlain by Jurassic clastic sedimentary rocks. The strata consist of turbidites and olistostromes that commonly include allochthonous blocks of chert, limestone, and greenstone of various age, shape, and size. The chert blocks yield Triassic conodonts and radiolarians. The limestone blocks are commonly fossiliferous and yield calcareous algae, fusulinaceans, and conodonts that suggest an Early to Middle Permian age.

Kanuma (1958a, b, 1959, 1960) extensively studied this area and divided the strata into four formations, namely, the Akuda, Kuchibora, Kayukawa, and Shimadani Formations in ascending order. The Akuda and Kuchibora Formations consist mainly of white to pale gray massive limestone and black bedded limestone, respectively. The Kayukawa Formation consists mainly of clastic sedimentary rocks. The Shimadani Formation is composed of bedded chert. Kanuma (1958a, b) described late Early Permian fusulinaceans collected from the limestone of the Akuda Formation.

Subsequently, Yoshida (1972) studied the structural geology of this area and analyzed some complicated folding structures. I restudied this area and discovered many Triassic conodonts from cherts of the Kayukawa and Kuchibora Formations (Hh. Igo, 1979) and provided new information concerning the geologic age of these formations. Furthermore, I confirmed that the cherts are allochthonous blocks or sheets embedded in both formations.

Wakita (1984) made regional mapping in the Hachiman area and pointed out that Jurassic clastic sedimentary rocks are extensively distributed in this area, intercalating allochthonous blocks of various kinds of sedimentary rocks. Moreover, these blocks show various sizes and ages. He subdivided the Jurassic rocks into five such units, the Nabigawa, Kodaragawa, Kajika, Furumichi, and Samondake Formations. Concerning the limestone of the Akuda Formation, he showed that it is a huge allochthonous block embedded in the Nabigawa Formation and it is designated as the Akuda Block.

I continued investigation of this area and reported a mixed conodont fauna preserved within fissure-filling deposits in the limestone of the Akuda Block (Hh. Igo, 1989). Furthermore, I discussed the origin of this mixing related with the sedimentary environment of the Akuda Limestone. Recently, Horibo (1990) documented the petrography of limestones which belong to the Akuda and Horikoshitoge Formations, and discussed their depositional environments.

During my consecutive field survey in the Hachiman area, I have collected many limestone samples from the Akuda and Horikoshitoge Formations in which abundant fusulinaceans are contained. Paleontological study of the samples elucidates that the fusulinaceans are similar to hitherto described species from allochthonous limestones embedded in the accreted Jurassic sedimentary rocks in the Mino Terrane, Central Japan. The purpose of the present paper is to describe the fusulinaceans in these two formations and to discuss the age and similarities of the fauna with that reported from other allochthonous limestones in the Mino Terrane. I discriminate a total of 37 species of

fusulinaceans belonging to 16 genera in this study, among which six species are new to science and four species left in open nomenclature.

Geologic setting

The Akuda Block of Wakita (1984) is an informally designated rock unit of limestone previously treated as a formation, the Akuda Formation (Kanuma, 1958, etc. ; Hh. Igo, 1989). Recently, Horibo (1990) restudied Wakita's Akuda Block based on the limestone petrography and analysis of biofacies. He subdivided the Akuda Block into the Akuda (s.s) and Horikoshitoge (newly designated) Formations by their lithic characters. Furthermore, Horibo showed that these formations are almost coeval but that the former was deposited in lagoons or sand bars while the latter accumulated in the marginal part of the bank. The two formations are now in fault contact.

In the present study, I follow Horibo's newly proposed definition of the Akuda and Horikoshitoge Formations. The Akuda Formation constitutes the main part of the Akuda Block, which is about 1.7 km in width and 12 km in lateral extent. It strikes E-W and dips 80° to 90°S or N. According to my observations, the Akuda Formation consists mainly of white to pale gray massive and thick-bedded limestones including limestone conglomerate and calcarenite, and variegated greenstones and volcaniclastics. The total thick-
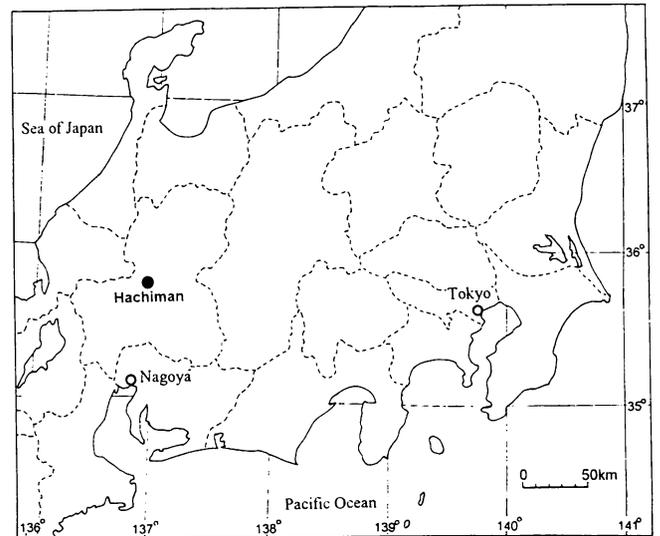
Figure 1. Index map of Hachiman town, Gujyo County, Gifu Prefecture.

ness of this formation was estimated to be 550 m by Hh. Igo (1989) and 500 m by Horibo (1990). The Akuda is well exposed along the roadcut from Nishi-Akuda to Akuda-
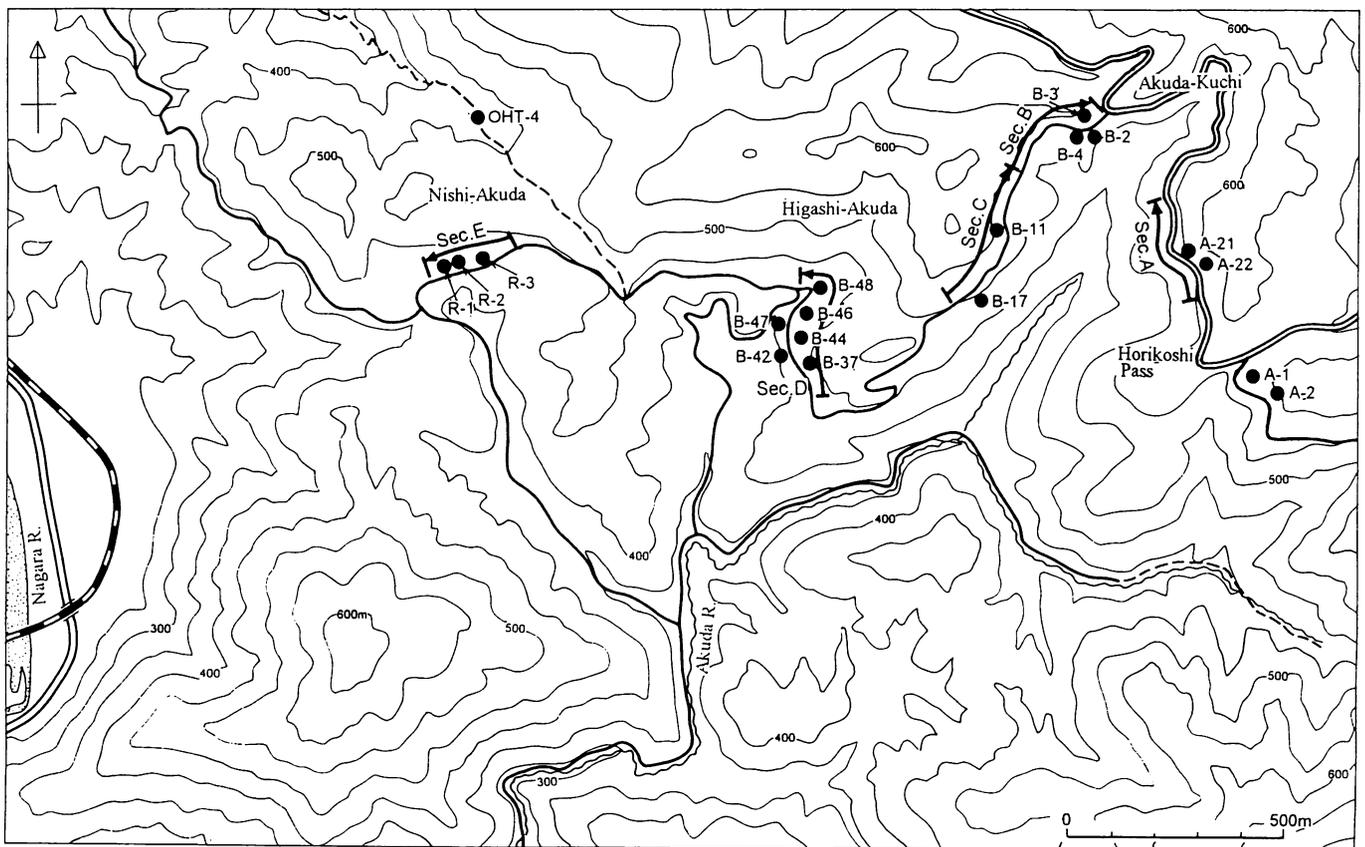
Figure 2. Map showing fusulinacean localities.

Kuchi (Sections B, C, E) and north of the Horikoshi Pass (Section A). Limestones in the Sections B and E are mostly pale gray to white and massive. Limestones along the Section C (B-17, B-11) are bedded and mostly dark gray with brownish tints.

Intercalations of limestone conglomerate (Horibo's limestone-breccia) are characteristic lithofacies of the Akuda Formation. This conglomerate consists of various-sized angular clasts of limestone and dolostone cemented with ill-sorted lime mud, lime sand, and red hematitic clay. The other type of conglomerate is volcanic conglomerate exposed along the roadcut at Nishi-Akuda (R-1). Limestone clasts of the conglomerate are commonly rounded and of boulder size cemented with variegated tuff.

The Horikoshitoge Formation at Higashi-Akuda consists mainly of gray to dark gray bioclastic bedded limestone, and attains a thickness of about 200 m. Along the Section D, limestones (B-37 to B-48) show typical lithology of the Horikoshitoge and their microfacies are lime mud/wacke-
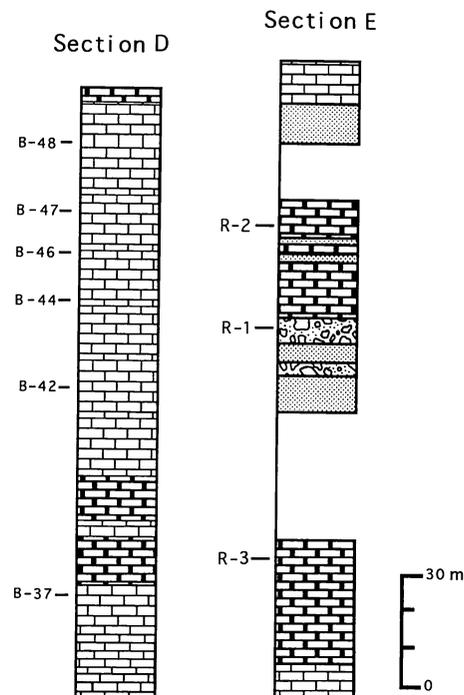
Figure 4. Geologic columns of the measured section with indications of fusulinacean-bearing levels. Section D is located near Nishi-Akuda; Section E is located at Higashi-Akuda refer to Figure 2. For lithologic symbols see Figure 3.

Figure 3. Geologic columns of the measured section with indications of fusulinacean-bearing levels. Section A is located north of the Horikoshi Pass; Sections B and C are located west of Akuda-Kuchi refer to Figure 2.

stone. These limestones yield abundant fusulinaceans.

Fusulinaceans from the Akuda and Horikoshitoge Formations

Volcanic conglomerate crops out at Nishi-Akuda (R-1) and abundantly includes limestone clasts containing well-preserved fusulinaceans. This conglomerate is assumed to be equivalent with limestone-breccia in the upper part of the Column B (Section 71) of Horibo (1990). This breccia occupies the upper part of the middle division of the Akuda Formation. The following fusulinaceans are discriminated from R-1: *Pseudoreichelina* sp., *Pamirina* (*Levenella*) *leveni* Kobayashi, *P.* (*L.*) *evoluta* Sheng and Sun, *Nankinella* sp., *N.* aff. *kotakiensis* (Fujimoto and Kawada), *Sphaerulina akudensis* Hh. Igo sp. nov., *Schubertella pseudoobscura* Chen, *Neofusulinella giraudi* Deprat, *Schwagerina shukoae* Hh. Igo sp. nov., *S. higashidaniensis* Hy. Igo, *S. kanumai* Hh. Igo sp. nov., *Pseudofusulina minoensis* Hh. Igo sp. nov., *P. miyamensis* Hh. Igo sp. nov., *P. regularis* (Schellwien), *P. houziguanica* Sheng, and *P.* sp. Massive limestone (R-2) situated about 30 m above R-1 yields *P. regularis* (Schellwien) and *Chalaroschwagerina* aff. *chinensis* (Chen). A single species, *S. kwangchiensis* Chen, was obtained from R-3 situated about 60 m below R-1.

Although the actual stratigraphic position is uncertain, I collected some samples from limestones exposed south of the Horikoshi Pass (A-1, A-2). These samples may repre-

sent the lower part of the Akuda Formation and contain *Pseudofusulina norikurensis* Hy. Igo and *P. paratschernyschewi* Kanuma. Collections were also made along the roadcut (Section A) north of the Horikoshi Pass. Limestones situated in the lower part of this section (A-21, A-22) yield *Neofusulinella lantenoisi* Deprat, *Minojapanella (M.) elongata* Fujimoto and Kanuma, *Dunbarula uenoi* Hh. Igo sp. nov., *Pseudofusulina horadaniensis* Hy. Igo, *Maklaya pamirica* (Leven), *M. saraburiensis* Kanmera and Toriyama, and *Armenia* sp.

Limestone samples were collected along the Section B, about 300 m north of the above-mentioned localities. They are at levels B-2, B-3, and B-4 and yield *Schwagerina shukoae* Hh. Igo sp. nov., *Acervoschwagerina fujimotoi* Kanuma, and others. Massive limestone in the lower part of the Section C (B-1) includes *Parafusulina ? sublineata* Hy. Igo and thickly bedded limestone in the upper part of this section yields *Parafusulina sotensis* Hy. Igo and others (B-11).

A single species, *Pseudofusulina krafft i* (Schellwien), was collected from a white massive limestone exposed at OHT-4, upstream of the Otohime-tani Valley, north of Nishi-Akuda.

I collected abundant fusulinacean specimens from thin-bedded limestones (B-37, B-42, B-44, B-46, B-47, B-48) exposed at Higashi-Akuda (Section D). These limestones are equivalent with the lower member of the Horikoshitoge Formation (Column A, section 59 of Horibo, 1990). The following fusulinaceans are discriminated from these levels : *Pamirina (Levenella) evoluta* Leven, *Neofusulinella giraudi* Deprat, *Toriyamaia laxiseptata* Kanmera, *Schwagerina muraii* Morikawa, *Pseudofusulina norikurensis* Hy. Igo, *P. paratschernyschewi* Kanuma, *P. horadaniensis* Hy. Igo, *P. isomiae* Hy. Igo, *P. duplithecata* Hy. Igo, *P. regularis* (Schellwien), *P. krotowi* (Schellwien), and others.

As already mentioned, the Akuda and Horikoshitoge Formations are a huge allochthonous block embedded in Jurassic rocks, and the detailed internal structure of this block is unclear. I measured several sections to collect fusulinaceans, but these specimens do not provide enough biostratigraphic value, and even the local correlation among measured sections is difficult. Fusulinaceans discriminated in this study, however, indicate that the formations are almost coeval as already pointed out by Horibo (1990).

The present fusulinacean fauna is characterized by species of *Pseudofusulina* with a large cylindrical shell, thick spirotheca, and dense axial filling. Characteristic *Schwagerina* species with a fusiform shell of medium size, thin spirotheca, and delicate septa are also important representatives. A similar schwagerinid but with an elongate shell identified to *Parafusulina* with reservations, is also characteristic. Although its occurrence is rare, the presence of *Acervoschwagerina* in this fauna is noteworthy. The fauna also contains *Neofusulinella, Sphaerulina, Schubertella, Minojapanella, Nankinella,* and other small fusulinaceans. The mentioned faunal characters are common features in the fauna reported from the upper Lower Permian (Yakhtashian) of the Tethyan Realm. The present fauna excludes typical *Parafusulina* species except for *Parafusulina sotensis* and species of *Misellina,* which are good indicators of the

Bolorian, are also lacking.

In the Section A, limestones of two different levels yield two species of *Maklaya,* and an unidentified species of *Armenia* in association with *Neofusulinella* and others. These levels may occupy higher levels than those of the aforementioned species and are correlated with the middle Middle Permian (Kubergandian).

The Jurassic accreted terrane, the Mino Terrane, in Central Japan commonly includes various-sized Upper Paleozoic limestones. Previous to our recognition of accreted terrane schemes, these limestones had long been considered to be autochthonous strata which were deposited in the shallow carbonate shelf, bank, reef, and other marine geosynclinal environments. Fusulinaceans of these limestones were studied by many specialists in the Lake Biwa area (Morikawa and Isomi, 1961), Akasaka Limestone (Ozawa, 1927, Morikawa, 1958, etc.), Ibuki Limestone (Kobayashi, 1957), Yoganeyama Limestone (Sashida, 1980), Hachiman area (Kanuma, 1958a, etc.), Nyukawa Group (Hy. Igo, 1964, etc.), Shirahone Limestone (Choi and Fujita, 1970), and others. There are other fusulinacean-bearing limestones in the Mino Terrane of Central Japan such as the Fujiwaradake, Ryozen, and Funafuseyama Limestones. Fusulinaceans contained in these limestones have not yet been fully studied, but the present fauna is similar to the fauna described from the Shiroi, Kono, and lower Sote Formations of the Nyukawa Group (Hy. Igo, 1964, 1965) exposed about 60 km northeast of the present area.

Systematic paleontology

Order Foraminiferida Eichwald, 1830
Suborder Fusulinina Wedekind, 1937
Superfamily Fusulinacea von Möller, 1878
Family Staffellidae Miklukho-Maklay, 1949
Genus **Pseudoreichelina** Leven, 1970

Type species.—*Pseudoreichelina darvasica* Leven, 1970

Pseudoreichelina sp.

Figures 10-15—20

Materials.—Axial section, TGUFU 1086 ; tangential sections, TGUFU 1084, 1085, 1087, 1089 ; sagittal section, TGUFU 1088.

Remarks.—The present specimens are mostly recrystallized and the spirothecal structure and other specific characters are obliterated. The shape of septa in the last uncoiled volution of the specimens indicates assignment to the genus *Pseudoreichelina.*

Occurrence.—All specimens collected from R-1 in Section E of Nishi-Akuda.

Genus **Pamirina** Leven, 1970 emend. Kobayashi, 1977

Type species.—*Pamirina darvasica* Leven, 1970
Subgenus *Levenia* Ueno, 1991
Subgenus **Levenella** Ueno, 1994

Type species.—Pamirina leveni Kobayashi, 1977

Pamirina (Levenella) leveni Kobayashi, 1977

Figures 11-20—31

Pamirina leveni Kobayashi, 1977, p. 11-14, pl. 1, figs. 13-38.
Pamirina (Levenia) leveni Kobayashi. Ueno, 1991, p. 746, 747, figs. 3-8—23.
Pamirina (Levenella) leveni Kobayashi. Ueno, 1994, p. 405.

Materials.—Axial sections, TGUFU 1110, 1111, 1112, 1113, 1114, 1115, 1116, 1117, 1120, 1121 ; sagittal sections, TGUFU 1118, 1119.

Remarks.—Ueno (1991) proposed the subgenus *Levenia*, which is characterized by a finer alveolar keriotheca than that of *Pamirina*. Subsequently, Ueno (1994) revised the genus name *Levenia* to *Levenella*. The Akuda specimens quite agree with the original ones described by Kobayashi (1977) from the Hanagiri Limestone and Otaki, Saitama Prefecture, Central Japan.

Occurrence.—All specimens collected from R-1 in Section E of Nishi-Akuda.

Pamirina (Levenella) evoluta
Sheng and Sun, 1975

Figures 11-32—34

Pamirina ? evoluta Sheng and Sun, 1975, p. 46, pl. 1, fig. 15.
Pamirina (Levenella) evoluta Sheng and Sun. Ueno, 1991, p. 747, 748, figs. 4-1—8.

Materials.—Axial sections, TGUFU 1122, 1123, 1124.

Remarks.—Recently, this species has been fully described by Ueno (1991) on the materials from the Akiyoshi Limestone Group. It has a larger proloculus than *P. (L.) leveni*. The specimens referable to this species are very rare in my collections.

Occurrence.—TGUFU 1122 from B-47 in Section D near Higashi-Akuda ; TGUFU 1123, 1124 from R-1 in Section E of Nishi-Akuda.

Family Staffellidae Miklukho-Maklay, 1949
Genus Nankinella Lee, 1934

Type species.—Staffella discoides Lee, 1931

Nankinella sp.

Figure 11-16

Material.—Tangential section, TGUFU 1106.

Remarks.—The present specimen is completely recrystallized and the inner structure of the shell is obscure, but the angular periphery and umbilicated axial areas indicate assignment to the genus *Nankinella*.

Occurrence.—One specimen from R-1 in Section E of Nishi-Akuda.

Nankinella aff. kotakiensis
(Fujimoto and Kawada, 1953)

Figures 11-17—19

Compare.—
Hayasakaina kotakiensis Fujimoto and Kawada, 1953, p. 119-121, figs. 1-10 ; Hy. Igo, 1956a, p. 172, 173, pl. 27, figs. 1, 6, 12-16.
Nankinella kotakiensis (Fujimoto and Kawada). Kanmera, 1958, p. 208-210, pl. 28, figs. 9-13.

Materials.—Axial sections, TGUFU 1107, 1108, 1109.

Description.—Shell very small, discoidal, subspherical with somewhat broadly rounded periphery. Mature shell consists of seven to eight volutions. In two specimens, axial length 1.83 to 1.86 mm, median width 1.83 to 1.86 mm, and form ratio 0.716 to 0.749.

Shell mostly recrystallized. Inner four volutions discoidal and planispiral having slightly angular periphery. Spirotheca thin, consisting of a tectum and recrystallized translucent layer. Proloculus very small and spherical. Chomata present in inner three to four volutions.

Remarks.—The present specimens closely resemble the type specimens of *Nankinella kotakiensis*, but the former differs from the latter in more angular periphery in inner volutions. *Nankinella orientalis* Miklukho-Maklay resembles the present specimens but differs from the latter in fewer volutions. *Nankinella inflata* (Colani) also resembles the present specimens but the former has a large shell and more angular periphery in inner volutions.

Occurrence.—All specimens from R-1 in Section E.

Genus Sphaerulina Lee, 1933

Type species.—Sphaerulina crassispira Lee, 1933

Sphaerulina akudensis Hh. Igo sp. nov.

Figures 11-9—14

Materials.—Axial section of holotype, TGUFU 1099 ; axial section of paratype, TGUFU 1104 ; tangential sections, TGUFU 1100, 1101 ; sagittal sections, TGUFU 1102, 1103.

Diagnosis.—Small *Sphaerulina* with an inflated oval shell, thick wall, fewer volutions, and unfluted septa.

Description.—Shell small, discoidal, and subspherical with slightly umbilicated axial regions and rounded periphery. Mature shell having six volutions, 1.03 mm in axial length, 1.40 mm in median width, and form ratio 0.736 in holotype.

Inner two volutions tightly coiled and have narrowly rounded periphery. Outer volutions expand rather rapidly. Radius vectors of holotype in first to sixth volutions 0.08, 0.15, 0.25, 0.38, 0.53, and 0.73 mm respectively. Proloculus very small, spherical, and having external diameter of 0.075 mm in holotype.

Spirotheca rather thick compared with shell size. It consists of a tectum and recrystallized dark calcite layer. In spirotheca of outer volutions except last volution appears a diaphanotheca-like transparent layer. Septa rather thick, plane, and having a lighter calcite layer than that of spirotheca. Chomata low, small, and asymmetrical.

Table 1. Measurements of *Sphaerulina akudensis* Hh. Igo sp. nov. (in mm)

Reg. no.		Fig.	L.	W.	F.R.	D.P.	Radius vector					
							1	2	3	4	5	6
1	TGUFU1099	11- 9	1.03	1.40	0.74	0.08	0.08	0.15	0.25	0.38	0.53	0.73
2	TGUFU1100	11-10	0.93	1.40	0.66	?	?	0.09	0.28	0.38	0.53	0.73
3	TGUFU1102	11-12	---	1.50	---	0.20	0.13	0.18	0.28	0.43	0.60	---
4	TGUFU1103	11-13	---	1.03	---	0.06	0.08	0.15	0.24	0.36	0.50	---
5	TGUFU1104	11-14	0.68	0.83	0.82	0.06	0.08	0.14	0.23	0.30	0.45	---

	Thickness of spirotheca					
	1	2	3	4	5	6
1	?	?	0.02	0.02	0.05	0.05
2	?	?	?	0.05	0.06	0.08
3	?	0.02	0.03	0.05	0.04	---
4	0.02	0.02	0.04	0.05	0.03	---
5	?	?	0.02	0.03	0.04	---

Remarks.—This new species resembles a species hitherto described as a *Pamirina*, but the former has a larger shell and thicker spirotheca than the latter. Recently, Hy. Igo *et al.* (1993) described *Sphaerulina* cf. *croatica* Kochansky-Devidé from the Wang Saphung Formation of northeastern Thailand. The Thailand species resembles *S. akudensis* but has an inflated shell and distinct chomata.

Etymology.—This species name is derived from a local name of Hachiman town.

Occurrence.—All specimens from R-1 in Section E.

Family Schubertellidae Skinner, 1931
Subfamily Schubertellinae Skinner, 1931
Genus **Schubertella** Staff and Wedekind, 1910

Type species.—*Schubertella transitoria* Staff and Wedekind, 1910

Schubertella pseudoobscura Chen, 1934

Figure 11-15

Schubertella pseudoobscura Chen, 1934, p. 16, 17, pl. 1, figs. 1, 2; Lin, 1984, p. 153, pl. 8, figs. 25, 26.

Material.—Axial section, TGUFU 1105.

Description.—Shell small and almost spherical with slightly umbilicated axial regions. This specimen has four volutions, 0.53 mm in axial length, 0.54 mm in width, and form ratio 0.98. Inner first to second volutions planispiral and coiling at a right angle to axis of outer volutions. Inner two volutions tightly and last one loosely coiled. Proloculus small, spherical, its outside diameter 0.05 mm. Spirotheca thin and composed of a single structureless layer. Chomata low, asymmetrically developed in third volution.

Remarks.—This specimen resembles the type species but the former is larger than the latter.

Occurrence.—One specimen from R-1 in Section E.

Genus **Neofusulinella** Deprat, 1912

Type species.—*Neofusulinella praecursor* Deprat, 1912

Neofusulinella giraudi Deprat, 1915

Figures 11-1—4

Neofusulinella giraudi Deprat, 1915, p. 11, pl. 1, figs. 6-11; Ozawa, 1927, p. 38, figs. 3-6, 16 c, pl. 39, figs. 4-6.
Schubertella giraudi (Deprat). Sheng, 1963, p. 34, 158, 159, pl. 4, figs. 1-9; Kobayashi, 1957, p. 263, 264, pl. 1, figs. 1-5; Kanmera, 1963, p. 88, 89, pl. 12, figs. 8-12; Hy. Igo, 1967, pl. 7, figs. 7, 8; Sashida, 1980, p. 300-302, pl. 34, figs. 7-9; Wang *et al.*, 1981, p. 19, pl. 15, figs. 3, 4; Sun *et al.*, 1983, p. 17, pl. 3, fig. 5; Wang and Tang, 1986, pl. 1, figs. 6, 8; Xiao *et al.*, 1986, p. 73, pl. 1, figs. 3, 10, 15, 24, 25; Zhou, 1991, pl. 2, figs. 13, 14.
Mesoschubertella giraudi (Deprat). Xia, 1994, pl. 18, fig. 6.

Materials.—Axial sections, TGUFU 1090, 1092; slightly oblique axial sections, TGUFU 1091, 1093.

Remarks.—This species resembles *Neofusulinella praecursor* but is easily distinguished from the latter in that its shell is not elongated. Sheng (1963) transferred this species to the genus *Schubertella* based on the general shape, form ratio, and development of chomata. I assign this species to *Neofusulinella* for several reasons. The size of shell in *Schubertella* is smaller than that of *Neofusulinella*. The early stage of *Schubertella* has sharply changed axis of coiling relative to later ones. Chomata of *Neofusulinella* are asymmetrical and highly elongate while *Schubertella* has asymmetrical massive chomata.

Occurrence.—TGUFU 1090 from R-1 in Section E; TGUFU 1091 from B-47; TGUFU 1092, 1093 from B-48 in Section D near Higashi-Akuda.

Neofusulinella lantenoisi Deprat, 1913

Figures 11-5—8

Neofusulinella praecursor Deprat, 1913, p. 41, 42, pl. 7, figs. 23-25; Thompson and Foster, 1937, p. 131, 132, pl. 24, figs. 1-4; Pitakpaivan, 1965, p. 24-26, pl. 1, fig. 16; Leven, 1967, p. 126,

pl. 1, figs. 9, 10 ; Toriyama *et al.*, 1969, p. 28-31, pl. 3, fig. 23, pl. 4, figs. 1-15 ; Xiao *et al.*, 1986, p. 75, pl. 1, figs. 11, 16.

Materials.—Slightly oblique axial section, TGUFU 1095 ; axial sections, TGUFU 1096, 1097, 1098.

Description.—Shell small to medium in size and thickly fusiform with straight axis of coiling and bluntly pointed poles. Mature shell having six volutions, 1.50 to 1.67 mm in axial length, 0.67 to 0.93 mm in width, and form ratio 1.8 to 2.2.

Proloculus small and spherical with outside diameter of 0.04 to 0.05 mm. Inner two volutions planispirally coiled and make a right angle with axis of outer volutions. Spirotheca thin, consists of a tectum, diaphanotheca, and lower thicker layer. Septa thin, numerous, and plane. Chomata developed in third to last volutions, low, massive, and asymmetrical. Septal pore distinct in almost all volutions except for the inner two volutions.

Remarks.—Recently, Li (1985) proposed a new genus *Multiavoella* with the holotype *M. guangxiensis* from the Lower Permian at Chongzuo, Guangxi, South China. *Multiavoella* may be a synonym of *Neofusulinella.*

Toriyama *et al.* (1969) described this species from the Khao Phlong Phrab section, Changwat Sara Buri, central Thailand and discussed the taxonomic status, validity, and the phylogeny of *Neofusulinella.*

Recently, Zhou and Sheng (1993) restudied Permian staffellids and proposed a new concept of classification in these subfamilies. They attributed the genera *Leella, Haoella, Sphaerulina* (in part), and *Caspiella* (in part) to the genus *Neofusulinella.*

Occurrence.—TGUFU 1095, 1097, 1098 from A-22 in Section A ; TGUFU 1096 from A-21 in the same section.

Subfamily Biwaellinae Davydov, 1984
Genus *Toriyamaia* Kanmera, 1956

Type species.—Toriyamaia laxiseptata Kanmera, 1956

Toriyamaia laxiseptata Kanmera, 1956

Figures 10-4, 5

Toriyamaia laxiseptata Kanmera, 1956, p. 252-255, pl. 36, figs. 1-14 ; Sheng, 1963, p. 33, 34, 157, pl. 4, figs. 36, 37 ; Kanmera, 1963, p. 87, 88, pl. 11, figs. 1-4, pl. 19, figs. 8, 9 ; Kanmera and Mikami, 1965, p. 277-279, pl. 46, figs. 9, 10 ; Choi, 1973, p. 20, pl. 2, figs. 8-10 ; Ozawa, 1975, pl. 7, fig. 18 ; Lin *et al.*, 1977, p. 19, pl. 3, fig. 17 ; Kahler and Kahler, 1979, p. 226, 227, pl. 4, fig. 7 ; Zhou *et al.*, 1987, pl. 2, fig. 7 ; Ueno, 1992, p. 1276-1278, figs. 4-1—7.

Materials.—Tangential sections, TGUFU 1073, 1074.

Remarks.—The present specimens closely resemble Kanmera's original ones described from the Kozaki Formation, Kyushu, Japan.

Occurrence.—All specimens from B-48 in Section D.

Family Boultoniidae Skinner and Wilde, 1954
Genus *Minojapanella* Fujimoto and Kanuma, 1953
Subgenus *Minojapanella* Fujimoto and Kanuma, 1953

Type species.—Minojapanella elongata Fujimoto and Kanuma, 1953

Minojapanella (M.) elongata Fujimoto and Kanuma, 1953

Figures 11-37, 38

Minojapanella elongata Fujimoto and Kanuma, 1953, p. 152, pl. 19, figs. 1-11 ; Thompson, 1954, pl. 2, figs. 1-5 (2-3, 5 ; same as pl. 19, figs. 1, 10, 11 of Fujimoto and Kanuma, 1953, p. 152) ; Morikawa and Isomi, 1961, p. 7, pl. 2, figs. 10-15 ; Choi, 1973, p. 14, 15, pl. 1, figs. 8-11 ; Xiao *et al.*, 1986, p. 77, pl. 1, figs. 26, 29 ; Ozawa and Kobayashi, 1990, pl. 8, fig. 7 ; Xia, 1994, pl. 18, fig. 20.
Minojapanella (M.) elongata Fujimoto and Kanuma. Sheng, 1965, p. 565, pl. 1, figs. 1-6, 10-15 ; Kahler and Kahler, 1980, p. 191, pl. 2, fig. 3 ; Ueno, 1992, p. 1278, figs. 4-2—31.

Materials.—Oblique section, TGUFU 1127 ; sagittal section, TGUFU 1128.

Remarks.—The present specimens coincide with the type specimens which were described from a limestone near Hachiman town, Gujyo County, Gifu Prefecture, Central Japan. Fujimoto and Kanuma (1953) did not designate any holotype in their paper, but Thompson (1954) subsequently designated as the holotype the specimen illustrated by Fujimoto and Kanuma in pl. 19, figs. 1a-c ; this specimen is in fact the lectotype, not the holotype (Kahler and Kahler 1966, p. 245). The actual locality of the type specimens was not mentioned in the original paper. Recently, I examined the type specimens ; and confirmed that the lectotype occurred in a limestone exposed at Houshimaru, Wara village, Gifu Prefecture.

Occurrence.—TGUFU 1127 from A-22 ; TGUFU 1128 from A-21 in Section A.

Genus *Dunbarula* Ciry, 1948

Type species.—Dunbarula mathieui Ciry, 1948

Dunbarula uenoi Hh. Igo sp. nov.

Figures 11-35, 36

Materials.—Axial section of holotype, TGUFU 1125 ; axial section of paratype, TGUFU 1126.

Diagnosis.—Elongate *Dunbarula* with a thin wall, and septa only fluted in polar regions.

Description.—Shell small, elongate cylindrical in shape and having a gently bent axis of coiling and broadly rounded polar ends. Juvenile volutions tightly coiled but shell loosely coiled in last volution. Inner first to second volutions at a large angle of coiling to the outer ones. Shell of holotype consists of 5 volutions, 2.13 mm in axial length, 0.43 mm in width, with a form ratio of 4.95. Proloculus small and spherical, its outside diameter 0.02 mm in holotype. Radius vectors of first to fifth volutions in holotype, 0.04, 0.05, 0.07, 0.12, and 0.20 mm, respectively.

Spirotheca thin and composed of a tectum and less dense layer. Thickness of spirotheca of first to fifth volutions of

holotype 0.010, 0.012, 0.025, 0.027, and 0.020 mm, respectively. Septa numerous and strongly fluted in polar regions. Septal pores present near polar regions.

Chomata small and developed in second to fourth volutions.

Remarks.—Skinner and Wilde (1967) redescribed topotypes of *Dunbarula mathieui* Ciry from Tunisia. *Dunbarula mathieui* has broad variations in shape, ranging from ellipsoidal through thickly to slender subcylindrical. The present new species has a characteristic elongate shell. Other biocharacters show that the species is assignable to the genus *Dunbarula*.

Etymology.—This species name is dedicated to Dr. Katsumi Ueno, Assistant Professor of the Institute of Geoscience, University of Tsukuba, for his active research on fusulinaceans.

Occurrence.—All specimens from A-22 in Section A.

Family Schwagerinidae Dunbar and Henbest, 1930
Subfamily Schwagerininae Dunbar and Henbest, 1930
Genus *Schwagerina* Möller, 1877

Type species.—*Borelis princeps* Ehrenberg, 1842

Schwagerina shukoae Hh. Igo sp. nov.

Figures 9-5—7

Materials.—Tangential section of immature specimen, TGUFU 1059; axial section of holotype, TGUFU 1060; slightly tangential axial section of paratype, TGUFU 1061.

Diagnosis.—Small *Schwagerina* with an inflated fusiform shell, small proloculus, regularly fluted septa, and without axial fillings.

Description.—Shell medium in size, tightly coiled, fusiform with an inflated median part and broadly rounded poles. In holotype, axial length 6.98 mm, median width 2.90 mm, and form ratio 2.39. Mature shells consist of 6 volutions.

Spirotheca thin, consists of a tectum and fine alveolar keriotheca. Proloculus small, spherical, with an outside diameter of about 0.02 mm. Septa numerous, highly and regularly fluted throughout shell. Septal folds regular in shape with broadly rounded crest.

Chomata lacking except for poor development on the surface of proloculus. Tunnel single, low, and narrow.

Remarks.—The present new species is characterized by an inflated fusiform shell and regularly fluted septa.

Hy. Igo (1964) proposed *Schwagerina higashidaniensis* from the Shiroi Formation of the Nyukawa Group. He illustrated one axial and one tangential sections and two sagittal sections. The specimen questionably identified by him (pl. 104, fig. 2) probably falls within the present new species.

Etymology.—This species name is dedicated to Dr. Shuko Adachi, Assistant Professor of the Institute of Geoscience, University of Tsukuba, for her active research on Carboniferous to Triassic foraminifers.

Occurrence.—Holotype TGUFU 1060 and tangential section TGUFU 1059 from R-1 in Section E; paratype TGUFU 1061 from B-2 in Section B near Akuda-Kuchi.

Schwagerina muraii Morikawa, 1955

Figure 5-4

Schwagerina muraii Morikawa, 1955, p. 104, 105, pl. 14, figs. 1-4, 13; Hy. Igo, 1965, pl. 29, fig. 1.

Material.—Axial section of mature specimen, TGUFU 1003.

Description.—Shell large, elongate fusiform with bluntly rounded poles. Equatorial part of shell somewhat constricted. This specimen has 6 volutions, and is 9.06 mm in axial length and 2.73 mm in median width, with a form ratio of 3.32. Radius vectors in first to sixth volutions 0.03, 0.48, 0.67, 0.78, 1.17, and 1.47 mm, respectively.

Spirotheca thick, consists of a thin tectum and coarse keriotheca. Thickness of spirotheca in sixth whorl 0.13 mm. Proloculus large, spherical, its outside diameter is 0.42 mm. Septa strongly and regularly fluted throughout shell. Heavy secondary deposition fills in tunnel area and polar regions

Table 2. Measurements of *Schwagerina shukoae* Hh. Igo sp. nov. (in mm)

Reg. no.		Fig.	L.	W.	F.R.	D.P.	Radius vector					
							1	2	3	4	5	6
1	TGUFU1060	9-6	6.93	2.90	2.39	0.20	0.20	0.33	0.53	0.75	1.00	1.27
2	TGUFU1061	9-7	9.19	3.46	2.66	0.27?	0.23	0.37	0.83	1.00	1.43	1.83

	Thickness of spirotheca					
	1	2	3	4	5	6
1	0.03	0.04	0.06	0.06	0.07	0.07
2	0.05	0.05	0.05	0.08	0.10	0.10

Figure 5. 1-3. *Pseudofusulina norikurensis* Hy. Igo, 1 : axial section, TGUFU 1000, 2 : slightly oblique axial section, TGUFU 1001, 3 : axial section of immature specimen, TGUFU 1002. 4. *Schwagerina muraii* Morikawa, axial section, TGUFU 1003. 5-8. *Pseudofusulina paratschernyschewi* Kanuma, 5-7 : axial sections, TGUFU 1004, 1005, 1006, 8 : axial section of immature specimen, TGUFU 1007. 9-11. *Pseudofusulina horadaniensis* Hy. Igo, axial sections, TGUFU 1008, 1009, 1010. All figures ×10.
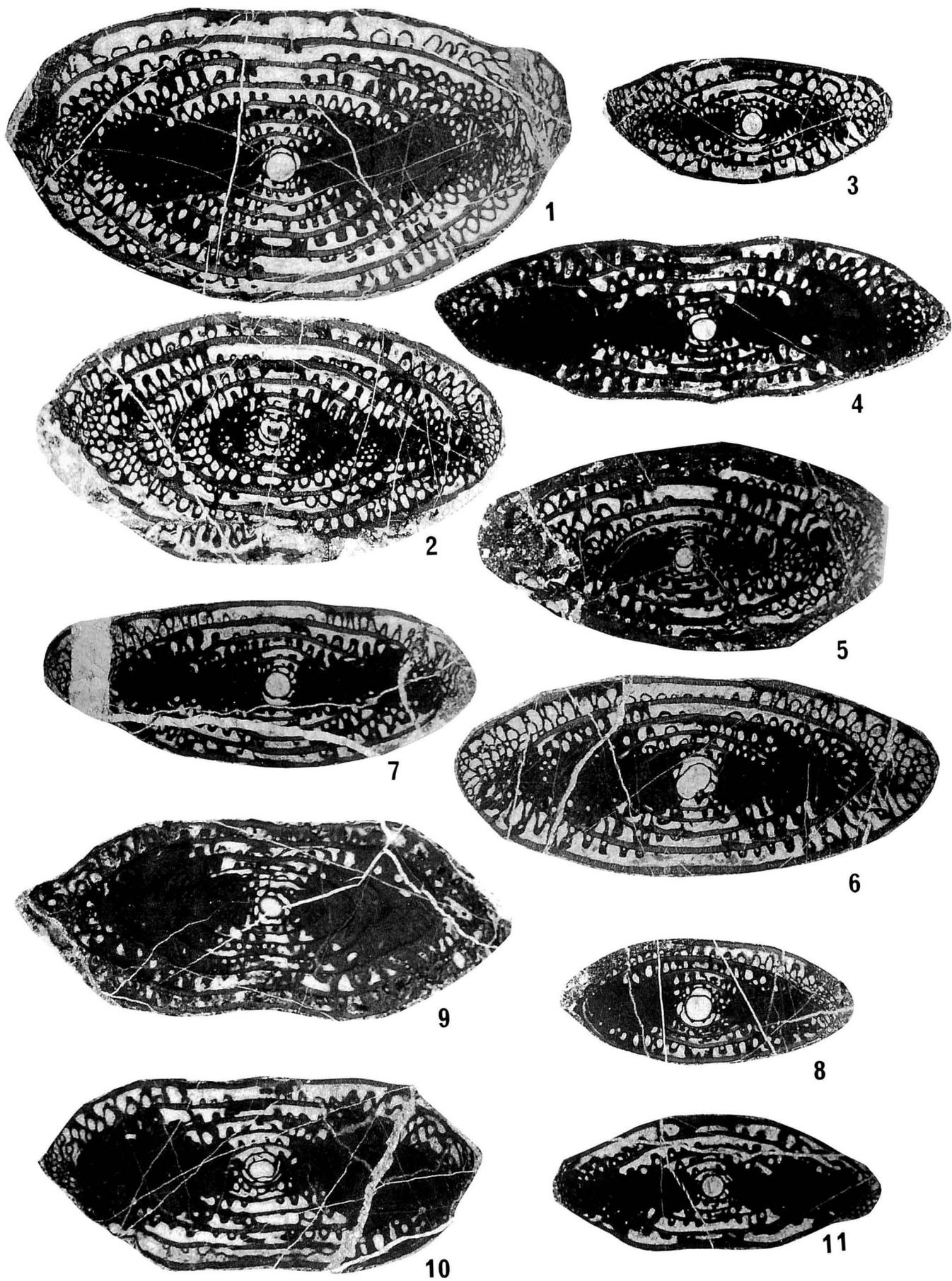
except for outermost whorl. Tunnel low and narrow. Chomata almost absent.

Remarks.—This species resembles *Pseudofusulina fusiformis* (Schellwien) in many respects, but the former differs from the latter in having heavy secondary deposition.

This species was described from the lower Sote Formation of the Nyukawa Group by Hy. Igo (1965). The present specimen is very similar to Igo's Sote specimen. This species also resembles *Pseudofusulina kraffti* (Schellwien), but the former is distinguishable from the latter in its elongate shell, pointed polar ends, and thin spirotheca.

Occurrence.—From B-44 in Section D.

Schwagerina kwangchiensis Chen, 1956

Figures 8-7—9

Schwagerina kwangchiensis Chen, 1956, p. 23, 24, pl. 1, figs. 17, 18; Sheng, 1963, p. 61, 62, 187, 188, pl. 14, figs. 19-21.

Materials.—Slightly oblique axial sections, TGUFU 1043, 1045; axial section, TGUFU 1044.

Description.—Shell medium in size, elongate fusiform to subcylindrical, more or less tightly coiled and having broadly rounded poles. Mature shell with seven volutions, 7.66 mm in length, 2.06 mm in median width, with a form ratio of 3.72.

Proloculus very small, spherical, 0.12 to 0.22 mm in outside diameter. Spirotheca thin, consists of a tectum and keriotheca with fine alveoli. Septa numerous, strongly and regularly fluted throughout shell. Septal folds regularly shaped and closely spaced.

Axial filling very weak in polar regions of younger volutions. Chomata almost lacking and tunnel indistinct.

Remarks.—The present species resembles *Pseudofusulina regularis* (Schellwien), but the former has a smaller proloculus. It also resembles *Pseudofusulina ambigua* (Deprat), but is distinguished from the latter in larger size of shell and proloculus.

The present species was originally described from the Wuhsueh Limestone in Hupeh, China, by Chen (1956). The limestone equivalent with the Maokou Limestone is exposed in southwestern China.

Occurrence.—All specimens from R-3 in Section E.

Schwagerina higashidaniensis Hy. Igo, 1964

Figures 8-16, 17

Schwagerina higashidaniensis Hy. Igo, 1964, p. 644, 645, pl. 104, figs. 1-4.

Materials.—Axial sections, TGUFU 1052, 1053.

Description.—Shell medium-sized, elongate fusiform to subcylindrical with broadly rounded poles and straight axis of coiling. Mature shell has five to six volutions and 6.32 to 8.00 mm in axial length, 1.53 to 1.83 mm in median width, with

a form ratio of 2.27 to 3.45. Inner second to third volutions tightly coiled with sharply pointed poles. Outer fourth to fifth volutions increase in height rather rapidly. Proloculus small, spherical, its outside diameter being 0.16 to 0.17 mm. Spirotheca thin, consists of a tectum and keriotheca with very fine alveoli. Septa numerous, thin, strongly and irregularly fluted. Phrenotheca absent in present specimens. Tunnel singular, low, and indistinct in outer volutions. Chomata present in first to second volutions but lacking outer volutions.

Remarks.—The present specimens coincide with Igo's holotype described from the Siroi Formation, Nyukawa Group. The present species is easily distinguishable from some species of the genus *Paraschwagerina*. The former has irregular septal fluting, but the latter has regular septal fluting. The former has extraordinarily thin spirotheca and septa.

Occurrence.—All specimens from R-1 in Section E.

Schwagerina kanumai Hh. Igo sp. nov.

Figures 9-1—4

Materials.—Axial section of holotype, TGUFU 1055; axial section of paratypes, TGUFU 1056, 1057, 1058.

Diagnosis.—Small *Schwagerina* with an inflated fusiform shell, small proloculus, and thin spirotheca. Septa regularly fluted. Axial filling lacking.

Description.—Shell medium in size, inflated fusiform, and biconical in shape. It has more or less acutely pointed poles and a straight axis of coiling. Mature shell consists of 6 volutions. Axial length 7.86 mm, median width 3.33 mm, and form ratio 2.36 in holotype.

Inner three volutions tightly coiled and outer three volutions increasing rather rapidly in height. Proloculus small, spherical, its outside diameter 0.23 mm in holotype.

Spirotheca thin and composed of a tectum and fine alveolar keriotheca. Thickness of spirotheca of each volution in holotype 0.03, 0.03, 0.03, 0.05, 0.06, and 0.08 mm, respectively. Septa very thin, regularly and intensely fluted. Septal folds across almost entire chamber in outer volutions.

Phrenotheca weak and rarely observed. Chomata almost lacking except for rudimentary ones on the surface of proloculus and first volution.

Remarks.—The present new species is quite similar to *Schwagerina ? annamitica* (Deprat), which was described from the Shiroi Formation, Nyukawa Group by Hy. Igo (1964). The former is distinguished from the latter in highly fluted septa.

Etymology.—This species name is dedicated to Dr. Mosaburo Kanuma, Professor Emeritus of the Department of Astronomy and Earth Sciences, Tokyo Gakugei University. He contributed to early studies of geology and fusulinaceans in the Hachiman area.

Occurrence.—All specimens from R-1 in Section E.

Figure 6. **1-7.** *Pseudofusulina isomie* Hy. Igo, 1, 3-5, 7 : axial sections, TGUFU 1011, 1013, 1014, 1015, 1017, 2 : sagittal section, TGUFU 1012, 6 : axial section of immature specimen, TGUFU 1016. **8, 9.** *Pseudofusulina duplithecata* Hy. Igo, 8 : axial section, TGUFU 1018, 9 : slightly oblique axial section, TGUFU 1019. **10.** *Pseudofusulina kraffti* (Schellwien), axial section, TGUFU 1020. All figures ×10.
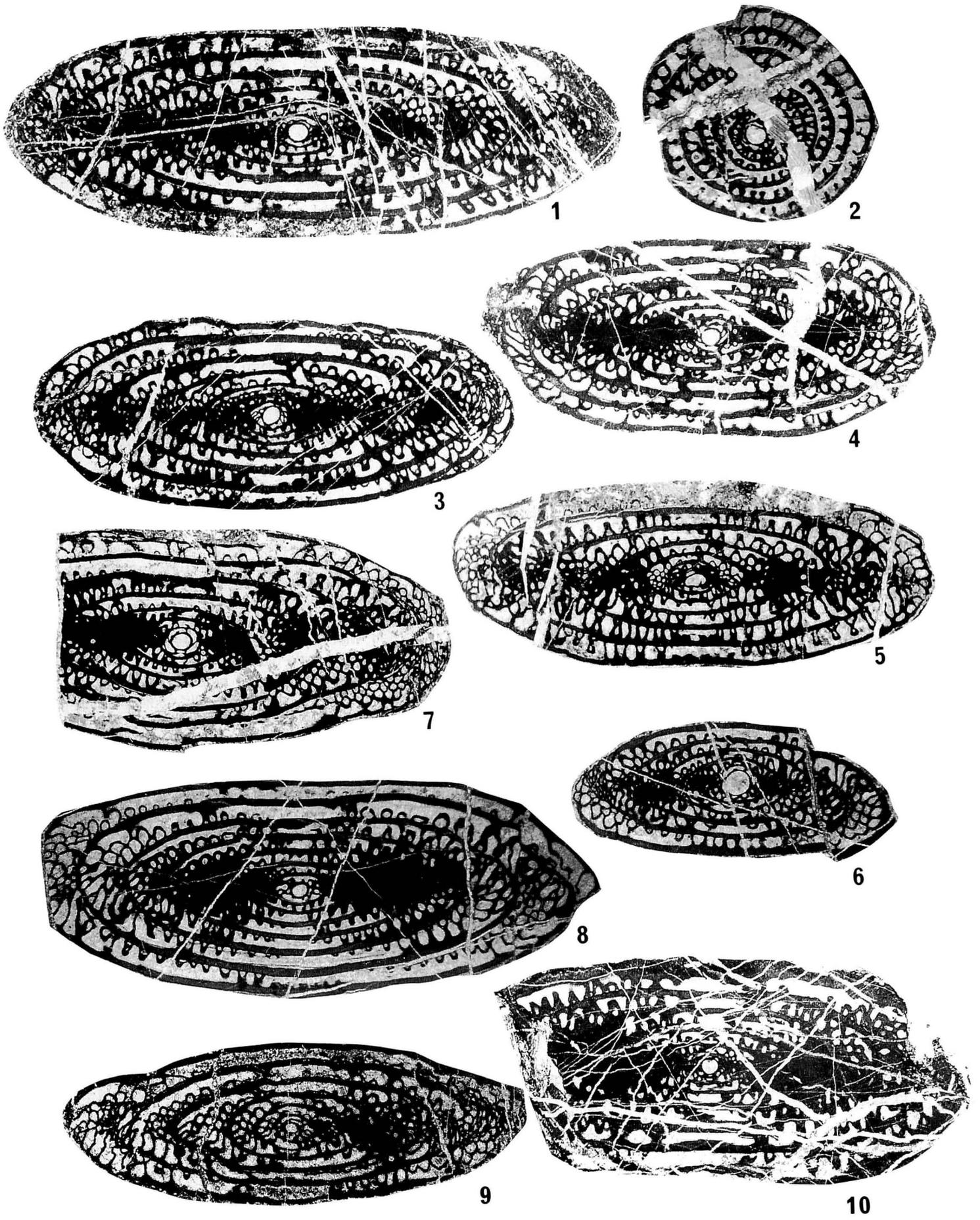
Table 3. Measurements of *Schwagerina kanumai* Hh. Igo sp. nov. (in mm)

Reg. no.		Fig.	L.	W.	F.R.	D.P.	Radius vector					
							1	2	3	4	5	6
1	TGUFU1055	9-1	7.83	3.33	2.36	0.23	0.19	0.30	0.46	1.80	1.23	1.68
2	TGUFU1056	9-2	4.81	1.93	2.50	0.27	0.20	0.31	0.47	0.73	1.71	---
3	TGUFU1057	9-3	4.40	1.83	2.40	0.18	0.17	0.24	0.37	0.57	0.88	---
4	TGUFU1058	9-4	3.92	2.66	1.47	0.27	0.20	0.30	0.47	0.70	---	---

	Thickness of spirotheca					
	1	2	3	4	5	6
1	0.03	0.03	0.03	0.05	0.06	0.08
2	0.03	0.03	0.04	0.03	0.04	---
3	0.01	0.02	0.03	0.05	0.05	---
4	0.02	0.02	0.02	0.04	---	---

Genus *Parafusulina* Dunbar and Skinner, 1931

Type species.—Parafusulina wordensis Dunbar and Skinner, 1931

Parafusulina ? sublineata Hy. Igo, 1965

Figures 9-8—15

Parafusulina sublineata Hy. Igo, 1965, p. 221, 222, pl. 30, figs. 1-3, pl. 32, figs. 1, 2.

Materials.—Axial sections, TGUFU 1063, 1065, 1066, 1068 ; slightly oblique axial sections, TGUFU 1062, 1064, 1069 ; tangential section, TGUFU 1067.

Description.—Shell large, highly elongate subcylindrical, having a slightly straight median part, irregularly undulated lateral slope, and truncated poles. Axis of coiling slightly bent. Mature shell consists of eight volutions. Axial length 7.33 to 12.00 mm, median width 1.64 to 3.2 mm, and form ratio 3.75 to 4.39.

First to third volutions tightly coiled, outer ones rapidly increase in height. Proloculus small, its outside diameter is 0.17 to 0.23 mm. Spirotheca thin, consists of a thin tectum and keriotheca but spirotheca of inner volutions recrystallized. Septa numerous, highly fluted throughout shell.

Septal folds form rounded crests, commonly extend across entire chamber. Phrenotheca almost absent. Vestigial chomata present in first to second volutions but lacking in outer ones. Axial filling almost lacking.

Remarks.—The present specimens agree closely with Hy. Igo's holotype specimen described from the Sote Formation, Nyukawa Group.

The Akuda specimens are larger than those of the Sote specimens. I could not obtain any complete specimens.

The holotype is also a broken specimen.

Occurrence.—All specimens from B-17 in Section D near Higashi-Akuda.

Parafusulina sotensis Hy. Igo, 1967

Figure 10-6

Parafusulina kawaii Morikawa *sotensis* Hy. Igo, 1967, p. 12, pl. 8, figs. 1-6.

Material.—Slightly oblique axial section, TGUFU 1075.

Description.—Shell large, elongate fusiform with more or less inflated median part and bluntly rounded poles. Present specimen consists of five volutions. Axial length 9.06 mm, median width 2.93 mm, and form ratio 3.09. Shell tightly coiled with a straight axis of coiling. Proloculus spherical with an outside diameter of 0.31 mm.

Spirotheca recrystallized, but probably composed of a tectum and keriotheca. Septa regularly fluted and septal loops with bluntly rounded to angular crests. Chomata lacking. Tunnel single narrow.

Axial filling weakly developed in polar regions of younger volutions.

Remarks.—The present specimen is weekly recrystallized, so that I could not determine detailed spirothecal structure. The Akuda specimen has less dense axial filling than that of Hy. Igo's holotype from the Sote Formation, Nyukawa Group.

Occurrence.—From B-11 in Section D.

Genus *Pseudofusulina* Dunbar and Skinner, 1931

Type species.—Pseudofusulina huecoensis Dunber and Skinner, 1931

Figure 7. 1-9. *Pseudofusulina minoensis* Hh. Igo sp. nov., 1, 3 : axial sections of paratypes, TGUFU 1021, 1023, 2 : axial section of holotype, TGUFU 1022, 4 : sagittal section, TGUFU 1024, 5-9 : axial sections of immature specimens, TGUFU 1025, 1026, 1027, 1028, 1029. **10, 11.** *Pseudofusulina miyamensis* Hh. Igo sp. nov., 10 : axial section of paratype, TGUFU 1030, 11 : axial section of holotype, TGUFU 1031. **12-16.** *Pseudofusulina* sp., 13, 14 : axial sections of mature specimens, TGUFU 1033, 1034, 12, 15, 16 : axial sections of immature specimens, TGUFU 1032, 1035, 1036. All figures ×10.
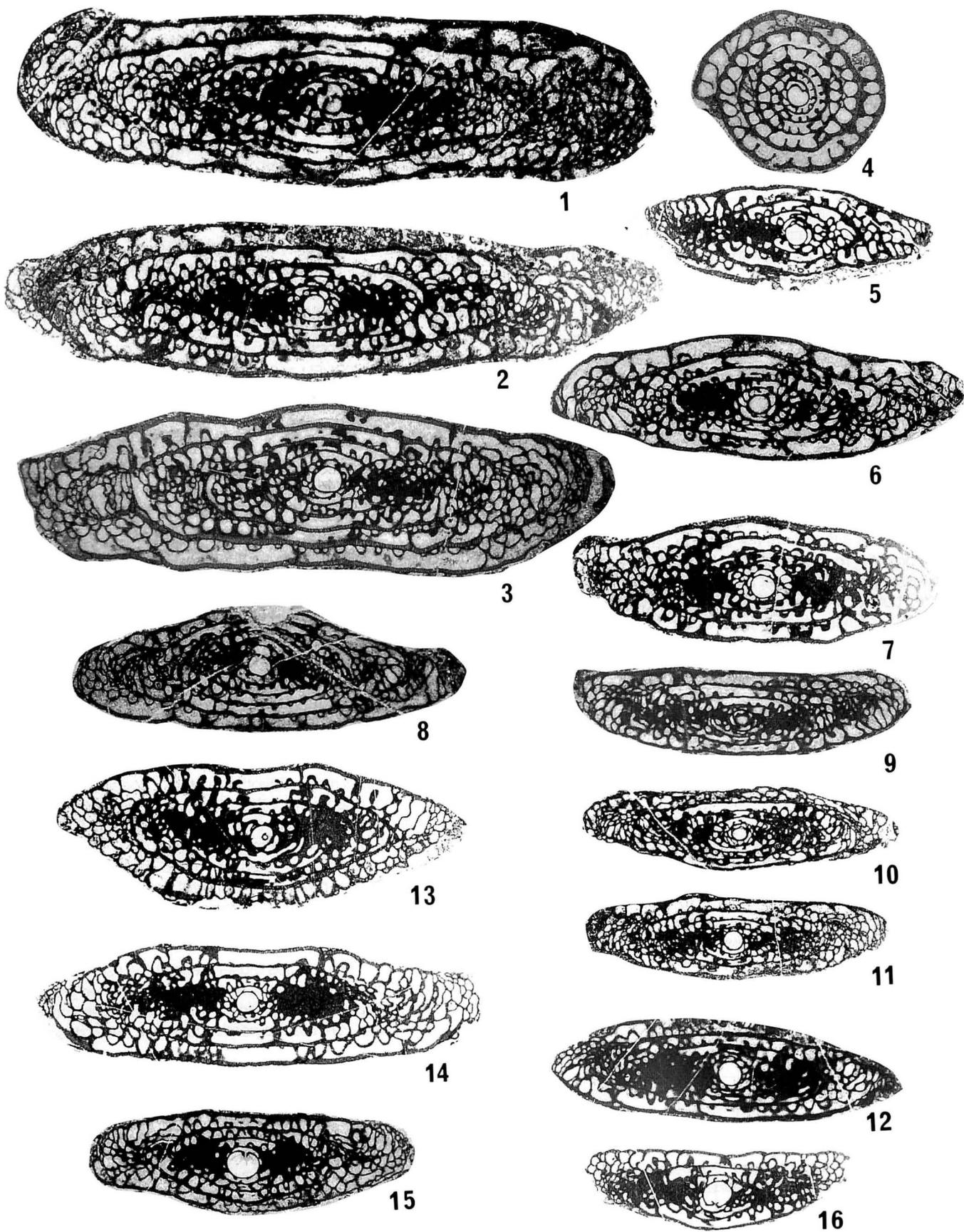
Pseudofusulina norikurensis Hy. Igo, 1959

Figures 5-1—3

Pseudofusulina kraffti (Schellwien) norikurensis Hy. Igo, 1959, p. 244, 245, pl. 2, figs. 1-3; Sashida, 1980, p. 296-298, pl. 34, figs. 3, 4.
Pseudofusulina norikurensis Hy. Igo. Morikawa and Isomi, 1961, p. 21, pl. 15, figs. 1-4, pl. 16, figs. 1-7.

Materials.—Axial sections, TGUFU 1000,1002; slightly oblique axial section, TGUFU 1001.

Description.—Shell large, inflated fusiform with broadly rounded poles. Mature shell consists of 8 to 9 volutions. Axial length 8.79 to 10.32 mm, median width 4.33 to 5.13 mm, and form ratio 2.01 to 2.03. Radius vectors in first to eighth volutions 0.40, 0.63, 0.83, 1.17, 1.53, 1.90, 2.30, and 2.76 mm, respectively.

Proloculus large, spherical with outside diameter of 0.50 to 0.57 mm. Spirotheca thick, consists of a thin distinct tectum and very coarse keriotheca. Upper keriotheca thin and 1/4 of whole thickness of keriotheca. Septa numerous, relatively intensely and regularly fluted along axial regions.

Cuniculi well developed in outer volutions. Phrenotheca poorly developed in lower part of chamber. Axial filling well developed in polar regions of inner five volutions. Tunnel low and narrow. Chomata lacking throughout shell.

Remarks.—This species resembles Parafusulina japonica (Gümbel), but differs from the latter in having an inflated shell with broadly rounded poles. This species was originally proposed by Hy. Igo (1959) as a subspecies of Pseudofusulina kraffti, but Morikawa and Isomi (1961) raised it to species level. I consider that this species is closely related to Parafusulina japonica in septal fluting and axial filling.

Occurrence.—TGUFU 1000, 1001 from A-1 south of the Horikoshi Pass; TGUFU 1002 from B-47 in Section D.

Pseudofusulina paratschernyschewi Kanuma, 1959

Figures 5-5—8

Pseudofusulina paratschernyschewi Kanuma, 1959, p. 67, 68, p. 6, figs. 4-7.

Materials.—Axial sections, TGUFU 1004, 1005, 1006, 1007.

Description.—Shell large and fusiform with almost straight axis of coiling and narrowly rounded poles. It is rather loosely coiled. Mature shell of 5 to 6 volutions 8.33 mm in axial length, and 3.40 mm in median width, giving a form ratio of 2.48. Radius vectors in first to sixth volutions, 0.47, 0.67, 0.93, 1.23, and 1.60 mm, respectively.

Proloculus relatively large, spherical to subspherical, with an outside diameter of 0.58 mm in mature shell. Spirotheca thick, consists of a thin tectum and coarse keriotheca.

Average thickness of spirotheca in first to last volutions in mature shell 0.05, 0.05, 0.10, 0.11, and 0.15 mm, respectively.

Septa numerous, rather regularly fluted nearly from pole to pole. Septal folds narrow, generally high, and commonly attain top of volutions. Cuniculi developed in outer volutions. Tunnel low and relatively narrow. Chomata almost lacking. Axial filling poorly developed in polar region of first to fourth volutions. Phrenotheca not present.

Remarks.—This species was first described by Kanuma (1959). He mentioned that this species accords closely with Parafusulina japonica (Gümbel) described by Chen (1934). He considered that Chen's P. japonica is related to Pseudofusulina tschernyschewi (Schellwien).

This species resembles P. tschernyschewi, but the former has a larger proloculus. This species also resembles Parafusulina japonica, but differs from the latter in having dense axial fillings and thick spirotheca.

Occurrence.—TGUFU 1004 from B-42; TGUFU 1005, 1006 from B- 47; TGUFU 1007 from A-1 south of the Horikoshi Pass.

Pseudofusulina horadaniensis Hy. Igo, 1964

Figures 5-9—11

Pseudofusulina horadaniensis Hy. Igo, 1964, p. 647, pl. 104, figs. 7-9.

Materials.—Axial sections, TGUFU 1008, 1009, 1010.

Description.—Shell large, cylindrical to elongate fusiform, and having straight median portion and truncated poles. Outline of shell elongate subhexagonal in axial section. Axial length 7.13 to 8.59 mm, median width 2.73 to 3.33 mm, and form ratio 2.10 to 2.58 in mature shells. Mature shell consists of six to seven volutions.

Radius vectors in first to seventh volution 0.33, 0.48, 0.66, 0.87, 1.13, 1.47, and 1.80 mm, respectively. Shell tightly coiled in first to third volutions.

Proloculus relatively large, spherical, with outside diameter of 0.40 to 0.43 mm. Spirotheca thick, consists of a thin tectum and coarse keriotheca with rather coarse alveoli. Thickness of spirotheca in first to sixth volutions 0.03, 0.05, 0.06, 0.08, 0.11, and 0.13 mm, respectively.

Septa numerous and intensely fluted. Septal folds about 1/2 as high as chamber. Phrenotheca absent. Tunnel single, low, and narrow. Chomata lacking. Axial filling strong and massive in polar regions. Outer one or two volutions lack axial filling.

Remarks.—This species closely resembles Pseudofusulina kraffti but differs from the latter in having pointed truncate poles and massive axial fillings. This species resembles in many respects Parafusulina postkraffti Leven (1967) described

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Figure 8. **1, 2.** Pseudofusulina fusiformis (Schellwien), axial sections, TGUFU 1037, 1038. **3-6.** Pseudofusulina regularis (Schellwien), 3, 5 : axial sections, TGUFU 1039, 1041, 4, 6 : slightly oblique axial sections, TGUFU 1040, 1042. **7-9.** Schwagerina kwangchiensis Chen, 7, 9 : slightly oblique axial sections, TGUFU 1043, 1045, 8 : axial section, TGUFU 1044. **10-13.** Pseudofusulina houziguanica Sheng, axial sections, TGUFU 1046, 1047, 1048, 1049. **14, 15.** Pseudofusulina krotowi (Schellwien), axial sections, TGUFU 1050, 1051. **16, 17.** Schwagerina higashidaniensis Hy. Igo, axial sections, TGUFU 1052, 1053. **18.** Chalaroschwagerina aff. chinensis (Chen), axial section, TGUFU 1054. All figures ×10.
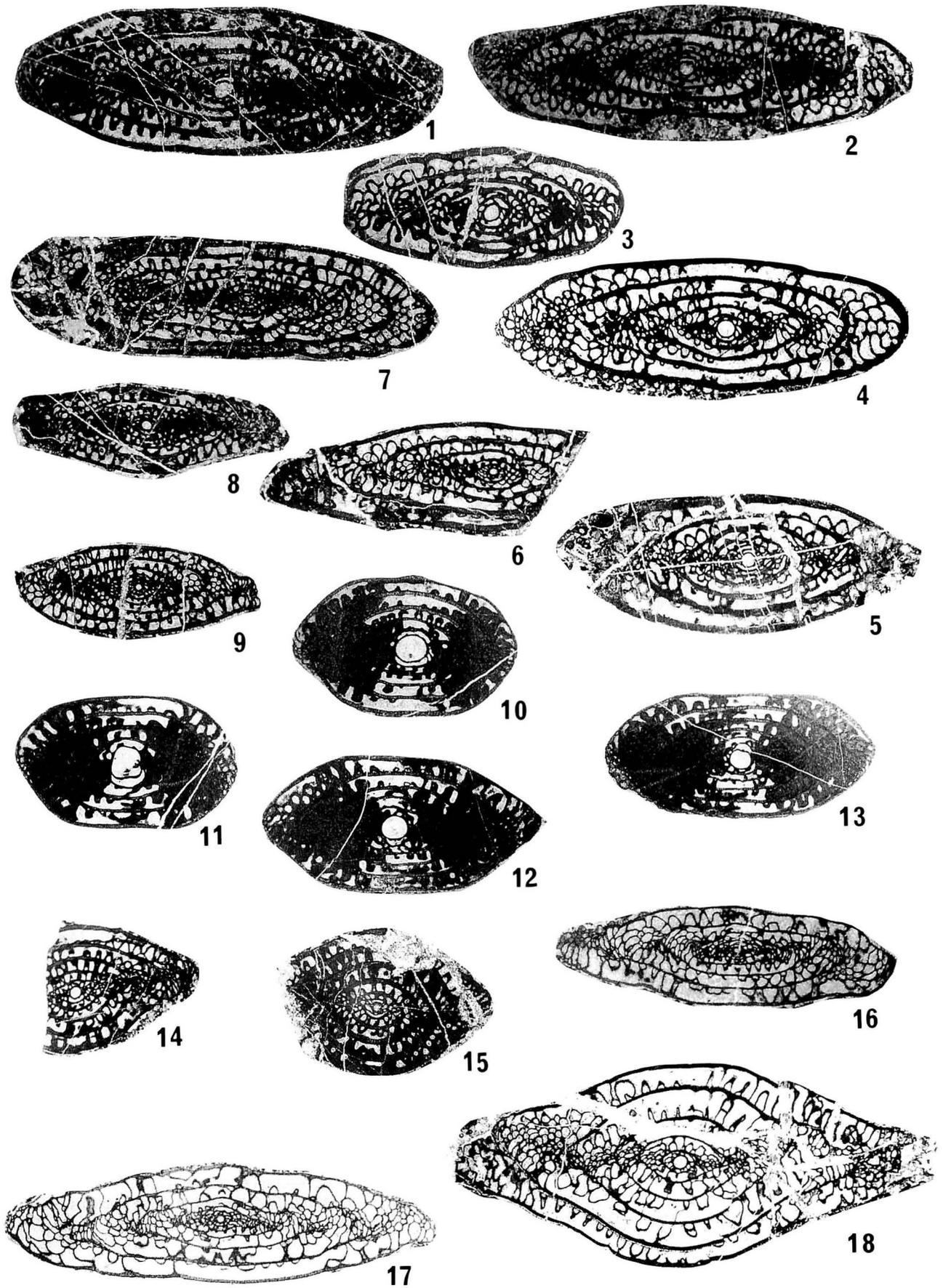
from the Pamirs but the latter has a large shell, intensely fluted septa, and well developed phrenotheca.

Occurrence.—TGUFU 1008 from B-48 ; TGUFU 1010 from B-44 in Section D ; TGUFU 1009 from A-2 south of the Horikoshi Pass.

Pseudofusulina isomie Hy. Igo, 1965

Figures 6-1—7

Pseudofusulina isomie Hy. Igo, 1965, p. 219, 220, pl. 29, fig. 6, pl. 30, figs. 5, 6, pl. 31, figs. 6, 7.

Materials.—Axial section of mature specimens, TGUFU 1011, 1013, 1014, 1015, 1017 ; axial section of immature specimen, TGUFU 1016 ; sagittal section of mature specimen, TGUFU 1012.

Description.—Shell large, cylindrical to elongate fusiform, and having slightly concave median part and bluntly rounded poles. Axial length 8.91 to 11.79 mm, median width 3.40 to 4.33 mm, and form ratio 2.45 to 3.00 in mature specimens. Mature shell has six to seven volutions.

Radius vectors in first to seventh volutions in largest specimen (TGUFU 1011) 0.33, 0.47, 0.73, 1.00, 1.37, and 1.73 mm, respectively. Shell rather tightly coiled in first to third volutions and having a straight axis of coiling. Proloculus large, spherical with an outside diameter of 0.37 to 0.73 mm.

Spirotheca thick, consists of a tectum and relatively coarse alveolar keriotheca. Upper keriothecal layer thin, 1/4 of whole thickness of keriotheca. Septa numerous, intensely fluted throughout length of shell and commonly extend across entire chamber. Fluting regular in median part of shell. Phrenotheca almost absent. Chomata lacking, tunnel low and narrow. Axial filling weekly developed in axial region of inner volutions.

Remarks.—In the Akuda specimens, axial filling is weaker than in the holotype from the Sote Formation. However, shape of shell and septal fluting are exactly the same in these specimens.

The Akuda specimens resemble *Parafusulina japonica* (Gümbel), which was illustrated by Toriyama (1975, pl. 5, figs. 48 ; pl. 6, figs. 1-8) but the latter specimens have an elongate fusiform shell and intense septal fluting.

This species closely resembles *Schwagerina toyamaensis* Suyari (1962). It differs from the latter in smaller proloculus, intense septal fluting, and thick spirothecae.

Occurrence.—TGUFU 1011 from B-37 ; TGUFU 1013, 1014, 1016 from B-42 ; TGUFU 1012, 1015, 1017 from B-47 in Section D.

Pseudofusulina duplithecata Hy. Igo, 1956

Figures 6-8, 9

Pseudofusulina duplithecata Hy. Igo, 1956, p. 297-299, pl. 18, figs. 1-10, pl. 19, figs. 1-3, 6 ; Hy. Igo, 1965, pl. 32, fig. 3.

Materials.—Axial section, TGUFU 1018 ; slightly oblique axial section, TGUFU 1019.

Description.—Shell large, cylindrical to elongate fusiform with an almost straight axis of coiling and having slightly straight median part and bluntly rounded poles. Mature shell has six to seven volutions.

Axial length 9.86 to 11.00 mm and median width 3.36 to 4.06 mm, giving a form ratio of 2.71 to 2.93. Shell tightly coiled throughout. Radius vectors in first to seventh volutions of largest specimen 0.28, 0.50, 0.70, 0.93, 1.23, 1.63, and 2.00 mm, respectively. Proloculus large, spherical, with outside diameter of 0.40 to 0.33 mm.

Spirotheca thick, consists of a tectum and upper and lower keriothecae. Discontinuous light layer observed in median part of the keriotheca. Outer surface of tectum is corrugated in fifth to sixth volutions of specimen illustrated in Fig. 6-9. Septa numerous, weakly fluted in polar regions. Septal loops low and 1/3 as high as chambers in outer volutions. Cuniculi developed in outer volutions. Chomata poorly developed in first to second volutions. Tunnel single, low, and wide. Axial fillings weekly developed in polar regions.

Remarks.—This species closely resembles *Pseudofusulina isomie* in its shell shape, but is distinguishable from the latter in weak and regular septal fluting. This species is characterized by possessing double spirotheca : the inner and outer keriothecae (Hy. Igo, 1956).

This double spirothecae appears in some specimens but is absent in others.

Occurrence.—All specimens from B-47 in Section D.

Pseudofusulina kraffti (Schellwien, 1909)

Figure 6-10

Fusulina kraffti Schellwien, 1909, p. 169, pl. 16, figs. 1-9.
Schellwienia kraffti (Schellwien). Ozawa, 1925, p. 25-27, pl. 6, fig. 7, pl. 7, fig. 4 ; Ozawa, 1927, p. 147, fig. 5.
Pseudofusulina kraffti (Schellwien). Fujimoto, 1936, p. 80, 81, pl. 14, figs. 3-8 ; Morikawa, 1955, p. 94, 95, pl. 7, figs. 15-17 ; Kanuma, 1959, p. 70, 71, pl. 7, figs. 1-3, 6 ; Morikawa and Isomi, 1961, p. 20, 21, pl. 14, figs. 1-10 ; pl. 15, figs. 5, 6 ; Sheng, 1963, p. 65, pl. 16, figs. 16-18 ; Chang, 1963, p. 206, pl. 4, fig. 11 ; Kalmykova, 1967, p. 183, 184, pl. 10, figs. 1-4 ; Leven, 1967, p. 146, 147, pl. 10, figs. 5, 6 ; Choi, 1970, p. 371, 372, pl. 1, figs. 6, 7 ; Choi, 1973, p. 52, pl. 6, figs. 1-5 ; Sashida, 1980, p. 296-298, pl. 34, figs. 3, 4 ; Xia, 1994, pl. 15, fig. 5.

Figure 9. 1-4. *Schwagerina kanumai* Hh. Igo sp. nov., 1 : axial section of holotype, TGUFU 1055, 2-4 : axial sections of paratypes, TGUFU 1056, 1057, 1058. **5-7.** *Schwagerina shukoae* Hh. Igo sp. nov., 5 : tangential section of immature specimen, TGUFU 1059, 6 : axial section of holotype, TGUFU 1060, 7 : slightly tangential section of paratype, TGUFU 1061. **8-15.** *Parafusulina ? sublineata* Hy. Igo, 8, 10, 15 : slightly oblique axial sections, TGUFU 1062, 1064, 1069, 9, 11, 12, 14 : axial sections, TGUFU 1063, 1065, 1066, 1068, 13 : tangential section, TGUFU 1067. All figures ×10.
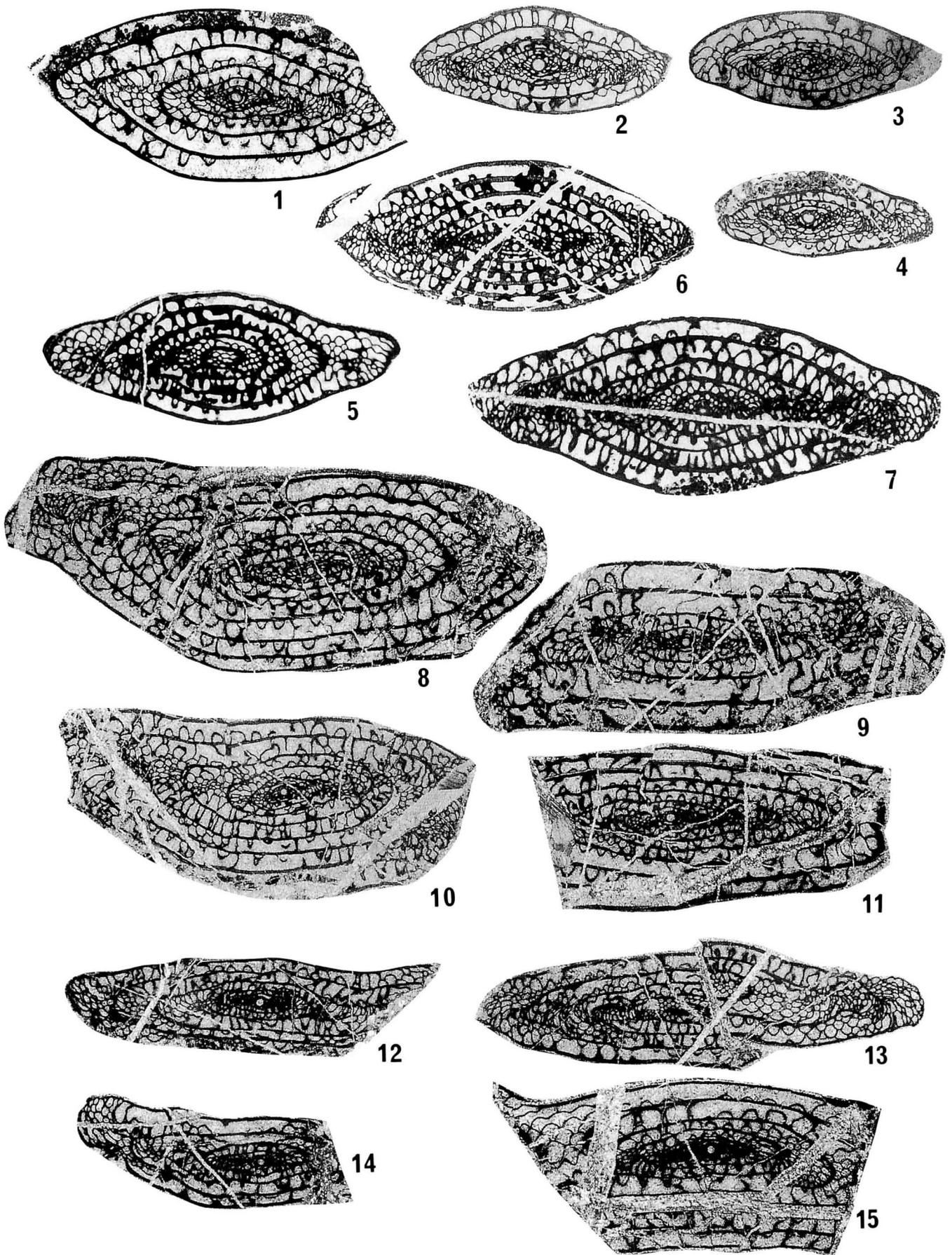
Pseudofusulina kraffti kraffti (Schellwien). Kanmera and Mikami, 1965, p. 299–301, pl. 44, fig. 7.

Pseudofusulina kraffti (Schellwien) forma A. Nogami, 1961, p. 217–219, pl. 10, figs. 5–8.

Material.—Axial section, TGUFU 1020.

Description.—Shell large, cylindrical to subcylindrical with broadly rounded poles. Mature shell has six to seven volutions. Axial length 10.66 mm and median width 4.33 mm, giving form ratio of 2.46. Shell tightly coiled in the first to third volutions and having a weekly bent axis of coiling. Radius vectors in first to sixth volutions 0.27, 0.38, 0.58, 0.90, 1.33? and 1.73 mm, respectively.

Proloculus large, spherical, with outside diameter of 0.37 mm. Spirotheca thick, consists of a tectum and coarse alveolar keriotheca. Septa numerous, intensely fluted near axis of coiling, most septal loops reach ceiling of chambers. Chomata poorly developed in first to second volutions. Tunnel single, low, and wide. Axial fillings developed in polar regions.

Remarks.—In the Akuda specimen, the spirotheca varies in thickness even in the same volution. This well known

species has broad variations in shell shape, septal fluting, size of shell, degree of axial filling, and other features. Many previous authors have already pointed out these variations.

Occurrence.—From OHT- 4 at Otohime-Tani.

Pseudofusulina minoensis Hh. Igo sp. nov.

Figures 7-1—9

Materials.—Axial section of holotype, TGUFU 1022; axial sections of paratypes, TGUFU 1021, 1023; axial sections of immature specimens, TGUFU 1025, 1026, 1027, 1028, 1029; sagittal section of mature specimen, TGUFU 1024.

Diagnosis.—Large *Pseudofusulina* with an elongate cylindrical shell and large proloculus. Septa regularly fluted.

Description.—Shell large, elongate subcylindrical to elongate fusiform, with a slightly flat median part and bluntly rounded poles. Axial length 11.32 to 10.52 mm, median width 3.33 to 2.73 mm, and form ratio 4.00 to 3.85 in mature specimens.

Shell rather tightly coiled in first to third volutions and

Table 4. Measurements of *Pseudofusulina minoensis* Hh. Igo sp. nov. (in mm)

Reg. no.		Fig.	L.	W.	F.R.	D.P.	Radius vector				
							1	2	3	4	5
1	TGUFU1021	7-1	11.32	3.33	3.40	0.49	0.35	0.50	0.75	1.25	1.45
2	TGUFU1022	7-2	11.52	2.73	4.22	0.38	0.30	0.47	0.63	0.93	1.32
3	TGUFU1023	7-3	10.52	2.86	3.68	0.53	0.37	0.53	0.77	1.03	1.37
4	TGUFU1024	7-4	---	3.40	---	0.43	0.37	0.50	0.73	1.03	1.40
5	TGUFU1025	7-5	5.73	1.86	3.03	0.43	0.33	0.50	0.70	0.90	---
6	TGUFU1026	7-6	7.79	2.34	3.33	0.37	0.35	0.50	0.73	1.03	1.33
7	TGUFU1027	7-7	7.33	2.40	3.05	0.49	0.33	0.50	0.70	1.00	1.30
8	TGUFU1028	7-8	6.79	2.20	3.09	0.42	0.37	0.53	0.73	0.90	1.17
9	TGUFU1029	7-9	5.40	1.50	3.60	0.26	0.18	0.28	0.42	0.60	---

	Thickness of spirotheca				
	1	2	3	4	5
1	0.06	0.05	0.06	0.06	0.08
2	0.03	0.03	0.04	0.08	0.09
3	0.03	0.04	0.06	0.09	0.08
4	0.03	0.03	0.02	0.07	0.08
5	0.03	0.04	0.05	0.06	---
6	0.03	0.05	0.03	0.09	0.11
7	0.03	0.04	0.05	0.07	0.08
8	0.06	0.04	0.06	0.08	0.08
9	0.02	0.03	0.04	0.05	---

Figure 10. 1-3. *Acervoschwagerina fujimotoi* Kanuma, 1, 2: oblique sections, TGUFU 1070, 1071, 3: slightly oblique axial section, TGUFU 1072, ×10. 4, 5. *Toriyamaia laxiseptata* Kanmera, tangential sections, TGUFU 1073, 1074, ×15. 6. *Parafusulina sotensis* Hy. Igo, slightly oblique axial section, TGUFU 1075, ×10. 7-10. *Maklaya pamirica* (Leven), 7, 9: slightly oblique axial sections, TGUFU 1076, 1078, 8, 10: axial sections, TGUFU 1077, 1079 ×17. 11, 12. *Maklaya saraburiensis* Kanmera and Toriyama, axial sections, TGUFU 1080, 1081, ×17. 13, 14. *Armenina* sp., axial sections, TGUFU 1082, 1083, ×17. 15-20. *Pseudoreichelina* sp., 15, 16, 18, 20: tangential sections, TGUFU 1084, 1085, 1087, 1089, 17: axial section, TGUFU 1086, 19: sagittal section, TGUFU 1088. 15-19 = ×30, 20 = ×50.
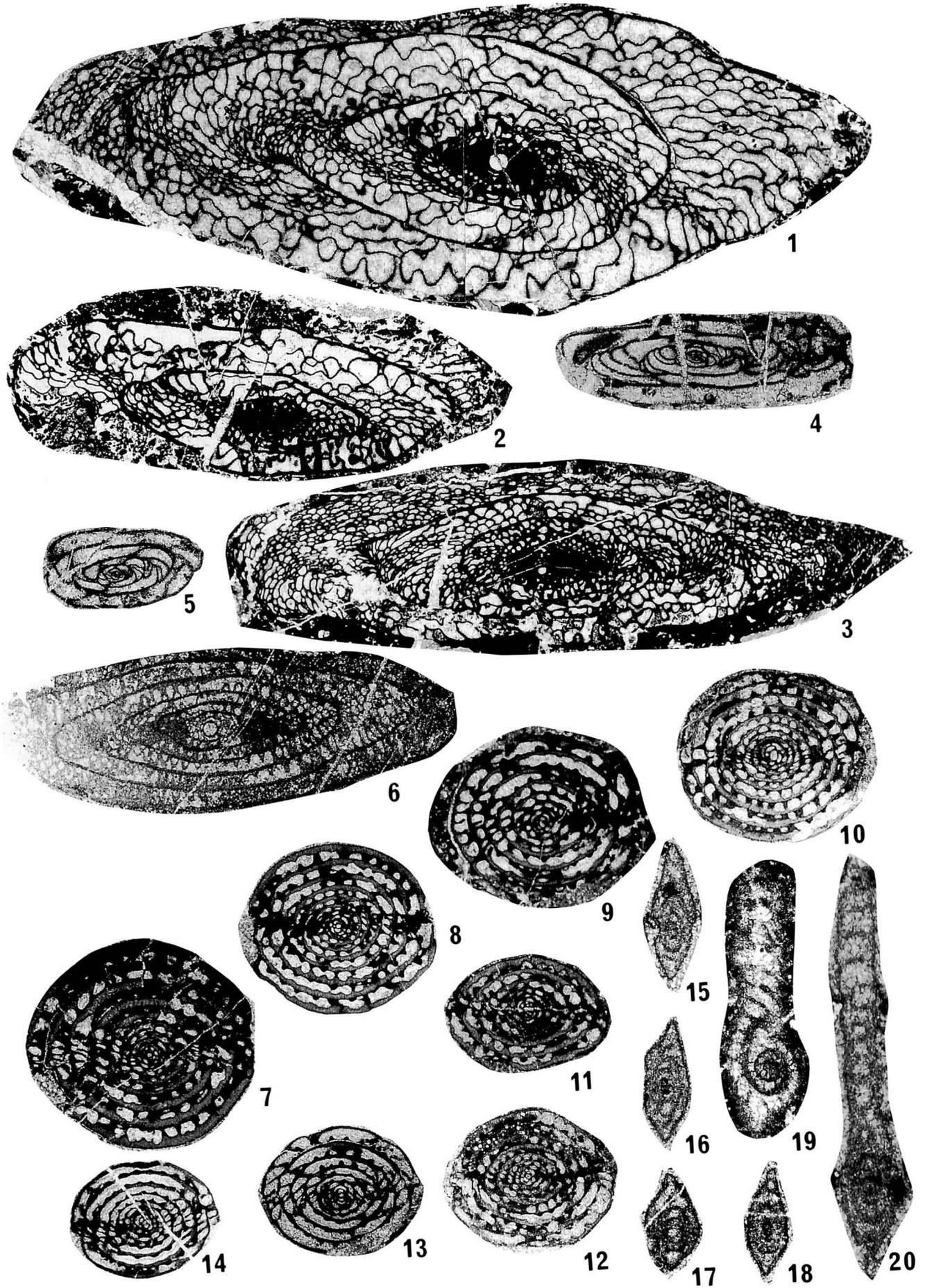
having a straight or slightly curved axis of coiling. Proloculus large, spherical, with an outside diameter of 0.53 to 0.26 mm.

Spirotheca thick, consists of a tectum and coarse alveolar keriotheca. Thickness of spirotheca in first to fifth volutions of holotype 0.03, 0.03, 0.04, 0.08, and 0.09 mm, respectively. Surface of tectum irregularly undulated.

Septa numerous, more or less regularly fluted, and most septal loops reach up to about 2/3 height of chamber. Phrenotheca present in outer volutions. Chomata lacking except for very poor development in first to second volutions. Tunnel singular, low, and narrow. Axial filling weekly developed in inner volutions.

Remarks.—This species very closely resembles *Pseudofusulina granumavenae* (Roemer) in many points. The former can be distinguished from the latter, however, in having fewer volutions and weak septal fluting.

Etymology.—This species name is derived from the ancient province name of Gifu Prefecture.

Occurrence.—Collected from R-1 in Section E of Nishi-Akuda.

Pseudofusulina miyamensis Hh. Igo sp. nov.

Figures 7-10—11

Materials.—Axial section of holotype, TGUFU 1031 ; axial section of paratype, TGUFU 1030.

Diagnosis.—Small *Pseudofusulina* with an elongate fusiform shell and thin spirotheca, and proloculus rather large compared with shell size.

Description.—Shell small, elongate fusiform with bluntly rounded poles and a straight axis of coiling. Axial length 5.66 and 5.86 mm, median width 1.53 and 1.57 mm, form ratio 3.83 and 3.61. Shell tightly coiled in first to third volutions. Radius vectors in first to fifth volutions of holotype 0.27, 0.40, 0.53, 0.73, and 0.87 mm, respectively. Proloculus large compared with shell size. Spirotheca thin, consists of a tectum and fine alveolar keriotheca. Thickness of spirotheca in first to fifth volutions of holotype 0.02, 0.03, 0,04, 0.06, and 0.05 mm, respectively. Septa regularly fluted, most loops reach to ceiling of chamber. Chomata lacking, but rudimentary ones observed on first volution. Tunnel singular and low. Axial filling very weekly developed in inner volutions.

Remarks.—This species resembles *Pseudofusulina minoensis* Hh. Igo, but the former has a smaller shell than the latter.

Etymology.—This species name is derived from the name of a village in the studied area.

Occurrence.—From R-1 in Section E of Nishi-Akuda.

Pseudofusulina fusiformis (Schellwien, 1909)

Figures 8-1, 2

Fusulina vulgaris var. *fusiformis* Schellwien, 1909, p. 165-168, pl. 15, figs. 1-4.
Pseudofusulina vulgaris var. *fusiformis* (Schellwien). Kanuma, 1959, p. 75, 76, figs. 7-11.
Pseudofusulina fusiformis (Schellwien). Thompson, 1948, pl. 12, fig. 3 (same as pl. 15, fig. 2 of Schellwien, 1909, p. 165-168) ; Morikawa, 1955, p. 98, 99, pl. 13, figs. 1-7 ; Hy. Igo, 1959, p. 246, 247, pl. 3, fig. 5 ; Morikawa and Isomi, 1961, p. 19, 20, pl. 7, figs. 11, 12, pl. 8, figs. 12, 13, pl. 10, figs. 1-10, pl. 11, figs. 1-10,

Table 5. Measurements of *Pseudofusulina miyamensis* Hh. Igo sp. nov. (in mm)

	Reg. no.	Fig.	L.	W.	F.R.	D.P.	Radius vector				
							1	2	3	4	5
1	TGUFU1030	7-10	5.86	1.53	3.83	0.29	0.20	0.33	0.47	0.63	0.83
2	TGUFU1031	7-11	5.66	1.57	3.61	0.40	0.27	0.40	0.53	0.73	0.87

	Thickness of spirotheca				
	1	2	3	4	5
1	0.03	0.02	0.02	0.05	0.06
2	0.02	0.03	0.04	0.06	0.05

Figure 11. **1-4.** *Neofusulinella giraudi* Deprat, 1, 3 : axial sections, TGUFU 1090, 1092, 2, 4 : slightly oblique axial sections, TGUFU 1091, 1093, ×30. **5-8.** *Neofusulinella lantenoisi* Deprat, 5 : slightly oblique axial section, TGUFU 1095, 6-8 : axial sections, TGUFU 1096, 1097, 1098, ×30. **9-14.** *Sphaerulina akudensis* Hh. Igo sp. nov., 9 : axial section of holotype, TGUFU 1099, 10, 11 : tangential sections, TGUFU 1100, 1101, 12, 13 : sagittal sections, TGUFU 1102, 1103, 14 : axial section of paratype, TGUFU 1104, ×30. **15.** *Schubertella pseudoobscura* Chen, axial section, TGUFU 1105, ×40. **16.** *Nankinella* sp., tangential section, TGUFU 1106, ×10. **17-19.** *Nankinella* aff. *kotakiensis* (Fujimoto and Kawada), axial sections, TGUFU 1107, 1108, 1109, ×15. **20-31.** *Pamirina(Levenella) leveni* Kobayashi, 20-27, 30, 31 : axial sections, TGUFU 1110, 1111, 1112, 1113, 1114, 1115, 1116, 1117, 1120, 1121, 28, 29 : sagittal sections, TGUFU 1118, 1119, ×30. **32-34.** *Pamirina (Levenella) evoluta* Sheng and Sun, axial sections, TGUFU 1122, 1123, 1124, ×60. **35, 36.** *Dunbarula uenoi* Hh. Igo sp. nov., 35 : axial section of holotype, TGUFU 1125, 36 : axial section of paratype, TGUFU 1126, ×30. **37, 38.** *Minojapanella (M.) elongata* Fujimoto and Kanuma, 37 : oblique section, TGUFU 1127, ×30, 38 : sagittal section, TGUFU 1128, ×50.
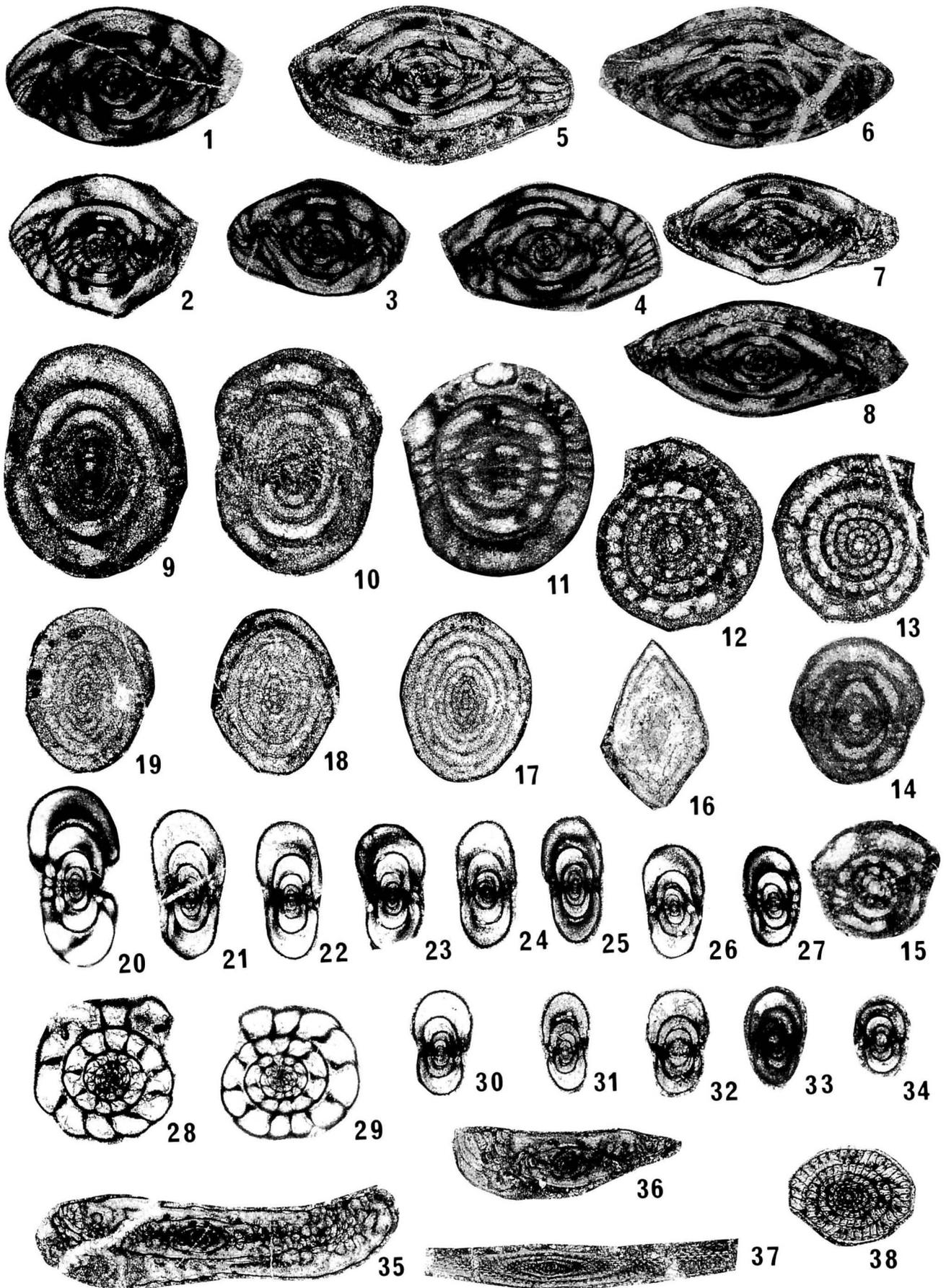
pl. 12, figs. 1-10, pl. 13, fig. 5 ; Sheng, 1963, p. 66, 192, 193, pl. 16, figs. 19-21 ; Kanmera and Mikami, 1965, p. 301, 302, pl. 52, figs. 1-6 ; Kalmykova, 1965, p. 122, 123, pl. 3, figs. 1-4 ; Kalmykova, 1967, p. 181, 182, pl. 9, figs. 1-5 ; Choi, 1972, pl. 2, fig. 7 ; Choi, 1973, p. 46, 47, pl. 9, figs. 1-3, pl. 11, fig. 4 ; Sakaguchi and Yamagiwa, 1975, p. 182, 183, pl. 2, figs. 1, 2, 11 ; Ozawa, 1975, pl. 9, fig. 16 ; Liu et al., 1978, p. 59, 60, pl. 13, fig. 1 ; Kahler and Kahler, 1980, p. 217-220, pl. 6, fig. 4, pl. 8, fig. 1 ; Ozawa and Kobayashi 1990, pl. 8, fig. 14 ; Ueno, 1992, p. 1283-1285, figs. 3-7—11.

Schwagerina fusiformis (Schellwien).   Suyari, 1962, p. 26, pl. 8, figs. 7-9.

Pseudofusulina cf. *fusiformis* (Schellwien).   Xia, 1994, pl. 16, fig. 15.

non *Schellwienia vulgaris* var. *fusiformis* (Schellwien).   Lee, 1927, p. 67, 68, pl. 9, figs. 3, 5.

Materials.—Axial sections of mature specimens, TGUFU 1037, 1038.

Remarks.—This well known species has been described from many localities in the Tethyan region. The Akuda specimens are identical to the original specimens described by Schellwien (1909).   Morphological variations in previously described *P. fusiformis* are limited, hence we can easily identify this species.   The Hirayu specimen (Hy. Igo, 1959), Yoganeyama specimen (Sashida, 1980), and the Akuda specimens (Kanuma, 1959 and this paper) well coincide morphologically with the original species.

Occurrence.—From B-37 in Section D near Higashi-Akuda.

Pseudofusulina regularis (Schellwien, 1898)

Figures 8-3—6

Fusulina regularis Schellwien, 1898, p. 250, pl. 19, figs. 1-6 ; Deprat, 1912, p. 28, pl. 7, figs. 14, 15.

Schellwienia regularis (Schellwien).   Lee, 1927, p. 50, pl. 7, figs. 8-10.

Pseudofusulina regularis (Schellwien).   Fujimoto, 1936, p. 94, pl. 10, figs. 9-11, pl. 18, fig. 1 ; Kanmera, 1958, p. 194, pl. 33, figs. 1-10 ; Saurin and Le-Thi-Vien, 1960, p. 396, pl. 1, figs. 16-18 ; Morikawa and Isomi, 1961, p. 15, pl. 7, figs. 1-10 ; Sada, 1964, p. 257, pl. 26, figs. 8-11, pl. 27, figs. 9, 10 ; Toriyama, 1975, p. 15, pl. 2, figs. 7, 8 ; Toriyama, 1982, pl. 3, figs. 2-4 ; Ishibashi, 1984, p. 211, 212, pl. 27, figs. 1-4.

Pseudofusulina (Daixina) regularis (Schellwien).   Hy. Igo, 1972, p. 105, pl. 16, figs. 10-16.

Schwagerina regularis (Schellwien).   Toriyama, 1958, p. 140, pl. 16, figs. 8-15 ; Kochansky-Devidé, 1959, p. 50, pl. 2, figs. 7-11 ; Suyari, 1962, p. 22, pl. 8, fig. 10 ; Liu et al., 1978, p. 44, 45, pl. 8, fig. 1 ; Zhou, 1991, pl. 2, figs. 6, 7.

Materials.—Axial sections of mature specimens, TGUFU 1039, 1041 ; slightly oblique axial sections, TGUFU 1040, 1042.

Description.—Shell moderate in size, elongate fusiform with a straight axis of coiling, having slightly inflated median part and bluntly pointed poles.   Mature shell composed of five to six volutions. Axial length 5.26 to 6.18 mm, median width 2.20 to 2.60 mm, and form ratio 2.38 to 2.39. Proloculus moderate in size, spherical, 0.33 to 0.28 mm in its outside diameter.   First volution subspherical in shape.

Spirotheca thick, composed of a tectum and alveolar keriotheca.   Septa fluted rather regularly, most septal loops attain a height about 2/3 that of the chamber.   Chomata poorly developed in first to second volutions.   Tunnel singular, rather low, and narrow.

Remarks.—The present specimens are similar to Schellwien's original specimens.   This species described by Kanmera (1958) from the Yayamadake Limestone is very similar to the Akuda specimens.

Hy. Igo (1972) described this species from North Thailand and discussed biocharacters and synonymous specimens of previous papers.

Occurrence.—TGUFU 1039, 1041 from B-47 and R-2 near Higashi- and Nishi-Akuda ; TGUFU 1040, 1042 from R-1 in Section E near Nishi-Akuda.

Pseudofusulina houziguanica Sheng, 1963

Figures 8-10—13

Pseudofusulina houziguanica Sheng, 1963, p. 67, 193, 194, pl. 16, figs. 11-14 ; Wang et al., 1981, p. 36, pl. 3, figs. 6, 7 ; Zhang and Dong, 1986, p. 100, pl. 14, fig. 7 ; Sun and Zhang, 1988, pl. 1, figs. 5, 14.

Pseudofusulina cfr. *houziguanica* Sheng.   Xiao, Wang, Zhang and Dong, 1986, p. 100, 101, pl. 10, fig. 17 ; Ueno, 1992, figs. 5-3, 4 ; Xia, 1994, pl. 16, fig. 18.

Materials.—Axial sections, TGUFU 1046, 1047, 1048, 1049.

Description.—Shell medium in size, rather tightly coiled, inflated fusiform or ellipsoidal, having straight median portion and broadly rounded poles. Mature shell consists of 5 to 6 volutions.   Axial length 4.06 to 5.00 mm, median width 2.20 to 2.46 mm, and form ratio 1.65 to 2.20.

Spirotheca rather thick compared with shell size and consists of a tectum and relatively coarse keriotheca. Septa numerous and regularly fluted throughout their length. Septal loops almost reach upper part of chamber.

Proloculus spherical or nearly rectangular, large compared with their shell size, thin-walled, and external diameter 0.37 to 0.50 mm.   Axial fillings rather heavy except central part of shell.   Chomata lacking except for very poorly developed ones on surface of proloculus.   Tunnel indistinct.

Remarks.—The present species is closely related to *Parafusulina funafusensis* Matsumaru described from the Funafuseyama Limestone of the northern Mino Terrane. *Parafusulina funafusensis* is probably a junior synonym of the present species.

Occurrence.—All specimens from R-1 in Section E of Nishi-Akuda.

Pseudofusulina krotowi (Schellwien, 1908)

Figures 8-14, 15

Fusulina krotowi Schellwien, 1908, p. 190-192, pl. 20, figs. 1-10.

Schellwienia krotowi (Schellwien).   Ozawa, 1925, p. 27, 28, pl. 7, figs. 5, 6.

Pseudofusulina krotowi (Schellwien).   Fujimoto, 1936, p. 82-84, pl. 15, figs. 1-5, 9-15 ; Rauzer-Chernousova, 1938, p. 143, 144, pl. 9, figs. 1, 2 ; Morikawa, 1955, p. 86, pl. 14, figs. 5, 6 ; Kanuma, 1959, p. 78, 79, pl. 8, figs. 1-3 ; Morikawa and

Isomi, 1961, p. 18, 19, pl. 8, figs. 1-11.
Schwagerina krotowi (Schellwien). Kanmera, 1958, p. 193, 194, pl. 24, fig. 20; pl. 35, figs. 13, 14; Toriyama, 1958, p. 134-138, pl. 15, figs. 8-19; Kawano, 1961, p. 84, 85, pl. 4, fig. 28; pl. 5, figs. 1-4; Ishizaki, 1962, p. 113, 114, pl. 29, figs. 6-10.

Materials.—Axial sections, TGUFU 1050, 1051.

Remarks.—The present specimens closely resemble Schellwien's original ones. This species was described from a limestone of the Okumyogata Formation about 15 km north of Hachiman town by Kanuma (1959).

Occurrence.—TGUFU 1049, 1050 from B-46 and B-48 in Section D near Higashi-Akuda.

Pseudofusulina sp.

Figures 7-12—16

Materials.—Axial sections of mature specimens, TGUFU 1033, 1034; axial sections of immature specimens, TGUFU 1032, 1035, 1036.

Description.—Shell medium in size, elongate fusiform, having somewhat bluntly rounded poles. Mature shell consists of four volutions. Axial length 7.60 to 8.59 mm, median width 2.26 to 2.73 mm, and form ratio 2.78 to 3.80 in mature specimens. Proloculus large, spherical, with outside diameter of 0.46 to 0.58 mm.

Spirotheca rather thin, consists of a tectum and coarse alveolar keriotheca, surface of tectum irregularly corrugated. Septa numerous, strongly fluted throughout shell. Septal loops rather high, almost reach top of chamber. Axial filling irregular in axial regions of inner volutions. Tunnel single, low, and narrow. Chomata lacking except for very poor development in first volution.

Remarks.—This species closely resembles Pseudofusulina minoensis Hh. Igo sp. nov., but has slightly stronger axial filling and septal fluting than in the latter.

Occurrence.—All specimens from R-1 in Section E of Nishi-Akuda.

Subfamily Pseudoschwagerininae Chang, 1963
Genus Acervoschwagerina Hanzawa, 1949

Type species.—Paraschwagerina (Acervoschwagerina) endoi Hanzawa, 1949

Acervoschwagerina fujimotoi Kanuma, 1959

Figures 10-1—3

Acervoschwagerina fujimotoi Kanuma, 1958, p. 62, 63, pl. 4, figs. 6-8; Ishii, 1964, p. 125, pl. 1, figs. 1, 2.

Materials.—Oblique sections, TGUFU 1070, 1071; slightly oblique axial section, TGUFU 1072.

Description.—Shell very large, elongate fusiform, and having inflated median part and broadly or narrowly rounded poles. Inner three or four volutions very tightly coiled, height suddenly increases in outer volutions.

Axial length of present specimens more than 15.98 mm and median width 6.00 mm or more. Proloculus spherical, small, and its outside diameter 0.27 to 0.47 mm. Spirotheca

very thin and consists of a tectum and keriotheca. Septa numerous and thin, fluting irregular throughout shell. Chomata poorly developed in first to second volutions.

Remarks.—The present specimens are deformed by compaction of sediments and the height of the outer volutions has consequently been lowered.

Occurrence.—TGUFU 1070 from B-2; TGUFU 1071 from B-3; TGUFU 1072 from B-4 in Section C near Akuda-kuchi.

Genus Chalaroschwagerina Skinner and Wilde, 1965

Type species.—Chalaroschwagerina inflata Skinner and Wilde, 1965

Chalaroschwagerina aff. chinensis (Chen, 1956)

Figures 8-18

Compare.—Schwagerina chinensis Chen, 1956, p. 6, 35, pl. 5, fig. 10.

Material.—Axial section of mature specimen, TGUFU 1054.

Description.—Shell large, highly inflated fusiform with rounded or elongate node-like poles and a rounded median part. Present specimen consists of six volutions. Axial length 9.32 mm, median width 5.06 mm, and form ratio 1.84. Inner volutions not so tightly coiled. Proloculus moderate in size, spherical, with an external diameter of 0.27 mm.

Spirotheca consists of a tectum and rather fine alveolar keriotheca. Thickness of spirotheca moderate with a maximum thickness of 0.08 mm. Septa numerous, moderately fluted throughout shell. Septal folds with bluntly pointed crests or obtuse crests extend almost halfway up the chamber. Phrenotheca weakly developed in median part of outer volutions. Chomata and axial filling lacking.

Remarks.—The present specimen closely resembles Schwagerina chinensis, which was described from Hupeh Province by Chen (1956). However, the former differs from the latter in the shape of septal fluting. The present specimen is similar to some species described as Paraschwagerina, but has a larger proloculus, more loosely coiled inner volutions, and regularly fluted septa.

Occurrence.—From R-2 in Section E of Nishi-Akuda.

Family Neoschwagerinidae Dunbar and Condra, 1927
Subfamily Neoschwagerininae Dunbar and Condra, 1927
Genus Maklaya Kanmera and Toriyama, 1968

Type species.—Cancellina pamirica Leven, 1967

Maklaya pamirica (Leven, 1967)

Figures 10-7—10

Cancellina pamirica Leven, 1967, p. 186, 187, pl. 32, figs. 1, 3; Sun and Zhang, 1988, pl. 4, fig. 21.
Maklaya pamirica (Leven). Kanmera and Toriyama, 1968, p. 34-37, pl. 4, figs. 1-16; Kahler and Kahler, 1979, p. 249, 250, pl. 8, fig. 6; Ishibashi, 1984, p. 222, 223, pl. 31, fig. 16; Yang, 1985, pl. 2, fig. 3; Ozawa and Kobayashi, 1990, pl. 9, figs. 10, 11; Fan et al., 1990, pl. 7, figs. 19, 27; Ueno, 1991, p. 994,

995, figs. 9-5—10.

Materials.—Axial sections, TGUFU 1076, 1077, 1078, 1079.

Description.—Shell medium in size, subspherical with broadly rounded poles. Mature specimens consist of 9 to 10 volutions. Axial length 2.10 to 2.56 mm, median width 1.83 to 2.33 mm, and form ratio 1.10 to 1.30. Proloculus minute, spherical, with an external diameter of 0.06 to 0.08 mm.

Spirotheca rather thick compared with shell size and composed of a tectum and alveolar keriotheca. Thickness of spirotheca in first to tenth volutions of mature specimen 0.005, 0.008, 0.020, 0.030, 0.030, 0.050, 0.050, 0.050, 0.070, and 0.070 mm, respectively. Short, broad, and fan-shaped primary transverse septula well developed in fourth or succeeding volutions. Septa thick and unfluted throughout shell. Parachomata nearly triangular in axial section, first appeaing in third volution. No axial septula present.

Remarks.—Recently, this species was described from the Akiyoshi Limestone by Ueno (1991). The Akuda specimens closely resemble the Akiyoshi specimens.

Occurrence.—TGUFU 1076, 1077, 1078 from A-21 ; TGUFU 1079 from A-22 in Section A near the Horikoshi Pass.

Maklaya saraburiensis Kanmera and Toriyama, 1968

Figures 10-11, 12

Maklaya saraburiensis Kanmera and Toriyama, 1968, p. 41-43, pl. 4, figs. 17-20 ; Ueno, 1991, p. 993, 994, figs. 9-1—4.
Neoschwagerina saraburiensis (Kanmera and Toriyama). Han, 1985, p. 685, pl. 2, figs. 14, 15.

Materials.—Axial sections of mature specimens, TGUFU 1080, 1081.

Description.—Shell small, subspherical with bluntly pointed poles. Mature specimens having seven and nine volutions, 1.83 and 1.86 mm in axial length, 1.27 and 1.57 mm in median width, and 1.18 and 1.44 in form ratio respectively. Inner two volutions planispiral with a short axis of coiling. Proloculus small, spherical, 0.05 mm in outside diameter. Spirotheca composed of a tectum and alveolar keriotheca. Thickness of spirotheca of first to seven volutions of Figure 10-11, 0.007, 0.007, 0.012, 0.025, 0.030, 0.050, and 0.060 mm, respectively. Short and low primary transverse septula first appear in fourth volution. Parachomata observed in third or succeeding volutions. No axial septula present.

Remarks.—This species is distinguished from *Maklaya pamirica* (Leven) by a larger shell and greater numbers of volutions. The Akuda specimens closely resemble the type specimen, which was described from the Rat Buri Limestone in the Khao Phlong Phrab area, central Thailand.

Occurrence.—TGUFU 1080, 1081 from A-22 in Section A near the Horikoshi Pass.

Family Verbeekinidae Staff and Wedekind, 1910
Subfamily Verbeekininae Staff and Wedekind, 1910
Genus *Armenina* Miklukho-Maklay, 1955

Type species.—*Armenina karinae* Miklukho-Maklay, 1955

Armenina sp.

Figures 10-13, 14

Materials.—Axial sections of mature specimens, TGUFU 1082, 1083.

Description.—Shell small, subspherical with rounded polar regions. Mature specimens having eight to nine volutions, 1.67 to 1.76 mm in axial length, 1.33 to 1.40 mm in median width, and form ratio 1.26 to 1.76. Inner 1/2 volutions planispiral, with a short axis of coiling and having a right angle to outer volutions. Inner three to four volutions tightly coiled and outer ones loosely coiled. Radius vectors of first to eighth volutions of axial section (Figure 10-13) 0.08, 0.11, 0.16, 0.25, 0.34, 0.45, 0.60, and 0.76 mm, respectively.

Proloculus small, spherical, and 0.05 mm in outside diameter. Spirotheca very thin for the genus, composed of a tectum and fine alveolar keriotheca except for the inner first to second volutions, which are a dense single layer. Thickness of spirotheca of first to ninth volutions (Figure 10-14) 0.007, 0.013, 0.013, 0.013, 0.010, 0.020, 0.030, 0.030, and 0.030 mm, respectively.

Parachomata small, low, narrow, and reach about 1/4 or 1/3 of chamber height. They appear in third volution. No axial septula present.

Remarks.—This species closely resembles *Verbeekina* (*Armenina*) *prisca* Toriyama and Kanmera, but differs from the latter in having a larger shell and rudimentary parachomata.

Occurrence.—From A-21 in Section A near the Horikoshi Pass.

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An early Middle Miocene warm-water molluscan fauna in southwestern Sakhalin — Molluscs from the Ausinskaya Formation around Novoselovo —

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Abstract. Thirty-two mollusc species were identified from two localities of the lower Middle Miocene Ausinskaya Formation around Novoselovo, southwestern Sakhalin. This fauna includes a number of warm-water taxa such as *Anadara watanabei, Glycymeris cisshuensis, Dosinia tugaruana, Tateiwaia* sp., *Euspira meisensis,* and *Cultellus izumoensis.* These taxa were previously unknown in the Ausinskaya Formation, except for *Cultellus izumoensis.* A *Dosinia-Anadara* association made up of subtropical to temperate-water euneritic dwellers is prominent in this fauna, as is a temperate- to cold-water, eu- to mesoneritic *Spisula* association that has been recognized in lower Middle Miocene strata of northwestern Hokkaido and northwestern Sakhalin. The cooccurrence of these two ecologically dissimilar faunal associations implies that adjacent warm (inshore) and cold (offshore) water masses were present within the temperate marine realm that prevailed in Hokkaido and in southwestern Sakhalin during the early Middle Miocene.

Key words : Early Middle Miocene, Ausinskaya Formation, warm-water, Mollusca, Sakhalin

Introduction

Neogene strata in southwestern Sakhalin consist of the Kholmskaya, Nevel'skaya, Chekhovskaya, Verkhneduiskaya, Ausinskaya, Kurasiiskaya and Maruyamskaya Formations, in ascending order (Table 1 ; Smekhov, 1948 ; Interdepartmental Committee on Stratigraphy, 1961, 1976). Of these, the upper part of the Chekhovskaya Formation near Novoselovo has yielded a K-Ar age of 16.9Ma (Okamura, 1994), and the Ausinskaya Formation in the Makarov Region of eastern Sakhalin has been correlated with the *Denticulopsis lauta* Zone of Koizumi (1985) by Arkhipova *et al.* (1992). Therefore, we regarded the age of the Ausinskaya Formation in southwestern Sakhalin as early Middle Miocene.

Molluscs from the Ausinskaya Formation were studied by Russian workers (Ilyina, 1954 ; Krishtofovich, 1964 ; Zhidkova *et al.,* 1968 ; Khudik, 1989). According to Zhidkova *et al.* (1968), the stratotype of the Ausinskaya Formation is situated along the Bezymyannaya (old name, Ausi ; now Tolkaya) River just south of the Arkansas River. Ilyina (1954) reported abundant mollusc species in the upper part of the Uglegorskaya Formation (=Ausinskaya Formation) between the Bezymyannaya and Novoselka Rivers, and she described and illustrated nine new species from there. Khudik (1989)

noted the following species present chiefly in the uppermost part of the Ausinskaya Formation : *Ciliatocardium shinjiense* (Khramova), *Serripes groenlandicus* (Bruguière), *Peronidia pulchra* (Slodkewitsch), *Macoma calcarea* (Gmelin), *Macoma nasuta* (Conrad), *Dosinia ausiensis* Ilyina, *Cultellus izumoensis* Yokoyama, *Panomya simotomensis* Otuka and *Mya cuneiformis* (Böhm). However, the fauna from the main part of the Ausinskaya Formation has never been thoroughly examined or compared with the early Middle Miocene

Table 1. Neogene stratigraphy of South Sakhalin (Smekhov, 1948 : Interdepartmental Committee on Stratigraphy, 1961, 1976).

Age	Formations
Pliocene	Maruyamskaya
	Kurasiiskaya
	Ausinskaya
Miocene	Verkhneduiskaya
	Chekhovskaya
	Nevel'skaya
	Kholmskaya
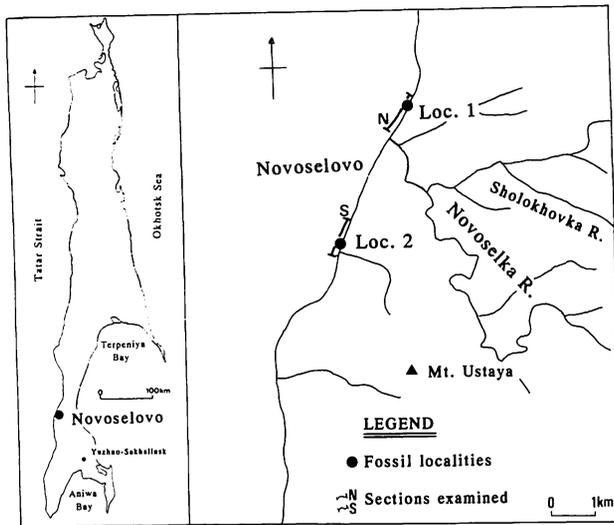
Figure 1. Fossil localities around Novoselovo in south-western Sakhalin.

faunas of Hokkaido, which are the geographically nearest coeval faunas.

In his summary of early Middle Miocene marine climates in northern Japan, Chinzei (1986) assigned the Chikubetsu fauna (Uozumi, 1962) of northwestern Hokkaido to the cold-water realm. He put northwestern Hokkaido in the subarctic (?) region on his proposed climato-geographic map. On the other hand, Ogasawara (1994) judged the Chikubetsu fauna to be a cool-temperate one, based on the cooccurrences of *Spisula equilateralis, Platyodon nipponica* and *Mercenaria* sp. along with *Anadara, Dosinia* and *Sinum* (Noda, 1992). None of these workers discussed coeval faunas of Sakhalin, such as the Ausinskaya fauna. The examination of Ausinskaya molluscs herein is made to address the differences in paleoclimatic interpretations noted above. To this end, we collected many mollusc species from the Ausinskaya Formation at the localities along the coast near Novoselovo (Figure 1). The purposes of this study are to describe these species, to compare them to species from coeval faunas in Japan, and to discuss their biogeographic significance.

Geologic setting and localities

The Chekhovskaya, Ausinskaya and Kurasiiskaya Formations are exposed around Novoselovo (Figure 1). The Chekhovskaya Formation is composed of lapilli tuff, tuff breccia and basaltic hyaloclastite (Figure 2), whereas the Ausinskaya Formation consists of fine- to medium-grained sandstone intercalated with two lignite seams and siltstone. An unconformable relationship between the Chekhovskaya and Ausinskaya Formations is observed in coastal cliffs about 800 m northeast of the mouth of the Novoselka River, where the basal conglomerate of the Ausinskaya Formation directly overlies the lapilli tuff of the Chekhovskaya Formation. The Ausinskaya sandstone bed in this area strikes N53°E and
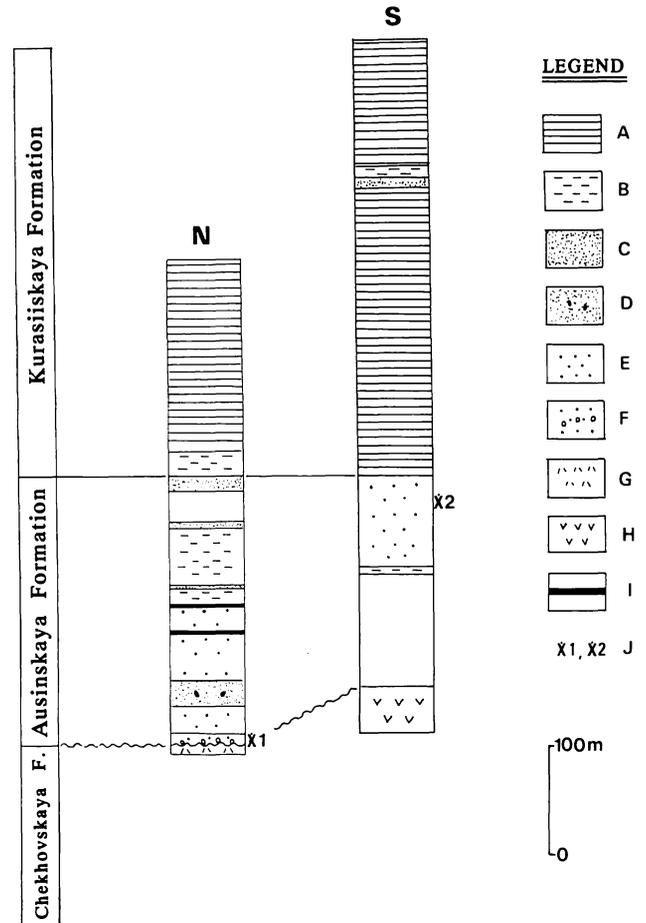
Figure 2. Columnar sections of Neogene formations around Novoselovo (N and S in Figure 1). Legend : A. mudstone ; B. siltstone ; C. fine-grained sandstone ; D. pebble-bearing fine-grained sandstone ; E. medium-grained sandstone ; F. pebble-bearing medium-grained sandstone ; G. lapilli tuff ; H. basaltic hyaloclastite ; I. lignite ; J. fossil horizons.

dips 16°W, while the Chekhovskaya tuff bed strikes N40°E and dips 15°E. The Kurasiiskaya Formation conformably overlies the Ausinskaya Formation and is subdivided into a lower part consisting of dark gray mudstone and an upper part made up of hard siltstone.

Both the Ausinskaya and Kurasiiskaya Formations have westward dips in an area between about 800 m east and 1.3 km west of the mouth of the Novoselka River. However, to the west of the present area, these strata strike N54-79°W and dip 17-40°E, which suggests the presence of a small basin-like structure in the area of Novoselovo.

We collected many mollusc fossils from the following two localities.

Loc. 1. Coastal cliff about 800 m northeast of the mouth of the Novoselka River ; tuffaceous pebble-bearing sandstone containing abundant plant debris, just above the basal conglomerate of the Ausinskaya Formation.

Loc. 2. Coastal cliff about 2.5 km southwest of the mouth

of the Novoselka River; medium-grained sandstone with calcareous concretions; upper part of the Ausinskaya Formation.

Molluscan associations in the Ausinskaya Formation

A total of 32 species of molluscs, including 25 bivalves and 7 gastropods, were collected from the two localities noted below (Table 2). Thirteen bivalve and four gastropod species were identified, of which only four species had been previously described and illustrated by Ilyina (1954) and Zhidkova *et al.* (1968) from the Ausinskaya Formation: *Modiolus tetragonalis, Dosinia ausiensis, Cultellus izumoensis* and *Reticunassa ausiensis*.

The living counterparts of the species from Loc. 1 dwell in various kinds of substrates, including rock (*Modiolus*), sand and gravel (*Chlamys*), muddy sand (*Dosinia*), and mud (*Tateiwaia*). Moreover, most bivalves at this locality occur as detached valves, suggesting an allochthonous nature.

Many sandy bottom dwellers such as *Dosinia* and *Anadara* were obtained from medium-grained sandstone at Loc. 2.

Most bivalves occur as articulated specimens, which suggest that the fauna is autochthonous. This assemblage comprises the *Dosinia-Anadara* association, consisting of *Dosinia* (*Phacosoma*) *tugaruana, D.* (*Kaneharaia*) *ausiensis, Anadara watanabei, Glycymeris cisshuensis, Cultellus izumoensis, Mercenaria yiizukai,* and *Euspira meisensis*.

The species composition of the *Dosinia-Anadara* association is similar to that of the *Mercenaria* assemblage (Noda, 1992) from the lower Middle Miocene Chikubetsu Formation in northwestern Hokkaido, and to the *Dosinia-Clinocardium* assemblage (Chinzei and Iwasaki, 1967) from the lower Middle Miocene Kadonosawa Formation in northeastern Honshu. According to Noda (1992), the *Mercenaria* assemblage is characterized by *Mercenaria yiizukai, Anadara ogawai, Dosinia* (*Kaneharaia*) *kaneharai kannoi* (=*D. ausiensis*) and *Cultellus izumoensis*. This assemblage is considered to have lived in the euneritic zone in subtropical to temperate waters.

The *Dosinia-Clinocardium* assemblage, on the other hand, is composed of *Dosinia* (*Phacosoma*) *nomurai, Clinocardium shinjiense, Anadara ninohensis, Clementia iizukai, Glycymeris*

Table 2. Molluscan fossils from the Ausinkaya Formation around Novoselovo. Numbers on the right are specimens from each locality.

Taxa Localities	1	2
Anadara (*Anadara*) *watanabei* (Kanehara)		3
A. ? sp.	1	
Glycymeris (Glycymeris) cisshuensis Makiyama		1
G.(G.) idensis Kanno		8
G.(G.) sp.		1
Modiolus tetragonalis Slodkewitsch	1	
Chlamys (Chlamys) arakawai (Nomura)	3	
C. (Chlamys) otukae Masuda and Sawada		1
C. sp.		1
Nanaochlamys sp.	1	
Clinocardium cf. decoratum (Grewingk)	1	
C. aff. nuttallii (Conrad)	1	
C. sp.		1
Macoma sp.	1	
Spisula (Pseudocardium) haboroensis (Yokoyama)		2
Oxyperas? sp.	1	
Solen sp.		1
Cultellus izumoensis Yokoyama		2
Mercenaria yiizukai (Kanehara)		3
Dosinia (Phacosoma) tugaruana Nomura	1	12
D. (Kaneharaia) ausiensis Ilyina	1	7
Saxidomus sp.	2	
Potamocorbula aff. amurensis (Schrenck)	1	
Panopea japonica A. Adams	1	
Thracia pertrapezoidea Nomura		1
Tateiwaia sp.	5	
Crepidula jimboana Yokoyama	1	
Euspira meisensis (Makiyama)	1	2
Glossaulax didyma coticazae (Makiyama)	4	1
Boreotrophon? sp.	1	
Reticunassa ausiensis (Ilyina)	6	
Plicifusus sp.	2	

cisshuensis, Siratoria siratoriensis, and *Euspira meisensis,* which are thought to be representatives of a sandy bottom habitat below the low-tide line (Chinzei and Iwasaki, 1967).

The bivalves, *Dosinia (Kaneharaia) ausiensis, Cultellus izumoensis* and *Mercenaria yiizukai* cooccur in the *Dosinia Anadara* association of the Ausinskaya Formation and the *Mercenaria* assemblage from the Chikubetsu Formation. These species are not present in the *Dosinia-Clinocardium* assemblage of the Kadonosawa Formation, although some warm-water taxa, including *Clementia iizukai* and *Siratoria siratoriensis,* are characteristic species only in the Kadono-sawa assemblage.

Biogeographic significance of the Ausinskaya fauna

The Ausinskaya fauna contains many subtropical to temperate water species (Uozumi, 1962 ; Ogasawara, 1994) such as *Anadara watanabei, Glycymeris cisshuensis, Cultellus izumoensis, Dosinia tugaruana, Tateiwaia* sp., and *Euspira-meisensis.* *Tateiwaia* is an especially characteristic genus of the tropical to subtropical Arcid-Potamid fauna (Tsuda, 1965).

It is noteworthy that the fauna around Novoselovo shares many species in common with the early Middle Miocene fauna of the Tanosawa Formation in Nishitsugaru district, Aomori Prefecture (Nomura, 1935 ; Ogasawara, 1977). These include *Glycymeris vestitoides* (= *G. cisshuensis*), *Chlamys arakawai, Cultellus izumoensis, Dosinia tugaruana, Thracia pertrapezoidea* and *Euspira meisensis.* The Nishi-tsugaru district at that time lay in a subtropical zone (Chinzei, 1986).

In contrast, only two cold-water species (Uozumi, 1962), *Spisula haboroensis* and *Mercenaria yiizukai,* were obtained from the upper horizon (Loc. 2) of the Ausinskaya Formation. *Mercenaria yiizukai* is one of the characteristic species of the Chikubetsu fauna of northwestern Hokkaido (Kanno and Matsuno, 1960).

The Chikubetsu fauna is subdivided into the *Penitella, Spisula,* and *Mercenaria* assemblages (Noda, 1992). The *Spisula* assemblage is characterized by the dominant occurrence of *Spisula equilateralis* (Clark) (= *S. voyi onnechiuria* (Otuka)), in association with *Clinocardium* spp., *Serripes groenlandicus* (Bruguière), *Megangulus tmatumotoi* (Otuka) (= *M. protovenulosus* (Nomura)) and *Macoma optiva* (Yo-koyama). Noda (1992) inferred that this assemblage flouri-shed in the eu- to mesoneritic zone in temperate to cold waters. We found this assemblage in the stratotype of the lower Middle Miocene Sertunaiskaya Formation along the coast near Mgachi, northwestern Sakhalin.

As noted above, the species composition of the *Dosinia-Anadara* association in the Ausinskaya fauna resembles that of the *Mercenaria* assemblage in the Chikubetsu fauna which is estimated to have lived in the euneritic zone of sub-tropical to temperate waters.

The cold-water *Spisula* and temperate water *Dosinia-Anadara* associations coexisted in Sakhalin and northwest-ern Hokkaido during the early Middle Miocene (Figure 3). It is suggested that such climatologically different faunal associations could hardly be reconciled to dwelling together,
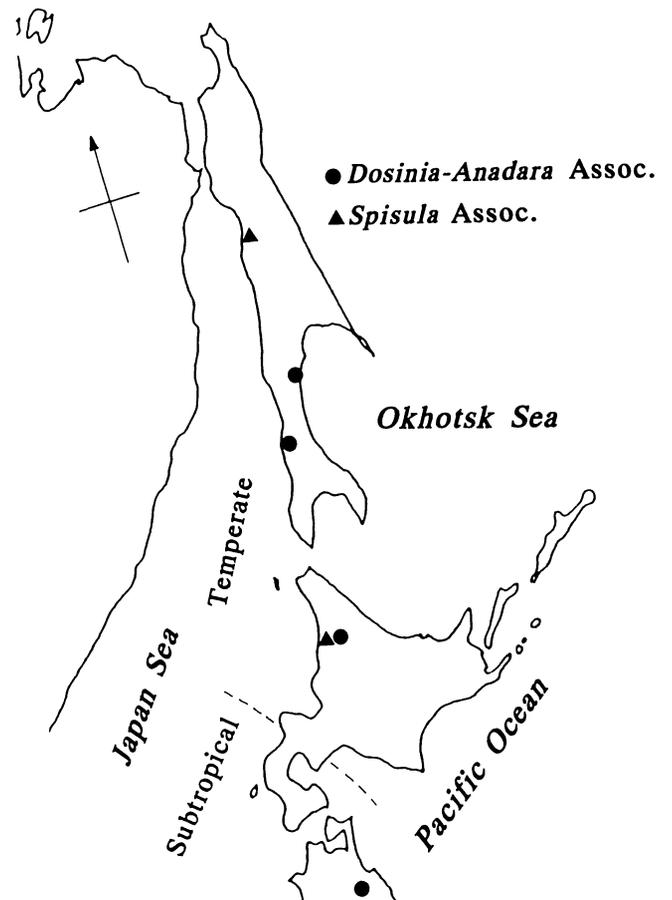
Figure 3. Distribution of *Dosinia-Anadara* and *Spisula* associations in northern Japan and Sakhalin during early Middle Miocene time.

but could have lived at distinctive depths, the cold-water *Spisula* association inhabiting slightly deeper water than the warm-water *Dosinia-Anadara* association. Uchimura and Majima (1992) noted for early Middle Miocene molluscs of the Furanui Formation in central Hokkaido that warm-water species were abundant in shallow-water deposits above normal wave base, whereas cold-water species lived in deeper water. These occurrences suggest that adjacent but thermally different water masses prevailed in both north-western Hokkaido and southwestern Sakhalin during the early Middle Miocene. A similar situation occurs today in mild-temperate waters along the Joban coast, Fukushima Prefecture, northeastern Honshu (Nemoto and Akimoto, 1990). Oxygen isotope paleotemperatures derived from the bivalves *Mya cuneiformis* and *Macoma nasuta* in the Ausins-kaya Formation are 15-16.5°C (Khudik *et al.,* 1984), which approximates the mean annual surface temperature along the modern Joban coast.

We conclude that southwestern Sakhalin lay in a temper-ate zone rather than a subboreal or subarctic zone during the early Middle Miocene. This climato-geographic scenario generally agrees with the coeval paleoclimate inferred for

northwestern Hokkaido by Ogasawara (1994). However, the subdivision of the early Middle Miocene temperate marine province of this region into warm, mild- and cool-temperate zones is difficult. The absence of clearly distinct temperature-based faunal associations in central Hokkaido and southwestern Sakhalin makes such subdivisions uncertain, as mentioned above.

Systematic notes on some species

Class Bivalvia
Family Pectinidae
Genus *Chlamys* Röding, 1798
Subgenus *Chlamys* Röding, 1798

Chlamys (*Chlamys*) *arakawai* (Nomura, 1935)

Figures 4-14, 15

Pecten islandicus Müller. Matsumoto, 1930, p. 104, pl. 40, fig. 9 (non Müller, 1776).

Pecten (*Pecten*) *arakawai* Nomura, 1935, p. 40, 41, pl. 4, figs. 1, 2.

Pecten (*Chlamys*) *arakawai* Nomura. Nomura, 1940, p. 17, pl. 2, figs. 1-3.

Coralichlamys shigemai Hirayama, 1954, p. 51, 52, pl. 3, fig. 2.

Chlamys arakawai (Nomura). Masuda, 1954, p. 150, 152, pl. 19, figs. 1-6; Sawada, 1962, p. 67, 68, pl. 6, fig. 20; Hirayama, 1967, p. 390, pl. 1, figs. 13-17; Ogasawara *et al.*, 1989, p. 77, pl. 3, fig. 1; Sato, 1991, p. 30-39, pl. 1, figs. 1-9, pl. 2, figs. 1-9, pl. 3, figs. 1-6; Kobayashi and Ueda, 1991, p. 132, pl. 4, figs. 4, 5.

Chlamys cf. *arakawai* (Nomura). Iwai, 1960, pl. 1, fig. 9.

Chlamys (*Chlamys*) *arakawai* (Nomura). Kotaka and Noda, 1967, pl. 2, fig. 3.

Remarks and comparison.—Three specimens were obtained from Loc. 1. *Chlamys arakawai* from the Ausinskaya Formation is large in size (maximum height=84.3 mm), higher than long, and moderately inflated. There are 23 weakly granulated radial ribs with one interstitial thread and 23 rounded radial ribs on the left valve. Anterior auricle of left valve is large, with eight radial threads.

Krishtofovich (1964, pl. 17, fig. 1) illustrated a species living around the Japanese Islands, *Chlamys* (*Chlamys*) *farreri nipponensis* Kuroda, from the Miocene Uandinskaya Formation in northwestern Sakhalin. His Uandinskaya specimen is closely allied to *Chlamys arakawai* in its shell size (height= 75.0 mm), proportions (height/length ratio=1.09), number of ribs (23?), and having granulated ribs with one interstitial

thread. However, Krishtofovich (1964) gave no description of the Uandinskaya specimen, so it is difficult to exactly compare it with *Chlamys arakawai*.

Measurements (*in mm*).—

Specimens	Length	Height	NR*	Valve
JUE no. 15574-1	57.1+	84.3	23	left
JUE no. 15574-2	—	59.6	23	right

* number of ribs

Distribution.—Ausinskaya Formation of Sakhalin; Kaigarabashi Member in southwestern Hokkaido; Tanosawa, Moniwa, Otsutsumi, Yanagawa and Orito Formations in Honshu; early Middle to late Middle Miocene.

Chlamys (*Chlamys*) *otukae* Masuda and Sawada, 1961

Figures 4-16

Chlamys sp. Otuka, 1935, pl. 55, fig. 142.

Chlamys cf. *hataii* Masuda and Akutsu, 1956, pl. 20, figs. 7-9.

Chlamys otukae Masuda and Sawada, 1961, p. 19, pl. 4, figs. 1-5; Masuda, 1962, p. 182, pl. 19, figs. 13, 14, pl. 21, fig. 12; Ogasawara, 1976, p. 41, 42, pl. 2, figs. 1, 2; Bito *et al.*, 1980, pl. 1, figs. 8, 10; Masuda *et al.*, 1989, p. 16, 17, pl. 2, figs. 7, 9, 10; Sato, 1991, p. 52-56, pl. 8, figs. 1-14.

Remarks and comparison.—One right valve was obtained from Loc. 2. The shell is small in size (length=19.1 mm), slightly inflated and somewhat higher than long. The valve is ornamented with 22 flat round-topped and smooth radial ribs. The radial ribs are broader than their interspaces, which have one intercalary thread.

The present species shows a wide range of variation in the bifurcation mode of its radial ribs (Sato, 1991). The early portion of the primary ribs of the Ausinskaya specimen is subdivided into two or three parts, making it look like a specimen from the Kaigarabashi Member in Hokkaido illustrated by Masuda and Sawada (1961, pl. 4, fig. 4).

The present species is morphologically very similar to *Chlamys akitana* (Yokoyama) but differs from the latter in having a less inflated shell and fewer radial ribs.

Measurements (*in mm*).—

Specimens	Length	Height	NR*	Valve
JUE no. 15575	18.1	19.1	22	right

* number of radial ribs

Distribution.—Ausinskaya Formation in Sakhalin; Kaiga-

Figure 4. All figures natural size, unless otherwise stated. **1.** *Glycymeris* (*Glycymeris*) *idensis* Kanno, Loc. 2, JUE no. 15582. **2.** *Modiolus tetragonalis* Slodkewitsch, Loc. 1, JUE no. 15583, ×1.5. **3, 8.** *Dosinia* (*Kaneharaia*) *ausiensis* Ilyina, Loc. 2, JUE nos. 15580-3, 15580-1. **4.** *Anadara* (*Anadara*) *watanabei* (Kanehara), Loc. 2, JUE no. 15584. **5.** *Panopea japonica* A. Adams, Loc. 1, JUE no. 15585. **6, 7.** *Dosinia* (*Phacosoma*) *tugaruana* Nomura, 6: Loc. 1, JUE no. 15577, 7: Loc. 2, JUE no. 15578-1, ×1.2. **9.** *Mercenaria yiizukai* (Kanehara), Loc. 2, JUE no. 15586. **10.** *Clinocardium* aff. *nuttallii* (Conrad), Loc. 1, JUE no. 15587. **11.** *Euspira meisensis* (Makiyama), Loc. 2, JUE no. 15588. **12.** *Glossaulax didyma coticazae* (Makiyama), Loc. 1, JUE no. 15589. **13.** *Glycymeris* (*Glycymeris*) *cisshuensis* Makiyama, Loc. 2, JUE no. 15590. **14, 15.** *Chlamys* (*Chlamys*) *arakawai* (Nomura), Loc. 1, JUE nos. 15574-1, 15574-2. **16.** *Chlamys* (*Chlamys*) *otukae* Masuda and Sawada, Loc. 2, JUE no. 15575, ×1.5. **17.** *Nanaochlamys* sp., Loc. 1, JUE no. 15576.
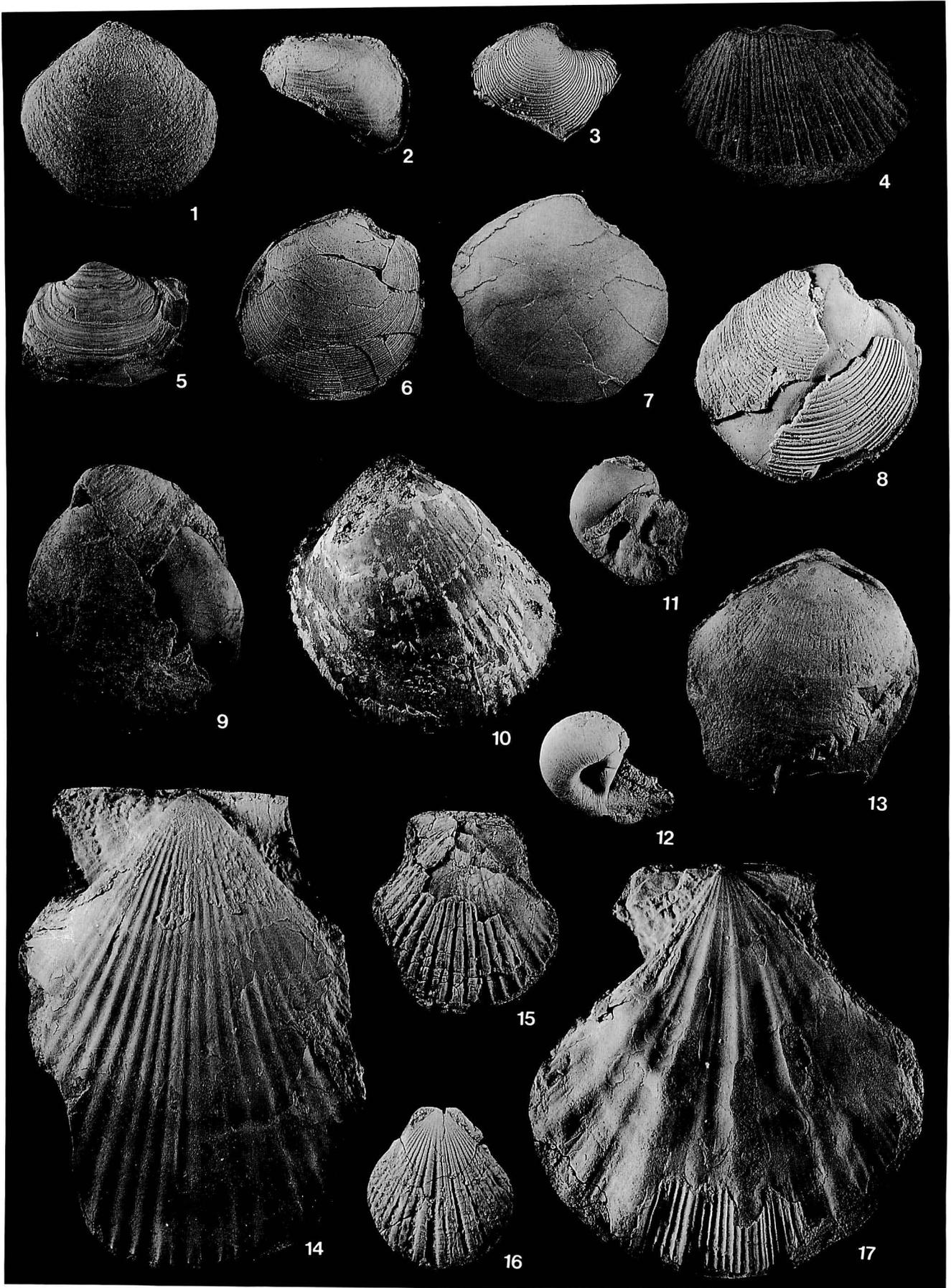
rabashi Member in Hokkaido; Metoki, Moniwa, Oido, Otsutsumi, Utsuno, Nanao, Ogane Formations in Honshu; early Middle to late Middle Miocene.

Genus *Nanaochlamys* Hatai and Masuda, 1953

Nanaochlamys sp.

Figure 4-17

Description.—One left valve was obtained from Loc. 1. Shell medium in size, flat and subequilateral except for auricles. Apical angle 95°. Surface ornamented with radial ribs and a weak concentric constriction. Primary radial ribs five, provided with six roof-shaped riblets separated by broader interspaces. Secondary radial ribs four, low, and ornamented with three riblets. Interspaces of primary and secondary ribs sculptured with three or four roof-shaped riblets. Anterior auricle much larger than posterior one, provided with five radial striations. Posterior auricle with six radial threads.

Measurements (in mm).—

Specimens	Length	Height	Valve
JUE no. 15576	63.1	69.6	left

Remarks and comparison.—The present specimen is very similar in appearance to *Nanaochlamys otutumiensis* (Nomura and Hatai, 1937), especially to specimens from the Middle Miocene Suenomatsuyama Formation illustrated by Masuda (1960, pl. 39, fig. 7). However, the present species differs from *N. otutumiensis* in having a flat shell and several roof-shaped riblets on the back of the primary and secondary ribs as well as within the interspaces between the ribs. In its early juvenile stage, *N. otutumiensis* sometimes has a flat left valve like the Ausinskaya specimen. So, it is possible to consider the Ausinskaya species as an ancestral form of *N. otutumiensis.*

It is easy to discriminate the Ausinskaya specimen from *Swiftopecten swiftii* (Bernardi), because it has a larger apical angle, a few secondary ribs, and many roof-shaped riblets.

Family Veneridae
Genus *Dosinia* Scopoli, 1777
Subgenus *Phacosoma* Jukes-Brown, 1912

Dosinia (Phacosoma) tugaruana Nomura, 1935

Figures 4-6, 7

Dosinia tugaruana Nomura, 1935, p. 58, 59, pl. 6, fig. 6.
Dosinia odosensis Nomura, 1935, p. 59, 60, pl. 6, fig. 2.
Dosinia (Phacosoma) tugaruana Nomura. Masuda, 1963, p. 32, 34, pl. 6, figs. 8-10; Gladenkov et al., 1987, p. 35, 36, pl. 7, figs. 2, 7, 8, 10, pl. 8, figs. 5, 6, 12.
Dosinorbis odosensis (Nomura). Itoigawa et al., 1974, p. 87, pl. 23, fig. 7.
Phacosoma odosensis (Nomura). Itoigawa et al., 1981, pl. 15, fig. 4; Itoigawa et al., 1982, p. 81, 82.

Remarks.—Twelve specimens were obtained from Loc. 2

and one from Loc.1. The Ausinskaya specimens are small to medium in size, moderately inflated, and subcircular in form. Pallial sinus narrow, bluntly pointed at end, extending to central part of valve.

Dosinia tugaruana and *D. odosensis* were described at the same time by Nomura (1935) from the Miocene Tanosawa Formation in Aomori Prefecture, northern Japan. As first noted by Masuda (1963), the two species are likely to be synonyms.

Iwai (1961) illustrated a specimen as *Dosinia tugaruana* from the Miocene Ainaigawa Formation and later (Iwai, 1965) illustrated it again under the name *Dosinia akaisiana* Nomura. Poor preservation of the Ainaigawa specimen prevents us from evaluating its species assignment.

Measurements (in mm).—

Specimens	Length	Height	Depth	Valve
JUE no. 15577	33.1	30.3	—	right
JUE no. 15578-1	33.1	30.6	12.9	both
JUE no. 15578-2	36.5	35.8	13.7	both
JUE no. 15578-3	17.7	17.1	8.2	both

Distribution.—Kakertskaya Formation and Ezhovii Horizon of Kamchatka; Ausinskaya Formation of Sakhalin; Tanosawa Formation and Mizunami Group of Honshu; all early Middle Miocene.

Subgenus *Kaneharaia* Makiyama, 1936

Dosinia (Kaneharaia) ausiensis Ilyina, 1954

Figures 4-3, 8

Dosinia ausiensis Ilyina, 1954, p. 228, 229, pl. 18, figs. 7, 8; Zhidkova et al., 1968, p. 107, 108, pl. 5, fig. 2, pl. 18, figs. 7, 8.
Dosinia mirabilis Uozumi (MS). Fujie et al., 1964, pl. 6, fig. 4.
Dosinia (Kaneharaia) kaneharai kannoi Masuda. Masuda, 1967, pl. 2, fig. 9; Noda, 1992, p. 83, 84, pl. 4, fig. 1.
Dosinia (Kaneharaia) kaneharai rumoiensis Amano, 1983, p. 50, 51, pl. 4, fig. 12, pl. 5, figs. 1, 5, 10.
Dosinia (Kaneharaia) kaneharai uandiensis Sinelnikova in Gladenkov et al., 1987, p. 35, pl. 7, figs. 4, 6.
Dosinia (Kaneharaia) ausiensis Ilyina. Gladenkov et al., 1987, p. 35, fig. 3; Amano and Sato, 1995, p. 7, figs. 4-3, 6, 12.
Dosinia (Kaneharaia) kaneharai Yokoyama. Shimizu and Fujii, 1995, fig. 6.

Remarks.—Only one specimen was collected from Loc. 1 and seven from Loc. 2. *Dosinia ausiensis* is small to medium in size (maximum length = 50.6 mm) and subcircular to ovately elongate in shape. Surface is sculptured by rather fine concentric cords which are rounded and elevated near the ventral margin. Number of cords between 1 cm and 2 cm from the beak is 15. Pallial sinus triangular, shallow, and wide.

The present species was established by Ilyina (1954), based on a specimen from the Uglegorskaya (now Ausinskaya) Formation at Bezymyannii (old Japanese name, Ausi). When he summarized Japanese *Kaneharaia,* Masuda (1967) illustrated a specimen from the Ausi River (type locality of

Dosinia ausiensis) under the name *D.* (*Kaneharaia*) *kaneharai kannoi*. Noda (1992) also described and illustrated *D.* (*K.*) *kaneharai kannoi* from the early Middle Miocene Chikubetsu Formation of northwestern Hokkaido. However, judging from his figure, Noda's (1992) Chikubetsu specimen is better identified with *D. ausiensis,* because of its subcircular shell form and many fine concentric cords.

Amano (1983) proposed *Dosinia* (*Kaneharaia*) *kaneharai rumoiensis* from the Middle Miocene Togeshita Formation of Hokkaido, and Sinel'nikova in Gladenkov *et al.* (1987) described *D.* (*K.*) *kaneharai uandiensis* from the Miocene Uandinskaya Formation in northwestern Sakhalin. However, it is difficult to separate these subspecies from *D. ausiensis* using ornamentation, shell size, shell shape or the form of the pallial sinus. Therefore, these subspecies are considered to be synonyms of the present species.

Comparison.—The present species is closely related to *Dosinia* (*Kaneharaia*) *kannoi* Masuda in its shell size and number of concentric cords (11–16 between 1 cm and 2 cm from the beak). However, this species differs slightly from *D.*

(*K.*) *kannoi* in having a more inflated shell and round-topped as well as elevated concentric cords near the ventral margin.

It is easy to distinguish *D.* (*K.*) *kaneharai* Yokoyama from *D.* (*K.*) *ausiensis,* because the former species has an ovate shell and fewer concentric cords (8–11 between 1 cm and 2 cm from the beak). *D.* (*K.*) *ausiensis* ranges from the lower Middle Miocene to the Lower Pliocene, whereas *D.* (*K.*) *kaneharai* ranges from Middle to Upper Miocene. Stratigraphically, the range of the latter species is shorter than that of the former.

Measurements (*in mm*).—

Specimens	Length	Height	Depth
JUE no. 15579	50.6	54.1	—
JUE no. 15580-1	39.2	37.2	19.0+
JUE no. 15580-2	30.6	26.5+	—

Distribution.—Early Middle Miocene Ausinskaya and Uandinskaya Formations in Sakhalin; early Middle Miocene
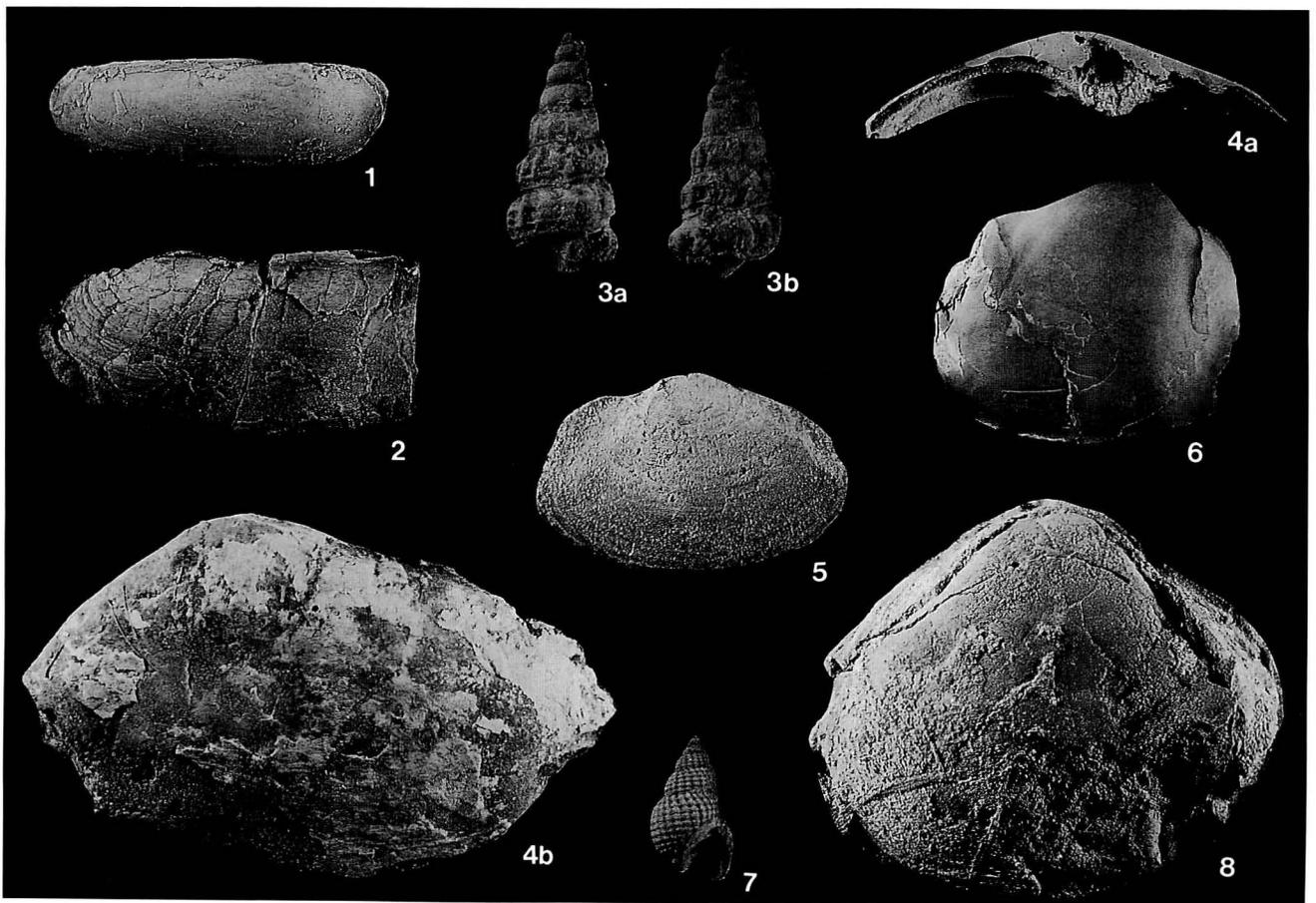
Figure 5. All figures natural size, unless otherwise stated. **1, 2.** *Cultellus izumoensis* Yokoyama, Loc. 2, JUE nos. 15591-1, 15591-2. **3a-b.** *Tateiwaia* sp., Loc. 1, JUE no. 15581, ×2. **4a-b.** *Oxyperas* ? sp., Loc. 1, JUE no. 15592. **5.** *Thracia pertrapezoidea* Nomura, Loc. 2, JUE no. 15594, ×1.45. **6.** *Saxidomus* sp., Loc. 1, JUE no. 15593. **7.** *Reticunassa ausiensis* (Ilyina), Loc. 1, JUE no. 15595, ×2.05. **8.** *Spisula* (*Pseudocardium*) *haboroensis* (Yokoyama), Loc. 2, JUE no. 15596.

Chikubetsu, Middle Miocene Togeshita and Tachikarau-shinai Formations in Hokkaido; Late Miocene? "Otogawa Formation" and Early Pliocene Joshita Formation in Honshu.

Class Gastropoda
Family Potamididae
Genus *Tateiwaia* Makiyama, 1936

Tateiwaia sp.

Figures 5-3a, b

Description.—Five specimens from Loc. 1 were examined. Shell small in size and turreted. Post-nucleus whorls seven in number; spire elevated and narrowly conical. Surface ornamented with three spiral threads and 14 axial ribs; upper spiral thread rather strong on shoulder, making weak nodes where it crosses each axial rib; middle spiral thread also strong; lowermost spiral thread weak and situated just above suture. Gently sloping area present above shoulder. Aperture poorly preserved.

Measurements (in mm).—

Specimens	Height	Diameter
JUE no. 15581	15.6	7.9

Remarks.—The Ausinskaya species resembles *Tateiwaia yamanarii* (Makiyama) in having three spiral threads. However, *T. yamanarii* has less numerous (8-9) axial ribs and higher whorls than the present species.

Tateiwaia yamanarii (Makiyama) and *T. tateiwai* (Makiyama) are characteristic elements of the subtropical intertidal association of early Middle Miocene age (Chinzei, 1986). According to Uozumi (1962), both species were previously known only from the early Middle Miocene Takinoue Stage in southwestern and central Hokkaido. Therefore, the present specimens record the northernmost occurrence of this warm-water genus.

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SHORT NOTES

| 37 | *Archaeodictyomitra apiarium* (Rüst), the correct specific name of *A. apiaria, A. apiara* and *A. apiarum* |

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The radiolarian species *Archaeodictyomitra apiarium* (Rüst) has occasionally occurred from the Upper Jurassic and Lower Cretaceous in the various areas of the world, for example, Japan, southern Tibet, Alaska, California, southern Alps and deep sea of the Pacific (e.g., Nakaseko and Nishimura, 1981 ; Wu, 1993 ; Pessagno, 1977 ; Kocher, 1981 ; Matsuoka, 1992). Although this species is an important index fossil of Upper Jurassic and Lower Cretaceous pelagic strata, its name has been variously rendered as *Archaeodictyomitra apiaria, A. apiara, A. apiarium,* and *A. apiarum* (e.g., Baumgartner, 1987 ; Pessagno, 1977 ; Matsuoka and Yao, 1985 ; Nakaseko *et al.,* 1979 and so on).

Archaeodictyomitra apiarium was first described as *Lithocampe apiarium* by Rüst (1885). His original description of *Lithocampe apiarium* is as follows : "Die Schale mit 8 bis 10 Gliedern hat die Form eines langen Bienenkorbes. Die mittleren Glieder mit 3, die oberen und unteren mit 2 Querreihen von Löchern."

Rüst mentioned the derivatio nominis of this species in his description as "Bienenkorb", namely beehive. The Latin word "apiarium" is a neuter noun in the nominative singular, not an adjective, so that inflection is not necessary in case of change of generic name. Article 31 b(ii) of the International Code of Zoological Nomenclature (Ride *et al.* eds., 1985) explains this point as follows : "A species-group name that is a simple or compound noun (or noun phrase) in apposition retains the same ending, whatever the gender of the generic name with which it is combined." Consequently, *Archaeodictyomitra apiarium* is the correct usage following the International Code of Zoological Nomenclature.

Acknowledgments.—I would like to express my sincere thanks to Prof. K. Chinzei of Kyoto University for critical discussion.

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A GUIDE FOR PREPARING MANUSCRIPTS

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Cover : A terminally resorbed maxillary tooth of iguanodontids (Ornithischia : Ornithopoda). The specimen is from the Kuwajima Formation, the Neocomian section of the Tetori Group, in Shiramine-mura, Ishikawa County, Ishikawa Prefecture, the west coast of Central Honshu, Japan (Shiramine-mura Board of Education, Coll. Cat. No. SBEI 001, 23 mm in dorsoventral length).

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┉┉┉┉┉┉┉┉ 行 事 予 定 ┉┉┉┉┉┉┉┉

◎1997年の第146回例会は6月28日(土)・29日(日)に豊橋市自然史博物館で開催の予定です。
　一般講演の申し込みの締め切りは5月10日です

◎日本地質学会第104年学術大会は,日本古生物学会のほかの参加した連合学術大会となります。日
　本古生物学会は10月10日にシンポジウムを実施いたします。シンポジウム企画案は1997年3月
　までにお申し込み下さい。

◎1998年年会・総会は1998年1月下旬に,神奈川県立生命の星・地球博物館で開催予定です。シン
　ポジウム企画案を募集しております。企画案の締め切りは6月中旬です。

◎訂正:9月発行の日本古生物学会報告・紀事 N.S. No.183 の551頁に記載の第145回例会 (新潟大
　学) の参加者数は174名の誤りです。お詫びして訂正いたします。

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