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, *l.* (Cr.) *ernst* Heinz and *l.* (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


*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 *l.* incon-
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, pl. 14, fig. 1; Meek, 1876, p. 146, pl. 2; Stanton, 1933, p. 85, pl. 15, fig. 2; Heinz, 1928b, p. 34, pl. 2, fig. 1; Seitz, 1929, p. 118; Dobrov and Pavlova, 1939, 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; Ciesiński and Blaszkiewicz, 1984, p. 96, pl. 16, fig. 1; Szaós, 1985, p. 161, 162, pl. 6, figs. 1a, b; Ciesiński and Blaszkiewicz, 1989, p. 159, fig. 1; Tarkowski, 1991, p. 107, pl. 15, fig. 1.

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

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

Inoceramus deformis Meek, Kauffman, 1978b, p. XII–2, list.

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

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


Cremnoceramus deformis (Meek). Walaszczyk, 1958, pl. 8, figs. 1, 2; Kopaczewich and Walaszczyk, 1990, pl. 4, figs. 4a, b; Walaszczyk, 1992, p. 52, 53, pl. 29, fig. 4, pl. 30, fig. 4.

Cremnoceramus (? deformis). 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.3H3016 from loc. Ob0012, JG.3H058 and 3060 from loc. Ob0013 in the Obira area, northwest Hokkaido.

Description.—Shell medium-sized, subequivale 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 commissural 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 asymmetricaly 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 Creampton (1988, p. 967, text-fig. 3 and p. 965, 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 developed, 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.3H3016. 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 (a) 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.3H3016 (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.3H3016 resembles closely the holotype of l. (Cr.) paradiformis Szász, 1965, 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 subquadrangular 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, (a) being about 85° whereas in the specimens from Romania, the ribs are strongly elongated toward the posterior part of the valve, (b) varying between 35°–45°. Even in specimens of l. paradiformis 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 l. paradiformis Szász, 1985, l. dobrogensis Szász, 1985 and l. babadagensis Szász, 1985 from the Babadag Basin, Dobrogea, resemble closely one another and are obviously related to l. 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.

l. (Cr.) deformis was established on the basis of a single
Table 1. Measurements of Inoceramus (Cremnoceramus) deformis Meek from Hokkaido. Linear dimension in mm.

<table>
<thead>
<tr>
<th>specimen</th>
<th>valve</th>
<th>h</th>
<th>l</th>
<th>b</th>
<th>s</th>
<th>H</th>
<th>L</th>
<th>α</th>
<th>γ</th>
<th>δ</th>
<th>δ_{h=60mm}</th>
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<tbody>
<tr>
<td>JG. H3016</td>
<td>L.</td>
<td>99.2</td>
<td>81.8</td>
<td>39.8</td>
<td>39.3</td>
<td>99.6</td>
<td>87.0</td>
<td>132°</td>
<td>102°</td>
<td>86°</td>
<td>84°</td>
</tr>
<tr>
<td></td>
<td>R.</td>
<td>77.4</td>
<td>70.4</td>
<td>29.7</td>
<td>33.0</td>
<td>81.8</td>
<td>74.8</td>
<td>132°</td>
<td>102°</td>
<td>76°</td>
<td>70°</td>
</tr>
<tr>
<td>JG. H3058</td>
<td>R.</td>
<td>51.8</td>
<td>53.6</td>
<td>14.0</td>
<td>29.2</td>
<td>52.0</td>
<td>59.3</td>
<td>123°</td>
<td>103°</td>
<td>74°</td>
<td></td>
</tr>
<tr>
<td>JG. H3060</td>
<td>L.</td>
<td>53.3</td>
<td>45.1</td>
<td>19.2</td>
<td>18.1</td>
<td>53.3</td>
<td>42.7</td>
<td>136°</td>
<td>104°</td>
<td>87°</td>
<td></td>
</tr>
</tbody>
</table>

specimen | valve | l/h | l_{h=60mm} | b/h | b_{h=40mm} | L/H | s/l | remarks |
<table>
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<th></th>
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</thead>
<tbody>
<tr>
<td>JG. H3016</td>
<td>L.</td>
<td>0.82</td>
<td>0.94</td>
<td>0.40</td>
<td>0.40</td>
<td>0.87</td>
<td>0.47</td>
<td></td>
</tr>
<tr>
<td></td>
<td>R.</td>
<td>0.91</td>
<td>0.86</td>
<td>0.38</td>
<td>0.31</td>
<td>0.91</td>
<td>0.47</td>
<td></td>
</tr>
<tr>
<td>JG. H3058</td>
<td>R.</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>secondarily deformed</td>
</tr>
<tr>
<td>JG. H3060</td>
<td>L.</td>
<td>0.85</td>
<td>0.36</td>
<td>—</td>
<td>—</td>
<td>0.80</td>
<td>0.40</td>
<td>less than 60 mm in H</td>
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</table>

For Abbreviations, refer to Noda (1996, table 1 and fig. 1).

Improper 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 Cobb, 1977; Kauffman, 1977) and biostratigraphic records by Scott and Cobb (1964), Hattin and Cobb (1977), Kauffman (1977, 1978a, b) and Kennedy and Cobb (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 Cobb (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 evolute, comparatively small beak, not so prominent umbo, vaulted shell with genicular, 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.) paradefonis* 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.) schoenbachi prattei* Heinz, 1928 figured by himself (1928, 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.
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 \textit{I. (Cr.) deformis} as the last representative of the lineage of \textit{I. (Cr.) waltersdorfensis} Andert—\textit{I. (Cr.) bronngniarti} Mantell—\textit{I. (Cr.) deformis} Meek. Besides, Kauffman (1978b) considered the lineage of \textit{I. (Cr.) deformis} as \textit{I. (Cr.) rotundatus} Feige—\textit{I. (Cr.) erectus} Meek—\textit{I. (Cr.) deformis} Meek—\textit{I. (Cr.) schloenbachii} Böhm. The Japanese material is too deficient, at present, to discuss the phylogeny of \textit{I. (Cr.) deformis}. Nevertheless the vaulted shell with blunt radial elevations shown by JG.H3016 may suggest some relationships with \textit{I. (Cordiceramus)}.

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


Range.—Locs. Ob0012 and 0013 are located in Unit Ub which immediately overlies Unit Ua2 (Tanaka, 1963). Unit Ua2 contains \textit{I. (Cr.) rotundatus} which is a good cosmopolitan zonal index of the lower lower Coniacian. Besides, one of the associated species, \textit{I. (I.) uwajimensis}, is a representative of the upper lower to middle Coniacian of Japan and adjacent areas. Thus the stratigraphic position of \textit{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 Cobb (1951), Scott and Cobb (1964), Kauffman (1978a, b), Kauffman et al. (1978), Cobb (1986) and Szász and Ion (1988), but there is disagreement among them. According to the recent work by Kennedy and Cobb (1991) in the Western Interior, \textit{I. (Cr.) deformis} indicates practically the lower part of the middle Coniacian. Besides, Kopaevich 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 \textit{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.

\textbf{Inoceramus (Cremnoceramus) ernsti} Heinz, 1928

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

\textit{Inoceramus americani} Parkinson (pars). Woods, 1912a, p. 325, fig. 85.

\textit{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 (Chomacerasus) ernstii Heinz. JG.193223 from Loc.O02/000, × ca 0.5 (coll. T. Shimamura, 1983).
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. López, 1990, p. 189, 193, pl. 5, figs. 6a, b; López, 1992, p. 2, 245–246, pl. 1, figs. 4, 5a, b.

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

Tethyceramus (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).


Description. — Shell medium to large, slightly inequivalve, inequilateral, much higher than long. Valve considerably convex from anterior to posterior and also along growth zone which is straight or somewhat concave to anterior. Anterior wall angularly bent from disk and deeply concave to commissural plane, posterior and posteriororal 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. Anterooral 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 (d) 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 commissural 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. (l) hobetsensis nonsultus, 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 Sachsens (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 López (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, figs. 2, 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.

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<thead>
<tr>
<th>specimen</th>
<th>valve</th>
<th>h</th>
<th>l</th>
<th>b</th>
<th>s</th>
<th>H</th>
<th>L</th>
<th>α</th>
<th>γ</th>
<th>δ</th>
<th>δθ = 90°</th>
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<tr>
<td>JG. H3017</td>
<td>L.</td>
<td>140.0</td>
<td>109.2</td>
<td>46.2</td>
<td>38.4</td>
<td>141.0</td>
<td>102.5</td>
<td>120°</td>
<td>140°</td>
<td>87°</td>
<td>83°</td>
</tr>
<tr>
<td></td>
<td>R.</td>
<td>109.0</td>
<td>95.9</td>
<td>33.8</td>
<td>35.9</td>
<td>111.6</td>
<td>90.0</td>
<td>121°</td>
<td>138°</td>
<td>81°</td>
<td>78°</td>
</tr>
<tr>
<td>JG. H3059</td>
<td>L.</td>
<td>52.1</td>
<td>45.3</td>
<td>25.5</td>
<td>19.8</td>
<td>57.6</td>
<td>36.4</td>
<td>136°</td>
<td>90°</td>
<td>86°</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>R.</td>
<td>34.7</td>
<td>30.1</td>
<td>19.1</td>
<td>15.0</td>
<td>35.4</td>
<td>29.5</td>
<td>117°</td>
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<th>l/hi – 100mm</th>
<th>b/h</th>
<th>b/hi – 100mm</th>
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<th>s/l</th>
<th>remarks</th>
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<td>0.93</td>
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<td>0.26</td>
<td>0.73</td>
<td>0.35</td>
<td>secondarily deformed</td>
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<td>0.89</td>
<td>0.31</td>
<td>0.28</td>
<td>0.81</td>
<td>0.37</td>
<td>less than 60 mm in H</td>
</tr>
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<td>JG. H3059</td>
<td>L.</td>
<td>0.87</td>
<td>—</td>
<td>0.49</td>
<td>—</td>
<td>0.63</td>
<td>0.34</td>
<td>—</td>
</tr>
<tr>
<td></td>
<td>R.</td>
<td>0.86</td>
<td>0.55</td>
<td>—</td>
<td>0.83</td>
<td>0.50</td>
<td>0.36</td>
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</tbody>
</table>

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

Phylogeny.—The lectotype of *L. (Cr.) ernsti* was originally regarded as a variety of *L. lamarccki* Parkinson which belongs undoubtedly to *L. (Inoceramus)*. Herm et al. (1979) pointed out the ambiguity of whether *L. rotundatus* Fiege and the group of *L. waltersdorfiensis* Andert are assigned to *L. (Inoceramus)* or to *L. (Cremnoceramus)*, which suggests a close phylogenetic relationship between *L. (Inoceramus)* and *L. (Cremnoceramus)*. The development of blunt radial elevations in some specimens of *L. (Cr.) ernsti* may foretell the characters of *L. (Cordiceramus)* in the upper Coniacian and subsequent stages. In other words, it may be a "transient" linking *L. (Cremnoceramus)* and *L. (Cordiceramus)*. *L. (Co.) kawashitai* Noda, 1986, from the upper Coniacian of some areas of Hokkaido and Kyushu is certainly a descendant of *L. (Cr.) ernsti*. On the other hand, Tröger (1969, p. 74) located *L. (Cr.) ernsti* as a linking species between *L. (L.) lamarccki* stumacki Heinz. 1926, from the middle Turonian and *L. (Volvicerasenu) koeneni* Müller, 1887, from the middle Coniacian (so-called lower Coniacian before Seibertz, 1979). I agree with Tröger's scheme (1969, p. 74, fig. 3) for the reason mentioned previously in the phylogeny of *L. (Volvicerasenu) koeneni* (Noda, 1996).

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

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

Loc. Ob0011. The opposite bank of loc. Ob0012 [see p. 576, for the locality of *L. (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 8. Diagram showing individual relative growth between l and h, and b and h of *Inoceramus* (Cr.) ernsti (specimen JG.H3017).

"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 \textit{L. (L.) uwa-jimensis} and \textit{L. (P.) troegeri}.


\textit{Loc.ik8617a}. For the locality map, see Noda (1996, fig. 9).

\textbf{Figure 9.} Diagram showing ontogenetic changes in selected characters of \textit{Inoceramus} (Cr.) emstf. 
A: l/h, B: b/h, C: obliquity.
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 Okuhidakimata-zawa (so-called Okusamato-zawa), about 450 m west of the fork along the left branch. Fine sandy allstone bed of Illb member (Matsumoto, 1965) of the Upper Yezo Group. Associated with l. (l.) lwaemenensis.

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 (Crempceramus) lueckendorfensis**
Tröger, 1967

*Inoceramus inconstansts* Woods, Dobrov and Pavlova, 1959, p. 137, pl. 5, figs. 1a, b.

*Inoceramus inconstansts lueckendorfensis* Tröger, 1967, p. 122-125, pl. 11, figs. 1a-c; Tarkowski, 1991, p. 198, pl. 13, fig. 8.

*Inoceramus "inconstans" lueckendorfensis* Tröger, 1967a, p. 102, 106, 107, pl. 1, figs. 8-11.

*Inoceramus (Crempceramus) inconstansts lueckendorfensis* Tröger, 1989, p. 917, 918, list.

*Holotype.*—Arbeitnr. 92F (Tröger, 1967, pl. 11, fig. 1) by original designation.

*Material.*—JG.H3097 and 3098 from loc. Ob0003f.

*Description.*—Shell large-sized, subequivaive 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, 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

![Figure 12](image)

**Table 3.** Measurements of *Inoceramus (Crempceramus) lueckendorfensis* Tröger from Hokkaido.

<table>
<thead>
<tr>
<th>specimen</th>
<th>valve</th>
<th>h</th>
<th>l</th>
<th>b</th>
<th>s</th>
<th>H</th>
<th>L</th>
<th>α</th>
<th>γ</th>
<th>δ</th>
<th>δ_H-stem</th>
</tr>
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<tbody>
<tr>
<td>JG.H3097</td>
<td>L</td>
<td>105.7</td>
<td>89.2</td>
<td>45.4</td>
<td>45.0</td>
<td>107.6</td>
<td>87.5</td>
<td>118'</td>
<td>120'</td>
<td>77</td>
<td>72'</td>
</tr>
<tr>
<td>JG.H3098</td>
<td>L</td>
<td>102.8</td>
<td>88.1</td>
<td>42.0</td>
<td>37.8</td>
<td>106.1</td>
<td>86.4</td>
<td>118'</td>
<td>—</td>
<td>73</td>
<td>66'</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>specimen</th>
<th>valve</th>
<th>l/h</th>
<th>l/H-stem</th>
<th>b/h</th>
<th>b/H-stem</th>
<th>L/H</th>
<th>s/l</th>
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</thead>
<tbody>
<tr>
<td>JG.H3097</td>
<td>L</td>
<td>0.84</td>
<td>0.90</td>
<td>0.43</td>
<td>0.24</td>
<td>0.81</td>
<td>0.50</td>
</tr>
<tr>
<td>JG.H3098</td>
<td>L</td>
<td>0.87</td>
<td>0.93</td>
<td>0.41</td>
<td>0.29</td>
<td>0.81</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Figure 11. *Inoceramus (Crempceramus) lueckendorfensis* Tröger. All figures natural size. 1a-c. JG.H3097 from loc. Ob0003f. 2a-c. JG.H3098, same locality (coll. T. Shimazuki, T. Matsumoto and M. Noda, 1993).
negative allometry for JG.H3097 and isometry for JG.H3098, and those of \( b / h \) 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 ( \( \gamma \) ) 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 \( b / h \) vs. \( h \) in each specimen.

Profiles of the specimens in two directions are illustrated in Figure 14. In the cross section, somewhat angular eleva-
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 Kolonkha 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. (Conoceramus*)


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.
(1.) lusatiae Andert, l. (V.) koeneni Müller, l. (Cr.) deformis Meek, l. (Cr.) ernstl Heinz and l. (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: l. (Inoceramus), l. (Cremnoceramus), l. (Cordiceramus) and l. (Volvicerasmus). The discussion of each species leads to an argument in favor of Tröger’s scheme (1969) and implies, in addition, that l. (Cordiceramus) may have been derived from l. (Cr.) ernstl, which is assumed to be the common ancestor of l. (Cordiceramus) and l. (Volvicerasmus).

3. With respect to taxonomic ranks, Inoceramus, Cremnoceramus and Volvicerasmus 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.

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