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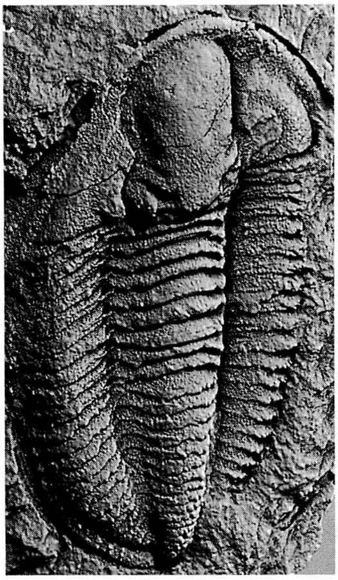

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June 30, 1990

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The fossil on the cover is *Phillipsia ohmorensis* Okubo, an Early Carboniferous trilobite from the Hikoroichi Formation in the Higuchizawa valley, Ofunato City, Iwate Prefecture, northeast Japan (Collected by A. Haga, PAt 5766, ×3.0; after Kobayashi and Hamada, 1980, pl. 6, fig. 4).

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898. ON *HAUERICERAS* DE GROSSOUVRE, 1894, A CRETACEOUS AMMONITE GENUS*

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Abstract. *Hauericeras* de Grossouvre, 1894 is a well known ammonite genus which occurs widely in the Upper Cretaceous of various regions. There are, however, three unsettled problems which are studied in this paper with the results as follows:

I. The type species, *Ammonites pseudogardeni* Schlüter, 1872 is redefined with designation of GBI. 48 (whose suture figured in the original paper) as its lectotype. This conforms with the concept of the same species by Müller and Wollemann (1906). *H. nodutum* (Schlüter, 1889) and *H. buszii* Wegner, 1905 fall in synonyms of *H. pseudogardeni* in the revised sense.

II. The sexual dimorphism exists evidently in the well studied species of *Hauericeras*. This is demonstrated by excellent specimens of *H. angustum* Yabe from Japan acquired by S.T. and Y.K. and also some more material. In *H. angustum* macroconchs are twice (or more) as large as microconchs in diameter. The apertural margin is distinctly sigmoidal in both conchs and lappeted in microconchs. *H. gardeni* (Baily) is likewise dimorphic. Many of the described specimens of *H. pseudogardeni* are macroconchs which may attain to 420 mm in diameter, whereas *H. mengedensis* (Schlüter) is probably a microconch of the same species.

III. The phylogenetic origin of *Hauericeras* is probably in a subgroup of *Puzosia* which has compressed nearly flat-sided whorls and weak or short ribs. The projected short ribs remain on the ventral part of *H. antiquum* Collignon, a Coniacian species, whereas an incipient keel occurs in a Turonian species of *Puzosia*. The two subgenera *H.* (*Hauericeras*) and *H.* (*Gardeniceras*) can be distinguished by the maintennance or disappearance of the ventral or ventrolateral riblets or nodes. They probably reflect the evolutionary stages. The proposal to combine the Hauericeratinae with Puzosiinae into the family Puzosiidae is approved.

Key words. *Hauericeras pseudogardeni*, *H. angustum*, dimorphism, *Puzosia*, *Hauericeras* (*Gardeniceras*).

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Introduction

Hauericeras de Grossouvre, 1894 is regarded as a well known ammonite genus which has been reported to occur widely in the Upper Cretaceous (Coniacian to Maastrichtian stages) of Europe, contiguous part of the USSR, South Africa, Madagascar, India, West Australia and the regions facing the North Pacific.

There are, however, at least three major problems about this genus which should be properly solved. First of all, I have a doubt on the current concept of *Ammonites pseudogardini* Schlüter, the type species of *Hauericeras*. Secondly, the idea of dimorphism seems to have been ignored in the hitherto published papers on the taxonomy and affinities of *Hauericeras*. Presence or absence of the dimorphs, and if present, what kind of dimorphism exists in the species of this genus should be worked out. Thirdly, the phylogenetic origin of *Hauericeras* is uncertain and debatable. On the ground of the renewed or improved knowledge concerning the above two points and also on other lines of evidence, I should give a reasonable interpretation on this problem.

In accordance with the procedures of research, three parts are set in this paper for the above three problems. I am primarily responsible for the overall reasoning. In Part II I invite S. Toshimitsu and Y. Kawashita as coauthors with me.

Part I. Restudy of the type species
(by T. Matsumoto)

The type species of the genus *Hauericeras* de Grossouvre, 1894 (p. 219) is *Ammonites pseudogardeni* Schlüter, 1872 (p. 54, pl. 16, figs. 3-6) as originally designated. This species was established on several syntypes, of which three of Schlüter's collection should be held in the Geological and Palaeontological Institute and Museum, University of Bonn (abbreviated here GBI.). I visited there in June 1965 and was afforded every facility to study Schlüter's collection of the Upper Cretaceous ammonites.

Of the two illustrated syntypes, GBI. 48 was there. It is the original specimen whose sutures were shown by Schlüter (1872, pl. 16, figs. 5, 6) and the drawing is correct. The other (ditto, pl. 16, figs. 3, 4) was missing and does not seem to be traced at present.

Considering the situation mentioned above, I designate herein GBI. No. 48, from the "Quadraten—Schichten" at Dülmen, Westfalen, as the lectotype of *Ammonites pseudogardeni*. This specimen is scarcely deformed secondarily but its surface is somewhat weathered. It is shown in Figure 1 and its dimensions are in Table 1. The measurements conform approximately with those by Kennedy and Summesberger (1987, p. 28). Anyhow, the specimen is wholly septate and 236 mm in diameter at its preserved end. On the assumption that this is the end of the phragmocone and that the body chamber occupied 240°, the entire shell diameter would be estimated roughly at 420 mm ($U=105$ mm, U/D assumed as 0.25). This size is the same order of magnitude as a macroconch of a certain species of *Puzosia*.

The whorl is compressed, with $B/H=0.40$ to 0.41, and fairly involute, nearly two thirds (in whorl-height) of the next inner whorl being overlapped by the outer one. The expansion ratio of the whorl is moderate, whereas the umbilicus is fairly narrow (see Table 1).

The outer whorl of the lectotype has several constrictions. They are probably six of which last two are distinct and others are more or less obscured by weathering. They are weak, narrow, gently flexuous, *i.e.* biconcave on sides with two shallow sinuses, and projected markedly on the venter.

The surface of the lectotype looks smooth on the interspaces between the constrictions, but this may be due to the weathering. Actually there are on the ventrolateral shoulder several faint nodes which have remained

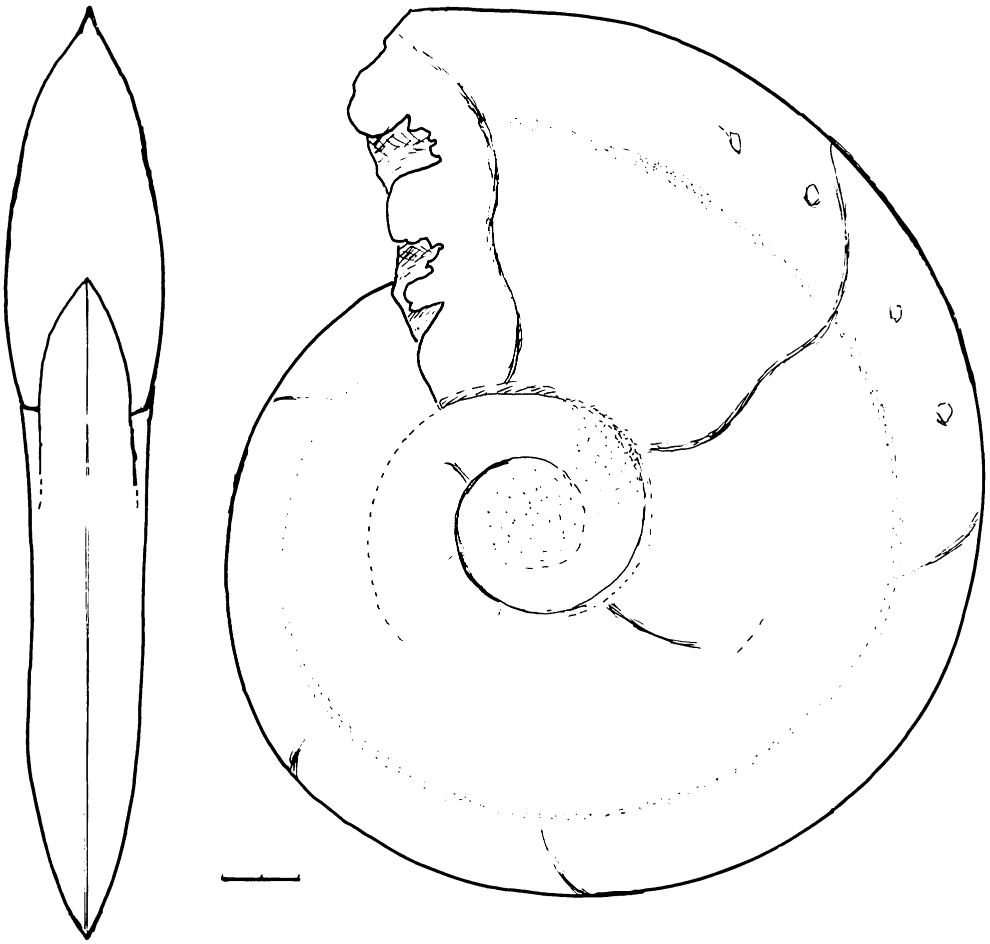


Figure 1. *Hauericeras pseudogardeni* (Schlüter). Lectotype, GIB. No. 48, wholly septate and secondarily weathered. Lateral and frontal views. Ventrolateral dotted zone = shallowly grooved. Scale bar = 20 mm. T.M. *delin.*

from the erosion. There must have been originally a row of small nodes or nodose riblets aligned on the ventrolateral shoulder. There is also a very shallowly depressed, spiral zone inside that row of ventrolateral nodes. Schlüter (1872) failed to recognize these characters and later (1899) reported a nodulous form as a variety *nodutus*, which is treated by some subsequent authors as an independent species, *Hauericeras nodutum* (Schlüter).

The specimens, from the "Lower Senonian" of Braunschweig and Broitzem, described under *Hauericeras pseudogardeni* (Schlüter) by Müller and Wollemann (1906, p. 14, pl. 4, fig. 1 ; pl. 8, fig. 3) are essentially similar to the lectotype in the fairly involute, high whorls, weakly marked and gently flexuous constrictions and a ventrolateral row of obliquely set, nodose riblets which occur clearly in the last septate whorl. As the authors remarked, the appearance of the ornament may vary owing to the state of preservation. There may be also an original variation. I agree with them in regarding *H. nodutum* as a synonym of *H. pseudogardeni*. One of Müller and Wollemann's specimens (ditto, pl. 4, fig. 1) preserves the beginning of

Table 1. Measurements of *Hauericeras pseudogardeni* (in mm).

Specimen (Position)		D	U	H	B	B/H	H/h	Inv.
Lectotype	(E)	236.0 (1)	58.0 (.25)	101.0 (.43)	*c*. 41.0 (.17)	0.41	1.31	0.63
〃	(E−130°)	195.0 (1)	46.0 (.24)	88.0 (.45)	35.5 (.18)	0.40	1.44	—
Sch. 16, 3-4	(E)	252.0 (1)	73.0 (.29)	102.0 (.40)	42.0 (.17)	0.41	1.32	0.66
Sch. 40, 9	(E)	73.0 (1)	21.0 (.29)	30.0 (.41)	—	—	1.36	0.67
M. and W. 4, 1	(E)	230.0 (1)	48.5 (.21)	106.0 (.46)	—	—	1.42	0.76

D = diameter, U = width of umbilicus, H = whorl-height, B = whorl-breadth, h = whorl-height at 180° adaptically from H, Inv. = involution = overlapped part/H of next inner whorl, *c*. = approximate, E = preserved end, Sch. 16, 3-4 = Schlüter, 1872, pl. 16, figs. 3-4 ; Sch. 40, 9 = ditto, 1876, pl. 40, fig. 9 as *Ammonites mengedensis* ; M. and W. 4, 1 = Müller and Wollemenn, 1906, pl. 4, fig. 1 ; These three are measured and calculated from the figures. The last one is so much compressed secondarily that the original form may have been modified to some extent, *e.g*. U narrowed and H enlarged.

the body chamber, where it is 263 mm in diameter. Therefore, its complete shell must have been very large.

The missing syntype illustrated by Schlüter (1872, pl. 16, figs. 3-4) is described as 252 mm in diameter at the preserved end, that is also the beginning of the body chamber. It must have been also very large, when it was in a complete state. The last three constrictions on the late part of its septate whorl are illustrated to be well marked and rather simply concave without flexuosity but the earlier ones look weak, narrow and very gently flexuous. Unless the actual specimen and others from the type locality are examined, I would avoid to decide whether it can be included in the variation of *H. pseudogardeni* or not.

In view of the undoubted evidence of dimorphism in a species from Japan (described in Part II), I should regard the above described lectotype and other large specimens of *H. pseudogardeni* as macroconchs. Then, how are microconchs of this species?

In the Museum of the University of Bonn, there was a small specimen from the "Emscher-Mergel" of the Alstaden Mine, southern Oberhaus, described under *Ammonites mengedensis* Schlüter (1876, p. 154, pl. 40, fig. 9). It is secondarily compressed and its right side is embedded in the rock matrix. It preserves the body chamber for about 220°, but its very apertural margin is not shown. It is only 73 mm in diameter but its measured proportions of U/D, H/D, H/h and involution are essentially similar to those of *H. pseudogardeni* (see Table 1). The constrictions of the actual specimen are not so deeply marked as those expressed by Schlüter's drawing but narrow, weak, gently flexuous on the main part of flank and markedly projected on the ventral part like those of *H. pseudogardeni*. Moreover, there are faint, ventrolateral riblets in the late part. This character was again overlooked by Schlüter. I suggest that this specimen may be a microconch of *H. pseudogardeni*.

H. buszii Wegner, 1905 (p. 208, pl. 8, figs. 1a, 1b), from the "Granulatenkreide" at several localities in western Münsterland, was originally described as closely allied to *H. pseudogardeni* and only distinguished by the presence of ventrolateral riblets or nodes. The latter species (*i.e. H. pseudogardeni*) is now revised to be characterized by the presence of ventrolateral nodes and/or riblets. In the illustrated specimens of *H. buszii*, the constrictions are narrow and gently flexuous on the main part of flanks, passing to a marked projection on the ventral part, as in the lectotype and Müller and Wollemann's specimens of *H. pseudogardeni*. Wegner's illustrations show the frequent constrictions, as in *H. mengedensis*, which also has ventrolateral riblets, as I mentioned above.

H. buszii was established on fairly numerous specimens, of which an example is recorded as very large (D = 420 mm), showing at the peristome a projected ventral rostrum and a distinctly biconcave outline on the flank with a broadly rounded lateral ear between the two sinuses. This must be a macroconch, although regrettably it was not illustrated.

To sum up, I suggest that *H. buszii* Wegner is highly possibly a junior synonym of *H. pseudogardeni* (Schlüter), although I should reserve the final conclusion until I could examine the original specimens of Wegner.

The extent of variation in *H. pseudogardeni* should be studied on the material of populations, but this is outside of my present capacity. According to Müller and Wollemann (1906), the variation does not seem large. I give below a revised specific diagnosis of *H. pseudogardeni* mainly on the ground of the observations described above.

Diagnosis.—Shell discoidal, consisting of much compressed whorls of moderate expansion and considerable involution, with nearly flat or only gently convex flanks, which converge to fastigiate and keeled venter. Umbilicus fairly narrow, surrounded by low but vertical wall and angular edge.

Periodic constrictions typically weak, narrow and gently flexuous; shallowly biconcave on the main part of flanks and markedly projected on the ventral part. A ventrolateral row of nodulose, prorsiradiate riblets or tiny nodes occur at least in some period of growth.

Suture finely and deeply incised, with tripartite lateral lobes and bifurcate saddles. L subsymmetric, somewhat deeper than, or nearly as deep as E; U2 and auxiliaries descending gradually toward the umbilical seam.

Microconch small; macroconch very large, sometimes three to five times as large as microconch in diameter.

Part II. Dimorphism in *Hsuericeras*

(by T. Matsumoto, S. Toshimitsu
and Y. Kawashita)

Foreword

Hauericeras angustum Yabe, 1904, which was redefined later by Matsumoto and Obata (1955) occurs fairly commonly in the Upper Cretaceous (Santonian and Campanian stages) of Japan and South Sakhalin. Our observations in field and museum works tell that some specimens of this species are fairly large and some others small or medium sized.

Meanwhile, Kawashita obtained on September 25, 1973 a fine specimen of complete preservation from the Haboro area of northwestern Hokkaido. Obata *et al.* (1978) studied the apertural features of this and other Cretaceous ammonites, with reference to functional implications.

When Matsumoto looked at this specimen, he thought at once that it must represent an adult microconch of *H. angustum* and much larger ones must be macroconchs. At T.M.'s suggestion, Toshimitsu has recently found a fine example of an adult macroconch of the same species in his large collection from the Haboro area. There are some more specimens which can be compared with these twos. We describe below these examples of dimorphism in more detail.

The repositories of the specimens dealt with in Part II are as follows, with abbreviated headings:

BM: British Museum (Natural History), London

GK: Department of Geology, Kyushu University, Fukuoka

MNHN: Museum Nationale d'Histoire Naturelle, Paris

UMUT: University Museum, University of Tokyo, Tokyo

YKC: Yoshitaro Kawashita's Collection, which will be eventually transferred to some museums as will be Y. Yokoi's Collection at Kenbuchi, Hokkaido.

Figure 2. *Hauericeras angustum* Yabe. GK. H8119, obtained by S.T. at loc. RH. 2532e, Haboro area. Macroconch preserved completely up to the peristome. Lateral view (**A**) and cross-section (**B**) along the fracture Q-R. Arrow = position of the last septum. Scale bar = 20 mm. Photos by M. Noda and S.T.

Macroconchs of *H. angustum*

Best example. —GK. H8119 (Figures 2-4) is the best preserved. It was obtained by S. T. from the Zone of *Inoceramus* (*Platyceramus*) *japonicus* at loc. RH. 2532e in the section along the Naka-no-futamata-gawa, a tributary to the River Haboro, northwestern Hokkaido (see Toshimitsu, 1988 for the location and stratigraphy).

This specimen is complete in showing the body chamber up to the peristome. The phragmocone ends with D = 155 mm and the succeeding body chamber is as long as 220° at the base of the apertural margin and 245° at the apex of the rostrum. The entire shell diameter measures 225 mm and 235 mm at the respective points mentioned above.

As the measurements in Table 2 shows, the rate of whorl expansion is rather low, degree of involution roughly 1/3, umbilicus of moderate width (roughly 1/3 of D), and the whorl is compressed, with B/H = 0.5 in the late part of the phragmocone. The body chamber is secondarily compressed. These characters and rather flat flanks converging to the keeled venter (which is less sharply fastigiate on the internal mould) conform with the diagnosis already given by Matsumoto and Obata (1955, p. 139).

The peristome is distinctly sigmoidal on the flank, passing to a markedly projected ventral rostrum. It shows a broad and moderately deep outer lateral sinus and a smaller but distinct umbilical sinus, with an obtusely convex, subrounded ear inbetween. This sigmoidal curve of the peristome is more pronounced than the gently flexuous growth lines or lirae on the main flank of the body chamber. There is a very shallow and wide zone of depression (8 to 10 mm in breadth) in parallel with and immediately behind a gently flexuous, weakly raised lira which is situated about 15 to 25 mm apart from the peristome (see Figure 3). This zone may be a kind of constriction which contracted the body chamber at the base of the apertural margin. As the body chamber of this specimen is secondarily compressed, the original degree of contraction may have been reduced. There is another, narrow and shallow, indistinct constriction on the body chamber about 180° back from the broader one mentioned above. Aside from the above described features, the surface of the body chamber is smooth, without any sign of ventrolateral riblets or nodes.

The constrictions on the septate whorl are infrequent and weak. The surface is smooth, except for flexuous lines of demarcation which may imply the occasional arrest of growth (Figure 4).

Table 2. Measurements of *Hauericeras angustum* (in mm).

Specimen	(Position)	D	U	H	B	B/H	H/h	Inv.
GK. H 8119	(M)	225.0 (1)	100.0 (.44)	69.0 (.31)	—	—	1.23	0.33
〃	(LS)	155.0 (1)	63.0 (.41)	52.0 (.34)	26.5 (.17)	0.50	1.30	0.35
〃	(LS − 180°)	118.0 (1)	45.5 (.39)	40.0 (.34)	20.0 (.17)	0.50	1.25	—
YKC. 480925	(M)	113.0 (1)	46.3 (.41)	38.2 (.34)	c. 17 (.15)	0.45	1.34	0.36
〃	(LS + 180°)	105.5 (1)	41.4 (.39)	35.0 (.33)	—	—	1.20	—
〃	(LS)	*c.* 75 (1)	27.8 (.37)	26.8 (.36)	*c.* 13 (.17)	0.49	—	—
UMUT. I-274	(LS + 180°)	93.0 (1)	37.2 (.40)	32.0 (.34)	*c.* 16 (.17)	0.50	1.34	0.37
GK. H 3322	(E)	123.0 (1)	48.0 (.39)	42.0 (.34)	22.3 (.18)	0.53	1.27	0.37
GK. H 8321	(LS + 180°)	98.0 (1)	36.0 (.37)	36.0 (.37)	15.4 (.16)	0.43	1.31	—

M = base of the apertural margin ; LS = last spetum ; others as in Table 1.
GK. H 3322 is measured on the internal mould. GK. H 8321 is distorted but measured as it is.

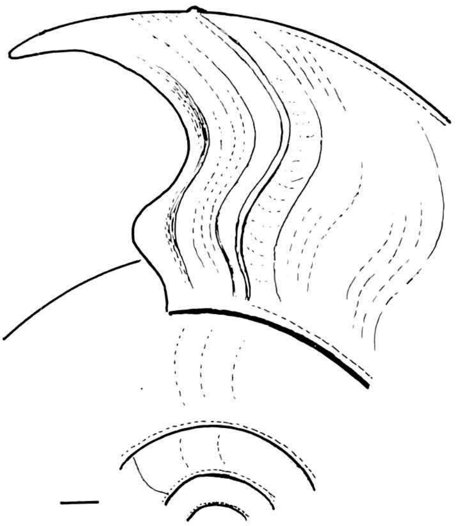


Figure 3. *Hauericeras angustum* Yabe. GK. H8119 (same as in Figure 2), showing the details of the apertural margin, growth lines (thin broken lines) and lines of demarcation (fine solid lines). Scale bar = 10 mm. T.M. *delin.*

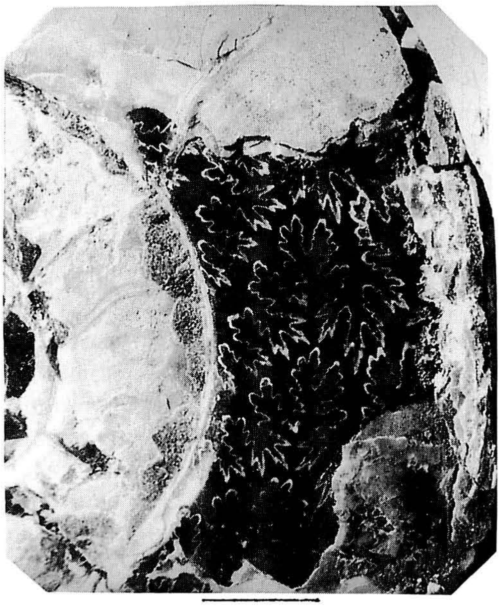


Figure 4. *Hauericeras angustum* Yabe. A part of the inner whorls of GK. H8119 (same as Figure. 2), showing sutures at about 2.5 whorls adapically from the peristome and also occasional lines of demarcation. Scale bar = 5 mm. Photo by S.T.

Other examples.—There is another macroconch specimen of *H. angustum* which shows the peristome. It was obtained by Mototaka Hayashi from the *Inoceramus* (*Platyceramus*) *japonicus* bearing formation at Onnebetsu-Hokusen, Shibetsu area of northwestern Hokkaido. It is now kept in Yokoi's Collection with No. 725. Although the specimen is badly damaged, one of us (T. M.) observed that it is roughly as large as GK. H8119, its body chamber as long as 230°, and that its peristome shows, though incompletely, a broader, outer lateral sinus, an obtusely convex ear and a smaller umbilical sinus ; its ventral rostrum was destroyed away.

Maeda obtained another example of a macroconch from northern Hokkaido. It shows incompletely the apertural margin. It is held in Kochi University.

There are more specimens which can be regarded as macroconchs of *H. angustum*. For example, GK. H5141 (Matsumoto and Obata, 1955, pl. 24, fig. 6) and GK. H5219 (ditto, pl. 28, fig. 1), both from South Sakhalin, are 125 mm and 115 mm in diameter at the last septum and the diameter of their entire shells may have been about 200 mm and 170 mm respectively, although the preserved body chambers are incomplete (and secondarily crushed in GK. H5141), without showing the apertural margin. Incidentally, in GK. H5141 the constrictions are fairly frequent in the period from the last part of the phragmocone to the beginning of the body chamber. Also in the late part of some macroconchs, raised lirae or subcostae may appear on the inner flank. They show gently convex curve as a part of the flexuous growth line. Moreover lines of demarcation occasionally appear, showing a moderate convexity on inner flank. They may occur in microconchs as well (Figure 5). The body chamber does not seem to broaden particularly in macroconchs, although it is often secondarily compressed or crushed.

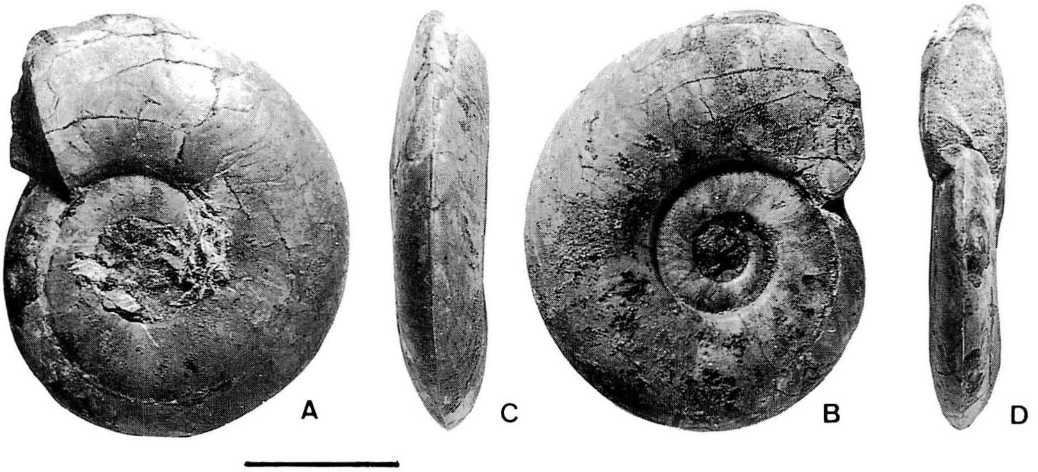


Figure 5. *Hauericeras angustum* Yabe. GK. H3534 from loc. U505, Ikandai, Urakawa area (T.M. Coll.), a juvenile showing occasional lines of demarcation on the surface of shell. Right (**A**) and left (**B**) lateral, back (**C**) and frontal (**D**) views, ×2. Scale bar = 10 mm. Photos by M. Noda.

Microconchs of *H. angustum*

Best example.—The best preserved microconch example of *H. angustum* is the specimen YKC. 480925 (Figures 6A, B). It was indicated as KC1002 by Obata *et al.* (1978, fig. 4; pl. 3, figs. 1a–d). It was obtained in 1973 by Y. Kawashita from the Ainu-zawa, a small tributary to the River Haboro.

This specimen is complete in showing the entire shell up to the apertural margin. The head of the last suture is at D = 75 mm and the last two sutures are approximated, suggesting that this ammonite was mature. The body chamber is 240° at the base of the apertural margin and 265° at the apex of the rostrum. Measured dimensions of this specimen at three positions are shown in Table 2.

The peristome of this specimen is marked by a fairly long and narrow, ventral rostrum, deep ventrolateral sinus, tongue like lappet and fairly deep, semi-sinus toward the umbilical edge. The lappet arises from its obtusely convex basal part at a point somewhat dorsad from the middle of flank and is elongated horizontally (instead of spirally), with its apex approaching to the middle of flank. It has dense and fine lirae, which show forward convex, short curves, and ends at a subrounded apex. On the left side of the shell there is a trace of injury in the basal part of the lappet, which however, went on to grow normally.

In this specimen the shelly material is preserved on the last half of the body chamber and a very thin inner shell layer may remain on some part of the posterior half. The fine lirae and striae in the basal zone of the apertural margin are moderately sigmoidal, showing a curvature similar to that of the peristome of a macroconch. There is a low elevation in parallel with the obtusely convex lirae on the basal part of the lappet. It is raised only on the inner flank, fading away outward.

In an early growth stage (D < 10 mm), irregular elevations with a convex curve are discernible on the inner flank (see Figure 6c) as in those of the holotype (UMUT. MM7573).

Incidentally, the scars of muscle attachment are well shown on the inner flanks in the adapical (*i.e.* posterior) part of the body chamber.

The phragmocone of this specimen is almost devoid of the external shell and

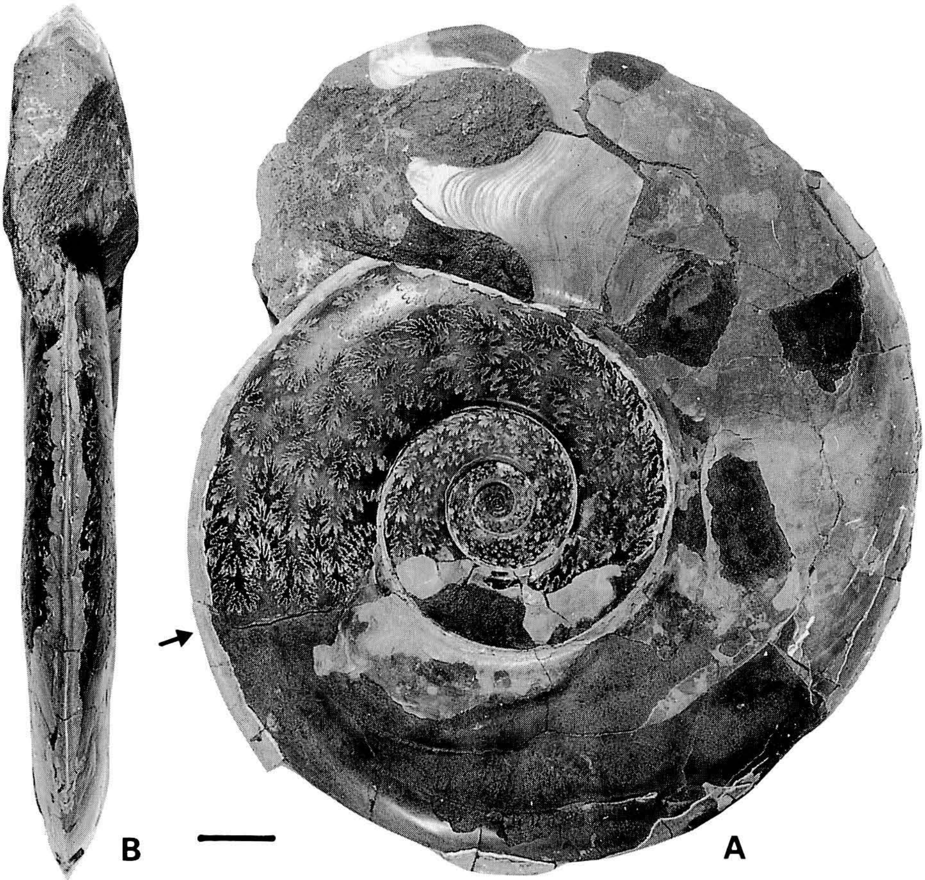
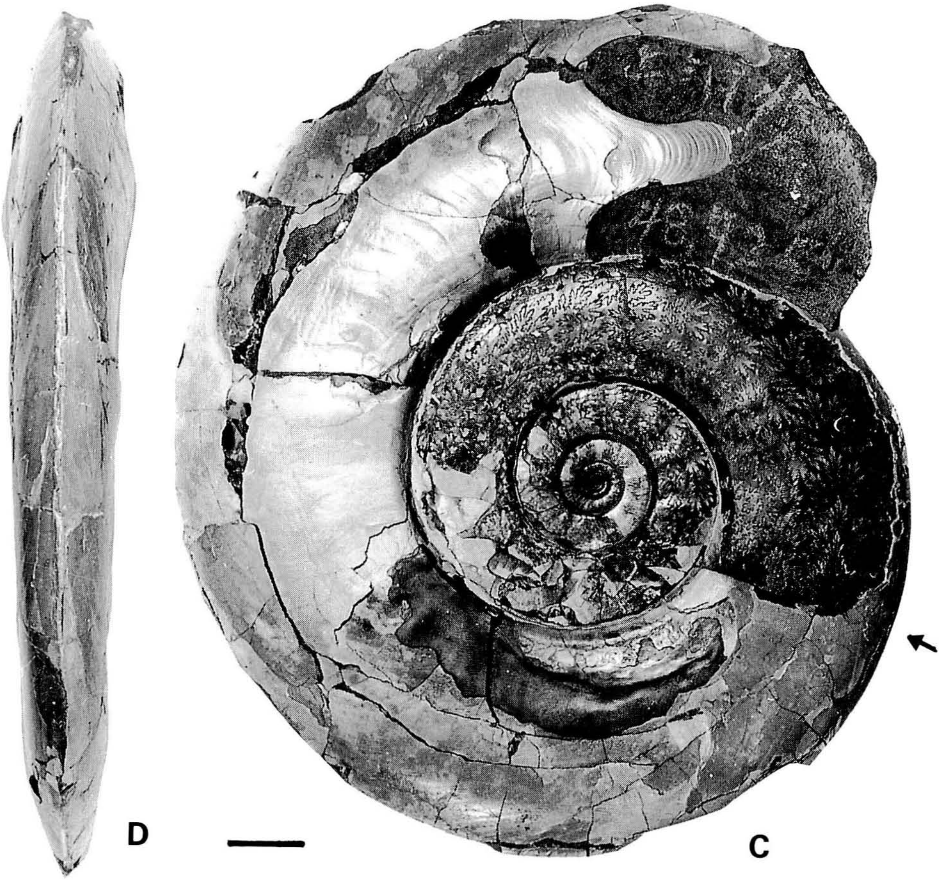


Figure 6. *Hauericeras angustum* Yabe. YKC. 480925 from the Ainu-zawa, Haboro area (Y.K. Coll.), an adult microconch preserved completely upto the peristome. Right (**A**) and left (**C**) lateral, frontal (**B**) and back (**D**) views, ×1. Arrow = head of the last suture. Scale bar = 10 mm. Photos by M. Noda. (to be continued to page 449)

sutures are finely exposed on the internal mould. L is nearly as deep as E and subsymmetrically tripartite. Saddle E/L is asymmetrically bifurcate with a smaller foliole on E side, and a larger branch on L side is again bifurcate. Saddle L/U2 is bifid. U2 nearly erect, about a half of L in size, and asymmetrically tripartite. Auxiliaries are descending abruptly toward the umbilical seam. This pattern of suture is essentially similar to that of a macroconch (see Figures 6, 4).

Other examples.—UMUT. MM7575 = GT. I-274, from Urakawa, is one of the specimens which were identified with *H. gardeni* (Baily) by Yabe (1904, p. 32). It was revised to *H. angustum* by Matsumoto and Obata (1955, p. 137, pl. 29, fig. 1). It is nearly 100 mm at the preserved end. Its body chamber is preserved for about 220° and the sutures in the last part of its phragmocone are approximated. Therefore, we can regard it as an adult microconch, whose last portion was regrettably destroyed away. Its diameter in a restored outline (on the assumption that the body chamber was 240° at the base of the apertural margin and 265° at the apex of the rostrum) can be inferred to be somewhere between 110 mm and 120 mm. This is nearly the same size as YKC. 480925, an undoubted microconch described above.



GK. H3322, from the Santonian of Urakawa, measured and illustrated by Matsumoto and Obata (1955, p. 139, pl. 28, figs. 1a, b) is probably an incomplete microconch, for its diameter is 123 mm at the preserved end (that is 230° from the beginning of the body chamber) and about 80 mm at the last septum. It is slightly (8% or so) larger than YKC. 480925, although its apertural margin is unpreserved. The growth lines or lirae on the surface of shell are gently flexuous on the flank and markedly projected on the ventral part.

GK. H8321 (Figures 7A—C) is a possible but questionable example of a microconch. It was acquired on July 19, 1988 by Noda, Takahashi and T. M. in a drifted nodule in the Hiromine-zawa at loc. Ik. 8049 p, 30 m upstream from the confluence with the Kikume-zawa in the Ikushumbets valley. Its derivation is uncertain, for some structural complexity in the geology of this local area. Although a bed of shale with *Inoceramus* (*Platyceranus*) *japonicus* is exposed at loc. Ik. 8101 about 50 m east from Ik. 8049, its extension in the Hiromine-zawa is still obscure.

Anyhow, it is secondarily distorted to an elliptical outline of 106 mm × 90 mm, but its body chamber, which occupies two thirds

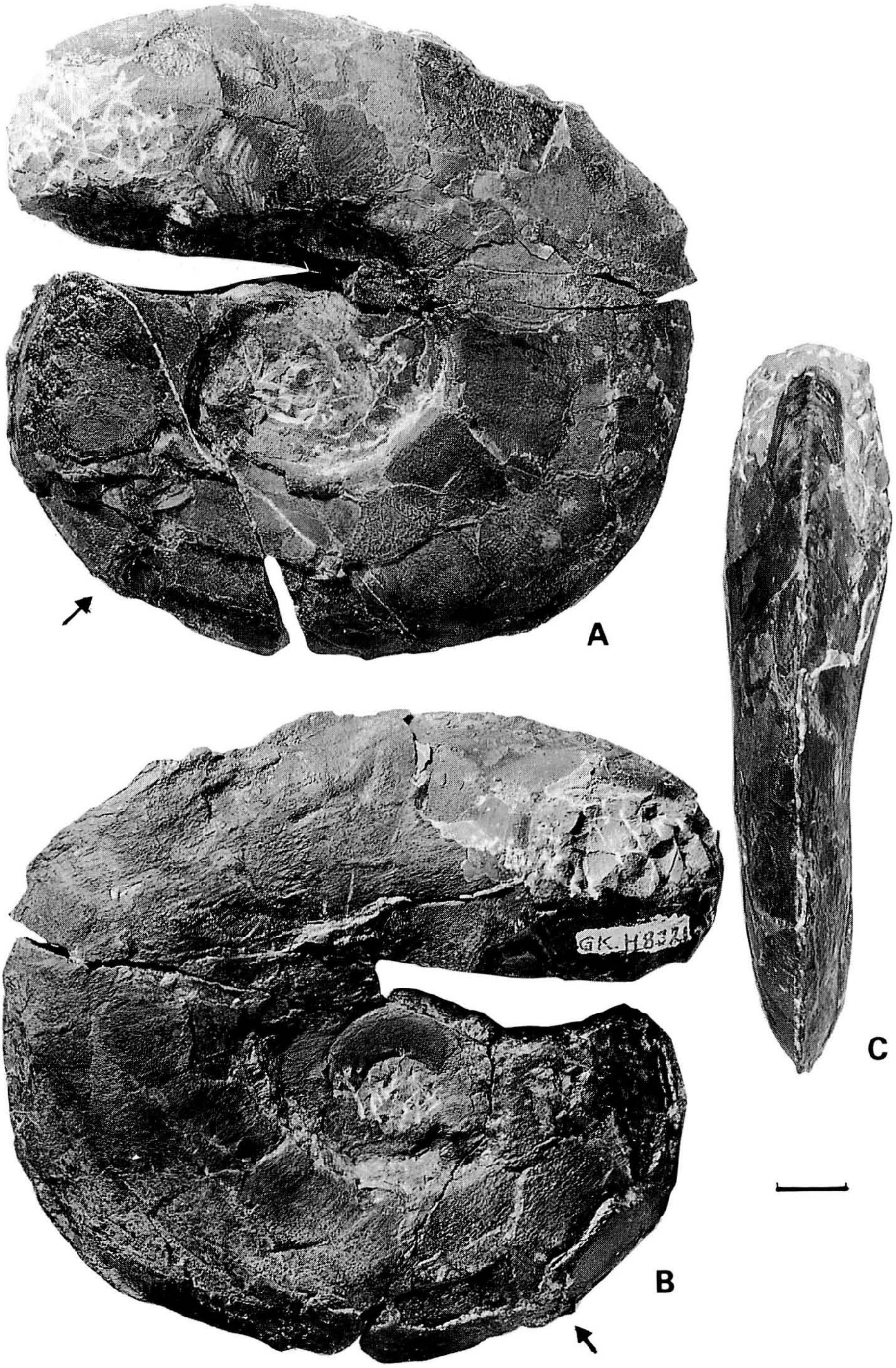


Figure 7. *Hauericeras angustum* Yabe. GK. H8321 from loc. Ik8049p, Kikume-zawa, Ikushumbets area, (M. Noda, T. Takahashi and T.M. Coll.) Probably a microconch, without lappets (secondarily destroyed or not yet grown), Right (**A**) and left (**B**) lateral and back (**C**) views, ×1. Arrow = approximate position of the last suture. Scale bar = 10 mm. Photos by M. Noda

(*i.e.* 240°) of the outer whorl, is preserved up to the apertural margin. It is slightly smaller than YKC. 480925 and may be roughly 20% smaller than GK. H3322 (see Table 2).

The peristome of this ammonite is considerably sigmoidal on the flank and markedly projected on the venter. Its flexuous curvature is quite similar to that of the basal zone on the apertural margin of YKC. 480925. For some reasons, it is devoid of tongue-like lappets on either side. Therefore, the curvature of its peristome is analogous to that of a macroconch, if the size difference is ignored.

As to the above features, three possible cases can be considered, *viz.* (1) the lappets existed originally but were destroyed away; (2) the ammonite died before the formation of long lappets; (3) this is a fossil of an immature or middle-aged female ammonite (macroconch) who was in a temporary repose during growth.

We have mentioned that the basal part of the lappet was injured on the left side of YKC. 480925 (Figure 6C) and then the lappet went on to grow completely. This tells us that there was a time of repose after the basal part of the apertural margin was formed and then the very peristome with long lappets may have been completed at the last growth stage. This seems to be favourable for the second case, but the third case (without lappets at all) cannot be ruled out. As the sutures are only partly observable in this specimen, it is difficult to decide whether this specimen is mature or immature from the approximation of the last sutures. There is a blunt elevation in the basal part of the apertural margin in this specimen as in YKC. 480925, but similar riblets or subcostae occur frequently in the inner flank of the body chamber and the preceding last part of the phragmocone of macroconchs. The mode of appearance of a single elevation favours the interpretation that this specimen is a microconch.

In a microconch (TTC. 53086) of *Mesopuzosia pacifica* Matsumoto (Matsumoto *et al.* in Matsumoto, 1988, fig. 8C), the lappet on its left side was cut off from the base of the apertural margin and going to be displaced to elsewhere, whereas the one on the right side was safe (ditto, fig. 8A). This fact suggests that the first case may be probable.

Anyhow, we are inclined to regard GK. H8321 as an example of a microconch. We have learned from the above observations that lappets may not be always preserved even in microconchs. Therefore, the distinct difference in size between the adult shells and the identity of the characters between the young to middle-aged shells are important to recognize the dimorphism in a given species.

Dimorphism in other species of *Hauericeras*

Dimorphism in *H. angustum* has been made clear on the basis of several specimens as described above. Then, how are other species of *Hauericeras* ?

H. pseudogardeni (Schlüter).—In Part I this species has been redefined. It has been suggested already that the lectotype and certain other large specimens of this species may be macroconchs, whereas the small form called *H. mengedensis* (Schlüter) may be a microconch of *H. pseudogardeni*.

H. gardeni (Bailey, 1855).—This is a well known species, which is allied to *H. angustum* but distinguished from the latter in its frequent and well marked, concave constrictions and somewhat broader whorl (*i.e.* larger B/H) (see Matsumoto and Obata, 1955, p. 140-144).

BM. C18518, from South Africa, is probably a microconch, although the apertural margin is not preserved. Its diameter is 135 mm at the preserved end and its body chamber occupies 230° (ditto, fig. 10). It is slightly larger than GK. H3322, a microconch example of *H. angustum*.

On the other hand, there are at least two illustrated specimens which probably represent macroconchs of *H. gardeni*. They are

MNHN. 2599 and MNHN. 2664, from the Lower Campanian of Madagascar and measured as D = 183 mm and 195 mm respectively at the preserved end (Collignon, 1961, pls. 28, 29). If the peristome is preserved, they must be somewhat larger, being nearly similar in size to GK. H8119, a macroconch example of *H. angustum*.

To sum up, the size difference between the dimorphic pair of *H. gardeni* is approximately comparable with that of *H. angustum*. The specimens of *H. gardeni* which show the apertural margin have yet to be searched for.

Other species.—In addition to the three species described above, there are more species of *Hauericeras*. For instance, *H. sulcatum* (Kner, 1850) (see also Kennedy and Summesberger, 1987, p. 27, pl. 1, figs. 1-7 ; pl. 13, fig. 2), *H. fayoli* de Grossouvre (1894, p. 220, pl. 27, fig. 3) (see Kennedy and Summesberger, 1984, p. 157, pl. 1, figs. 8, 12 ; pl. 2, figs. 4, 13-15) and *H. buszii* Wegner (1905, p. 208, pl. 8, figs. 1a, b) are well known and often cited, but we have had no opportunity to examine the actual specimens of them. According to Wegner, a large specimen of *H. buszii* seems to have a flexuous peristome with a broadly rounded ear, It may be a macroconch. Moreover, *H. buszii* may be a synonym of *H. pseudogardeni* (see Part I).

H. rembda (Forbes, 1846), from the Maastrichtian stage of southern India and Japan, are represented by very small specimens. They may be microconchs but larger, possible macroconchs, as well as its complete specimens with peristomes, have yet to be searched for. There is a fairly large specimen (with D more than 200 mm) of *Hauericeras* which was obtained from the upper (but not uppermost) part of the Maastrichtian formation exposed at Senposhi on the coast of Akkeshi Bay, eastern Hokkaido, by Tsunemasa Saito, who showed it to T.M. It is so badly crushed that it is hardly identified. It is now held in Department of Earth Sciences, Yamagata University. Noteworthy is the fact that even in the late Maastrichtian species of *Hauericeras* a macroconch was fairly large.

Part III. Affinities of *Hauericeras*
(by T. Matsumoto)

The genus *Hauericeras* has so distinctive characters that it is not affiliated to the Desmoceratinae nor to the Puzosiinae. Hence, the subfamily Hauericeratinae was proposed by Matsumoto (1938) and has been maintained (*e.g.*, Wright, 1981, p. 169).

The phylogenetic origin of *Hauericeras* is uncertain. Wright (1955, p. 567) suggested it in a compressed species of *Tragodesmoceroides* Matsumoto, 1942, a Turonian member of the Desmoceratinae. Matsumoto and Obata (1955, p. 134) noted a close affinity of *Hauericeras* with *Tragodesmoceras* Spath, 1922 of the Muniericeratidae. Wright (1957, p. L371) stated that the origin of the Haueriticeratinae is doubtful but probably in the Desmoceratinae close to the point of origin of the Muniericeratidae. Unlike *Hauericeras*, the latter is an ornate group.

Although Wright (1955, p. 567) once postulated a much compressed, unornamented species of *Puzosia* as another possible origin, he complained of the absence of such species in the Upper Turonian and Coniacian in the available material at that date.

The idea of *Puzosia* origin should now be reconsidered. *Puzosia manasoaensis* Collignon, 1961 (p. 34, pl. 5, fig. 2), from the Coniacian of Madagascar, is much compressed, very feebly ornamented and medium sized. A form which was found rarely from the Coniacian of Hokkaido and described under *P.* cf. *manasoaenis* by Matsumoto and Kera (in Matsumoto, 1988, p. 43, fig. 7) is flat-sided, much compressed, nearly smooth and very large. The former may be a microconch and the latter a macroconch. Anyhow, these ammonites meet the requirement of Wright mentioned above.

Hauericeras antiquum Collignon (1961, p. 75, fig. 12), from the Coniacian of Madagascar, is very interesting in that it has numerous, projected but short ribs on the ventral part. This species and *Puzosia* cf. *manasoaensis* cited above are so far represented respectively by a single, incompletely preserved specimen, but could be regarded as rare but valuable forms which may link a typical species of *Hauericeras* with that of *Puzosia*. The riblets or small nodes on the ventrolateral shoulders of *H. pseudogardeni* and probably synonymous *H. buszii* could be interpreted as ornaments which survived, with some modification, from the short ribs of such a species as *H. antiquum*.

Puzosia kuratai Tokunaga et Shimizu, 1926 (p. 196, pl. 22, fig. 6, pl. 23, figs. 4, 5, pl. 24), from the Coniacian of the Futaba area (about 200 km northeast of Tokyo), could be another linking species, but there is some difficulty about it (Matsumoto *et al*., 1989).

Still more interesting is the recent find of a keeled species of *Puzosia* from the mid-Turonian of northern Mexico. That is *Puzosia* (*P.*) *serratocarinata* Kennedy et Cobban (1988, p. 595, fig. 2 ; fig. 4 : 1-3), whose shell-form in gross view is similar to that of *Hauericeras*. The riblets on the outer part of the whorl of this species are similar to those of *H. antiquum* mentioned above. The keel of *Hauericeras* was described as septate by some authors, but actually it is solid (see Matsumoto and Obata, 1955, p. 144 ; also see Figures 1, 2B of this paper). Therefore, *P. serratocarinata* could possibly be transferred to *Hauericeras*. As it exhibits an obtusely fastigiate, keeled venter and sutures of the typical *Puzosia* pattern, I would agree at least for the time-being with Kennedy and Cobban in their assignment of it to *Puzosia*. Anyhow, it does have an incipient keel, showing a tendency to give rise such species as *H. antiquum*.

It should be noted that a young shell of *Hauericeras* has no keel (see Matsumoto and Obata, 1955, fig. 5), being quite similar to that or *Puzosia* or *Mesopuzosia* (see Matsumoto, 1954, fig. 2).

The evolute species of *Hauericeras*, such as *H. gardeni* and *H. angustum*, have a distinctly retracted umbilical lobe, as in *Puzosia*. In the more involute species, *e.g. H. pseudogardeni*, the auxiliaries are descending gradually. This feature is, however, analogous to that in the species of *Bhimaites*, an involute genus of the Puzosiinae. In the suture of *Hauericeras*, regardless of the degree of the retracted feature, L is not so large nor so asymmetric as in that of *Puzosia* and *Bhimaites*. This difference could be formed by some modification in the ontogenetic development.

In the discussion of the affinities, I should take dimorphism into consideration. The diameter of macroconchs in restored outline is 430 mm or so in the studied specimens of *P. elegans* Matsumoto, 1988 (much compressed and weakly ornamented species from the Upper Cenomanian of Japan) and *P.* cf. *manasoaensis* (mentioned above). That of the lectotype (probably macroconch) of *H. pseudogardeni* in restored outline is 420 mm, as described in Part I. Thus, as to the absolute size of macroconchs, the type species of *Hauericeras* has the same order of magnitude as certain species of *Puzosia*.

I presumed in Part I that the lectotype of *Ammonites mengedensis* may be a microconch example of *H. pseudogardeni*. Its diameter is only 75 mm to 80 mm in a restored outline. This difference in size is approximately comparable with that between macro- and micro-conch examples of *Puzosia subcorbarica* Matsumoto, which show 400 mm versus 90 mm (see Matsumoto, 1988, fig. 1).

In the examined species of the Desmoceratinae, I have not seen any example of such a large size nor such a great difference in size between dimorphs, if any, as in some species of the Puzosiinae and *Hauericeras*. There is, however, little knowledge as to the dimorphism in the members of the Desmoceratinae. Therefore, I attempt, together with some friends of mine, to collect the material which may be useful for this problem.

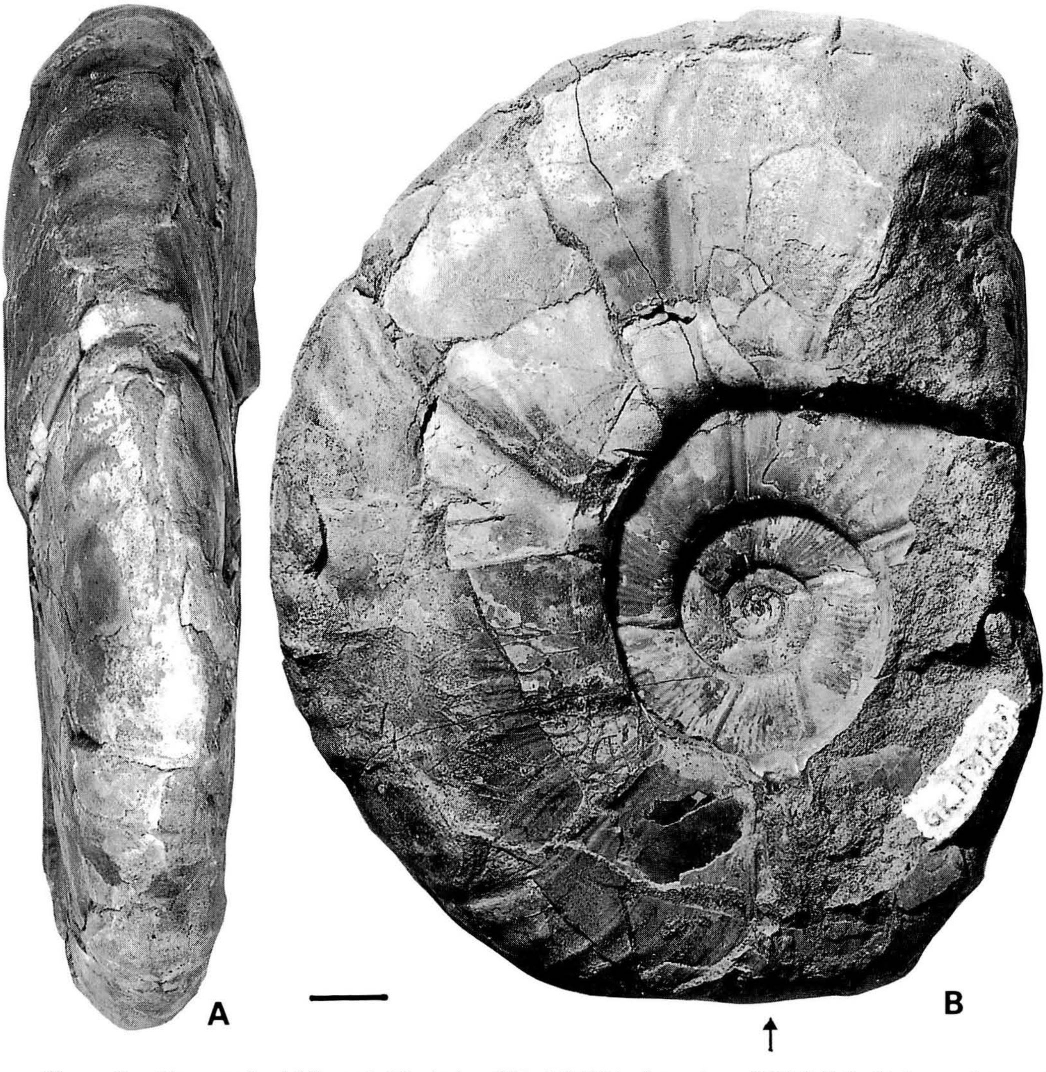


Figure 8. *Neopuzosia ishikawai* (Jimbo). GK. H8128A from loc. RH2511h2, Naka-no-futamata-gawa, Haboro area (S. Toshimitsu Coll.). An adult macroconch preserved up to the apertural margin. Back (**A**), left (**B**) and right (**C**) lateral views, ×1. Arrow = position of the last suture. Scale bar = 10 mm. Photos by M. Noda. (to be continued to page 455)

As to the apertural margin of the body chamber, the markedly rostrate and lappeted peristome is common between the microconchs of *Hauericeras* and *Puzosia* or *Mesopuzosia* or even *Neopuzosia*. The peristome of a macroconch of *Hauericeras*, as observed in *H. angustum*, has a long ventral rostrum and is distinctly flexuous and fairly deeply biconcave on sides, with obtusely convex ear between a wide and moderately deep outer sinus and a small but fairly deep, inner (probably ocular) sinus. This is somewhat similar to but not identical with the distinctly flexuous constrictions on the body chamber of *Desmoceras (Pseudouhligella) japonicum* Yabe, 1904. The peristome of the latter shows a more pronounced flexuosity, having moderately to rather narrowly rounded ears and a long projected rostrum with a moderately rounded apex.

In my preliminary obsevations, there are some differences between several species of *D.* (*Pseudouhligella*) as to the curvature of the peristome or that of constrictions. Therefore, it is too hasty to give general remarks on the difference of apertural margin between *Hauericeras* and *Desmoceras* or any other genera of Desmoceratinae.

The peristomes of the investigated macroconchs of the Puzosiinae are simply concave to gently flexuous on the flank and moderately to strongly projected on the venter with a flare or constriction behind it (see Stoliczka, 1865, pl. 68 for *Puzosia* ; Matsumoto, 1988, fig. 40, for *Jimboiceras* ; Matsumoto, 1989, pls. 1, 2, text-fig. 1 for *Pachydesmoceras).* This is considerably different from the peristome of *Hauericeras* macroconchs described above.

Macroconchs of *Neopuzosia* and *Kit-*

chinites, are smaller than those of undoubted genera of the Puzosiinae and their peristome is only gently flexuous on the flank, with very shallow ventrolateral sinuses, and a rather short rostrum on the venter (see Matsumoto, 1988, figs. 31A, 32A, 35; also this paper, Figure 8). Despite the similarity in the apertural margin of microconchs, *Hauericeras* is distinct from *Neopuzosia* and *Kitchinites* in the character of the peristome of macroconchs.

It is interesting to see that in some species of *Kitchinites*, *e.g*. *K. spathi* Henderson et MacNamara (1985, p. 57, pl. 4, figs. 5-6, 9-10, 14-15), whorls of early growth-stage are smooth and short riblets appear on the late whorl, showing an apparent similarity to microconchs of *Hauericeras pseudogardeni*. As *Kitchinites* (s.s.) appeared later in age than *Hauericeras*, the former cannot be an ancestor of the latter. Thus, the similarity is a homeomorphy between different but somewhat allied phylogenetic groups. There is another example of the reduction in ornaments in the Puzosiinae. That is the genus *Epipuzosia* Matsumoto, 1988 of Cenomanian-Turonian age, but it maintained the thick whorls of probably ancestral *Pachydesmoceras*.

Taking all the aspects of the above observations into consideration, I am rather inclined to ascribe the phylogenetic origin of *Hauericeras* in a much compressed and weakly ribbed subgroup of *Puzosia*. Should this view be warranted, my recent proposal (Matsumoto, 1988, p. 6) to combine the subfamilies Puzosiinae (in my sense, *loc. cit.*) with Hauericeratinae in to the family Puzosiidae would be approved.

Many, if not all, genera and species of the Puzosiidae have probably sexual dimorphs of great difference in size and their adult female shells (*i.e.* macroconchs) are large or gigantic and often show modified shell-forms and/or peculiar ornaments of their own. These features are significant not only morphologically but also anatomically and physiologically. I would evaluate them to be sufficient for the rank of family.

The above is my tentative proposal. There are yet some incomplete or questional points to be investigated further, as I have discussed above. For this reason, someone may favour a conservative attitude to keep the subfamilies Desmoceratinae, Puzosiinae, Hauericeratinae, Beudanticeratinae and Silesitoidinae to be grouped into the family Desmoceratidae, without giving a special importance to the peculiar features which I stressed.

Incidentally, the subgenus *Hauericeras* (*Gardeniceras*) Matsumoto et Obata, 1955, which was suppressed by some subsequent authors, can be redefined as a subgroup of *Hauericeras* in which ventral or ventrolateral riblets or nodes disappeared completely, whereas *Hauericeras* (*Hauericeras*) is the subgroup in which ventral or ventrolateral, prorsiradiate riblets or nodes remain at least in certain stages of growth.

As Matsumoto and Obata (1955, p. 139) have mentioned, in some specimens of *H.* (*G.*) *angustum*, faint, gently convex and radial elevations may appear irregularly on the inner half of flank. In the holotype, which is immature, they are well discernible in an early growth-stage, but in some other specimens (*e.g*., GK. H5213 and GK. H5141) they occur on the outer whorl.

The available records of occurrences tell that *H.* (*Hauericeras*) ranges from the Coniacian to Santonian and that *H.* (*Gardeniceras*) ranges from the upper part of the Santonian to fairly upper part of the Maastrichtian. In my view, the two subgenera may reflect stages of an evolutionary change.

Acknowledgements

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Dr. Seiichi Toshimitsu and Mr. Yoshitaro Kawashita kindly joined me in the study of dimorphism with supply of fine specimens of their collections. Mr. Katsujo Yokoi, Dr. Haruyoshi Maeda and again Dr. S. Toshimitsu generously showed me the relevant specimens of their collections with fruitful discussions. Professor Tsunemasa Saito and Dr. Hirotsugu Nishi kindly showed me a specimen from eastern Hokkaido with necessary information. Dr. Masayuki Noda friendly took photographs of selected specimens. Dr. Noda also helped me, together with Mr. Takemi Takahashi (Mikasa), in the field work (1988) of the Ikushumbets area. Miss Kazuko Hara faithfully assisted me in preparing the typescript.

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白亜紀アンモナイト属 *Hauericeras* について：本属は世界諸地域の上部白亜系に産し広く知られている。しかし私は次の 3 点が未解決であることに気付いた。これに対する研究結果を記す。(I) 模式種 *Ammonites pseudogardeni* の概念が不明確であった。今回後模式を指定して再定義した。外側部に短肋 (時に小突起) があるのが本種の 1 特質である。(II) 二型性の存否が問題であった。本邦産 *H. angustum* について殻口縁の保存されている M 殻•m 殻の好例を示し，模式種や *H. gardeni* においても二型のあることを説いた。(III) 本属の系統上の位置付けが未解決であった。本属における二型 M•m 殻の大きさの比と M 殻の絶対値は *Puzosia* のそれにほぼ匹敵するが, *Desmoceras* の場合 (研究中) とは異なる。コニ·アシアンにキールは無いが殻形が *Hauericeras* に似て狭い平板形で肋の発達の悪い *Puzosia* の種，他方キールがあり短肋がその両側にある *Hauericeras* の種が産する。さらに稀ではあるがチューロニアンに短肋が外面部だけにあり初生的のキールをもつ種 (*Puzosia serratocarinata*) が最近報告されている。また個体発生をたどると *Hauericeras* の幼殻はキールを欠きその形質は *Puzosia* の幼殻と酷似する。これらの諸事実から，*Hauericeras* の初期の種は *Puzosia* の中で殻形が挟い平板状で肋の発達が不十分な部類 (subgroup) の種から由来したとみなされる。短肋や小突起は亜属 *H.* (*Hauericeras*) では残存しているが, 亜属 *H.* (*Gardeniceras*) では全く消失した。また亜科 Puzosiinae と Hauericeratinae とを併せて，科 Puzosiidae とするのがよい。 松本達郎

(II は松本達郎・利光誠一・川下由太郎)。

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899. LATE MIDDLE MIOCENE FORAMINIFERA FROM THE MATSUE FORMATION, SHIMANE PREFECTURE*

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Abstract. Late Middle Miocene benthic foraminifera from the Matsue Formation in northern Shimane Prefecture are described, based on one boring well (depth 300 m). Foraminiferal assemblages consist of 38 taxa, which include *Ammonia* cf. *beccarii, Elphidium izumoense*, n. sp., *Elphidium matsuense*, n. sp., *Buliminella elegantissima, Buccella* cf. *kuromatsunaiensis, Elphidiella praesomaensis*, n. sp., *Elphidium perforatum*, n. sp., *Pseudononion japonicum* and *Trichohyalus* sp.

A Q-mode principal component analysis reveals that the lower horizon is represented by the *E. perforatum, E. praesomaensis*, and *E. matsuense* end-member assemblages and the upper stratigraphic horizon by *A.* cf. *beccarii*. These end member assemblages indicate that the Matsue Formation was not only deposited in a shallow-warm water environment but also influenced by a cold water. Generally, the assemblages of the Matsue Formation are closely correlated with the present-day shallow-water assemblages of northern Japan. Based on the results of principal component comparison, sediments of the lower horizon of the Matsue Formation were deposited in an outer bay environment along with cold water elements. The upper Matsue Formation is suggested to have been deposited in an inner bay environment of about 3 m water depth similar to Matsushima Bay, Northeast Honshu, Japan.

These results reveal that cold water elements extended to shallow area of San'in sedimentary basin on the southern Japan Sea borderland at the late Middle Miocene age.

Key words. Benthic foraminifera, late Middle Miocene, Matsue Formation, Shimane Prefecture.

Introduction

The foraminiferal fauna of the Tertiary deposits in Matsue City, Shimane Prefecture, has been recognized by Tai (1959, 1973) as the uppermost biostratigraphic unit in western Honshu, Japan. This biostratigraphic unit named *Ammonia* cf. *beccarii* Zone is only represented by the Matsue Formation in the Shinjiko-Nakanoumi Lowland. At the proposal of this zone, Tai (1959) recognized the upper *Rotalia-Bulimina* faunule and the lower *Nonion-Elphidium-Rotalia* faunule, and considered the Matsue Formation to be Pliocene in age. His work was, however, based on a limited number of samples and there are no subsequent micropaleontological investigations.

Molluscan fossils from the Matsue Formation have been studied by Otuka (1938) and Nomura and Hatai (1939), and more recently by Takayasu (1980). Molluscan assemblages recorded by these investigators are considered to be of Middle to Late Miocene, based on the recent progress in biostratigraphy of Japan (Tsuchi *et al.*, 1981). However, a more precise age determination is hindered by the non-occurrence of age-index microfossils

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from the formation. On the other hand, Kano and Nakano (1985) dated the basaltic andesite and assigned this formation to an age of late Middle Miocene (11.5±0.6 and 11.9±0.6 Ma).

This work is intended to provide fundamental data for the study of late Middle Miocene shallow-water benthic foraminifera of the San'in region and to present a quantitative analysis for the paleoenvironmental interpretation of the Matsue Formation.

Remarks on the lithostratigraphy of the Matsue Formation

The Miocene sequences in the San'in region are most typically exposed in the northern part of Shimane Prefecture, where the Matsue Formation has the dimensions of about 12 km in E-W direction and 7 km in N-S direction. The Matsue Formation unconformably overlies the Furue Formation in the northern part of the Shimane Peninsula and the Fujina Formation in southern hills. About one-third of the distributional area of the Matsue Formation is overlain by the Upper Miocene Wakurayama Andesite (6.5 Ma; Kano and Nakano, 1985). The stratigraphic succession recognized in the Shimane Peninsula is as follows:

Upper Miocene	···Wakurayama Andesite
Middle Miocene	Matsue Formation ······ unconformity ······ Furue Formation Fijina Formation Aishiro Formation Josoji Formation
Lower Miocene....	Koura Formation

The Matsue Formation consists of coarse- to fine-grained sandstone, intercalated basalt and mudstone in various horizons. Tai (1952, 1955, 1959) recognized three members in the Matsue Formation, noting the basaltic tuff layers in the middle horizons. They are the Teratsu Sandstone Member, Kawatsu Tuff Member, and Kuroda Sandstone Member in ascending order. Miyazima *et al.* (1972) recognized six basaltic layers and two tuff layers intercalated in sandstone, and showed their stratigraphic relationship in a profile section. According to them, the Matsue Formation attains a maximum thickness over 400 m at Yada, west of Matsue City.

Core lithology

Samples analyzed in this paper are from a well drilled for investigation of the water resources in northern area of Matsue City.

The well was drilled in 1983 by the Nishi-nippon Kensetsu Consultant Co., at Asakumi-cho of the City (Lat. 35°28.0′N; Long. 133°6.9′E). It was cored to a depth of 300 m from the surface which is 50 m above sea level (Figure 1). Referred to the report of Miyazima *et al.* (1972), a 300 m of the well cores would include almost all horizons of the Matsue Formation. The cores consist of a wide variety of clastic sediments, devoiding the basaltic tuff layers exposed in the environs.

Based on the sedimentary units consisting of bluish coarse- to medium-grained sandstone and mudstone, two horizons are recognized from bottom to top (Figure 2). The lower horizon (110.4-300 m depth) consists mostly of medium-grained sandstone, whereas the upper horizon (10-110.4 m depth) is characterized by frequent intercalation of mudstone layers and thinner sandstone layers. In addition, conglomerate layers containing granite, andesite and basalt are present at 14.8-14.9, 56.0-56.4, 201.5-201.6 m deep, respectively. Lignite layers ranging from 3 cm to 90 cm thick are also present in the depths of 27.5, 39.6, 70.5, 105.5, 111.0, 120.1, 198.5 and 211.5 m from the surface.

These sedimentary facies show that the environment of the basin changed upward, in correspondence with the upheaval of the Miocene basin during the depositional stage of the Matsue Formation (Nomura, 1986a).

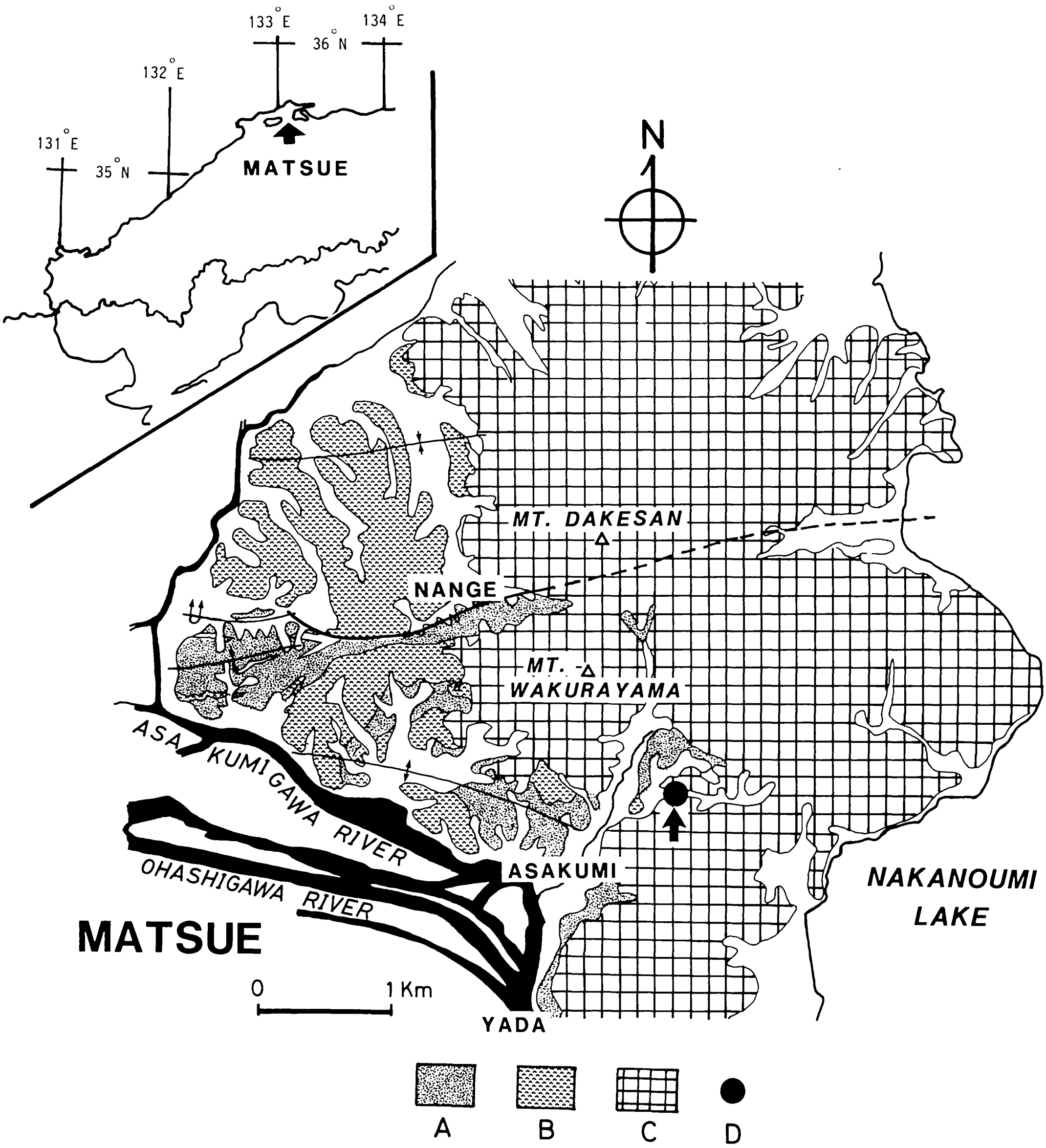


Figure 1. Geologic map near Matsue City, Shimane Prefecture and location of boring core. **A**, Sandstone and mudstone of the Matsue Formation ; **B**, Basalt of the Matsue Formation ; **C**, Wakurayama Andesite ; **D**, Drilled site.

Various sedimentary structures such as laminations and sandpipes are usually developed in sandstone, and concretions consisting mainly of *Ostrea* are included in the sandstone and mudstone.

Foraminiferal assemblage

Each sample weighing 80 g was disintegrated with the use of Na_2SO_4 solution and naphtha, then sieved on 200 mesh (74 μm opening) screen, and foraminifera were picked from the residue. Of the 78 samples

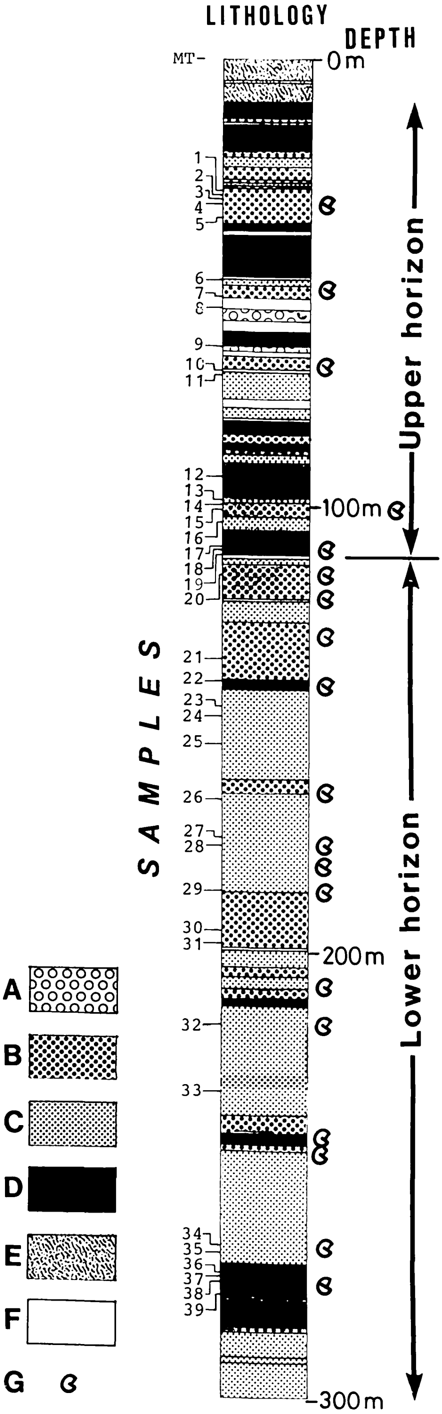


Figure 2. Lithology of core. **A**, Conglomerate; **B**, Coarse-grained sandstone; **C**, Medium-grained sandstone; **D**, Mudstone; **E**, Alluvial deposits; **F**, Not recovered interval; **G**, molluscs.

analyzed, 39 samples yielded foraminifera whose stratigraphic horizons are shown in Figure 2.

Foraminifera are generally rich and well-preserved in mudstone, while they are usually rare and badly preserved in sandstone. In all, the foraminifera of the Matsue Formation were represented by 25 different genera. *Elphidium matsuense*, n. sp. and *Elphidiella perforatum*, n. sp. occur consistently throughout the core and appear to be characteristic to the Matsue Formation. The upper part of the lower horizon and lower part of the upper horizon are characterized by a greater number of species, including *Trichohyalus* sp., *Buliminella elegantissima, Buccella* cf. *kuromatsunaiensis, B. frigida, Pseudononion japonicum*. Diversity is generally low in the uppermost upper horizon. *Ammonia* cf. *beccarii* dominates in the upper horizon and *Elphidium* spp. and *E. praesomaensis* in the lower horizon (Figure 3; Appendix).

Assemblage mainly consisting of the elphidiid and rotaliid foraminifera in the lower horizon is similar to the lower assemblage (*Nonion-Elphidium-Rotalia* faunule) of Tai (1959) in composition. However, three species, *Gaudryina* cf. *yabei* Asano, *Nonion nikobarense* Cushman, and *Elphidium etigoense* Husezima and Maruhasi, are not found, though Tai described as dominant. The upper horizon dominated by *Ammonia* cf. *beccarii* is not clearly correlated with Tai's *Rotalia*(=*Ammonia*)-*Bulimina* faunule because of the absence of his component taxa such as *Haplophragmoides, Trochammina Bulimina* and *Nonion*.

In the upper part of the lower horizon, the foraminiferal assemblage, characterized by the aforementioned species, consists mostly of hyaline calcareous forms but is rarely associated with porcelaneous forms represented by dwarf specimens of *Quinqueloculina*. Of particular interest is the presence of agglutinated forms such as *Cribrostomoides* sp., *Plectina* sp. and *Proteonina compressa*. Their deformed tests are similar to those of

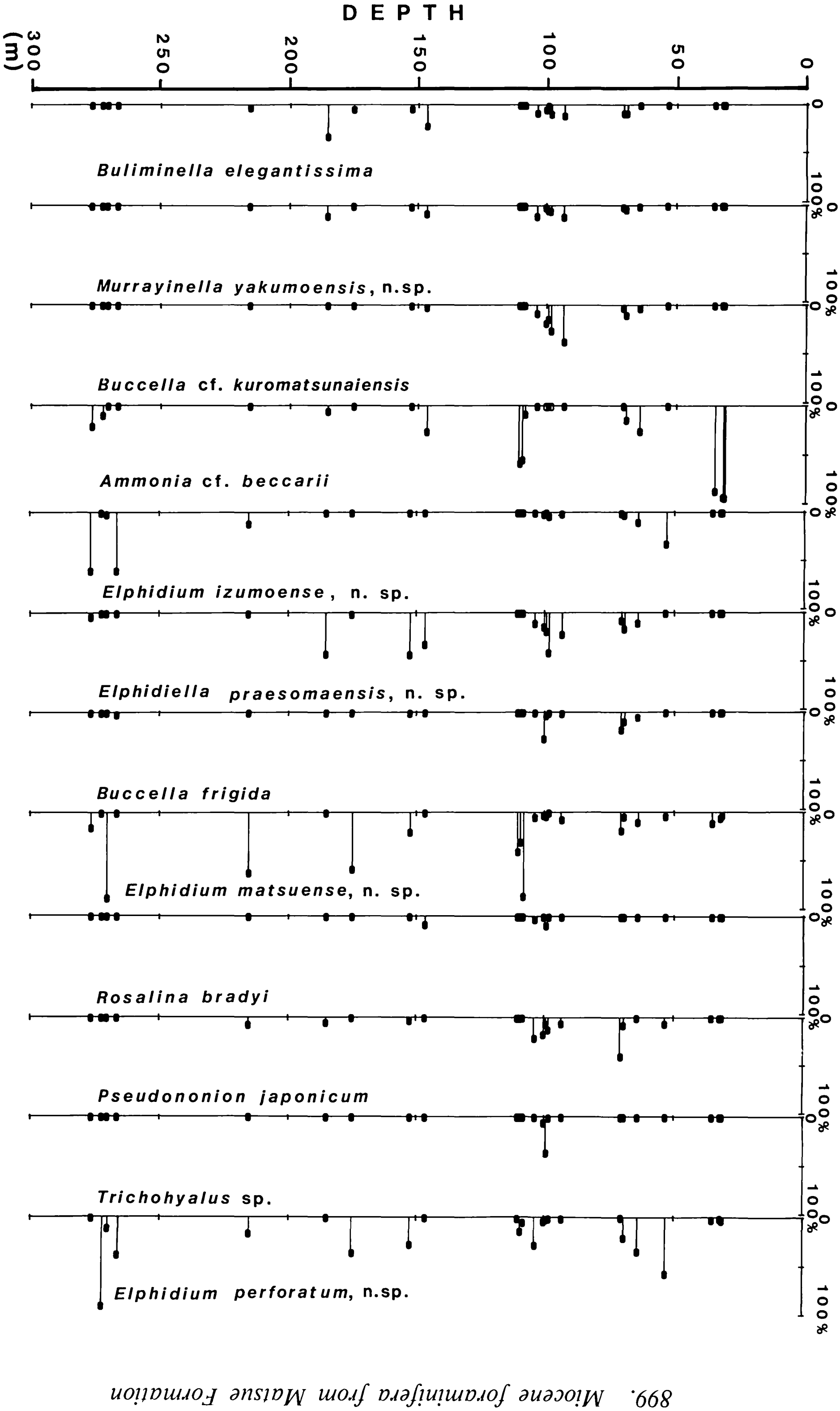


Figure 3. Frequency distribution of main foraminiferal taxa.

the agglutinated foraminifera found in the underlying Furue Formation, in which deformed foraminifera are very abundant (Nomura, 1986b). This indicates that the agglutinated foraminifera, having a physically stout test, are derived from the Furue Formation, which is supported by the unconformable relationship between the Matsue and Furue formations (Miyazima *et al.*, 1972 ; Yamauchi and Yoshitani, 1981 ; Nomura, 1986a).

Quantitative analysis

Of 38 taxa initially identified, 15 most common taxa (>4% within a sample) are considered here for further analysis. Q-mode principal component analysis was applied to reduce the census data for 24 samples yielding more than 50 specimens to a few principal components (hereafter PC for short) (Table 1). As described in Davis (1973), each principal component is independent and forms a trend in the data representing particular end-member foraminiferal assemblage.

Table 1. Results of principal component analyses

15 species from the Matsue Formation

Principal Component	Eigenvalue	Cum. Var.
1	6.722	37.35
2	3.892	58.97
3	2.786	74.44
4	1.769	84.27
5	0.895	89.24
6	0.836	93.88
7	0.594	97.18
8	0.349	99.12
9	0.138	99.89
10	0.017	99.98

11 species from Matsushima Bay

Principal Component	Eigenvalue	Cum. Var.
1	31.965	68.01
2	10.306	89.94
3	3.094	96.52
4	0.809	98.24
5	0.597	99.51
6	0.131	99.79
7	0.055	99.91

The first PC, which accounts for 37% of the total variance, is less value for faunal analysis. The factor scores on the first PC are all positive and no negative scores are obtained. As in usual cases, it only describes a deviation from the mean faunal composition of the samples (Lohmann, 1978). The second PC is defined by two end-member assemblages. One is only represented by *Ammonia* cf. *beccarii*, which is abundant in the upper horizon, MT-3, 5, 17, 19. The other, higher positive factor loadings are found in MT-12, 13 and 15, is dominated by *Elphidiella praesomaensis* and *Buccella* cf. *kuromatsunaiensis* (Figures 4, 5). The distribution pattern of the second PC indicates a hydrographic difference in relation to the bathymetry as discussed later.

The third PC reveals the *E. matsuense* end-member assemblage and the *Ammonia* cf. *beccarii* and *Elphidiella praesomaensis* end-member assemblage. The *E. matsuense* end-member has higher loadings in the lower horizon. The fourth PC shows the *Elphidium perforatum* and *Buccella* cf. *kuromatsunaiensis* end-members. The accumulated proportion of these four components accounts for 84% of the total, which may be sufficient for further paleoenvironmental consideration (Figures 4, 5).

Although ecological information of newly recognized species can not be obtained here, *Elphidium perforatum* is morphologically similar to *E. subarcticum* which is widely distributed in the arctic to subarctic regions and *Elphidiella praesomaensis* is similar to *Elphidium somaense* recorded from the shallow area neighboring the bay environment of northeast Honshu, Japan.

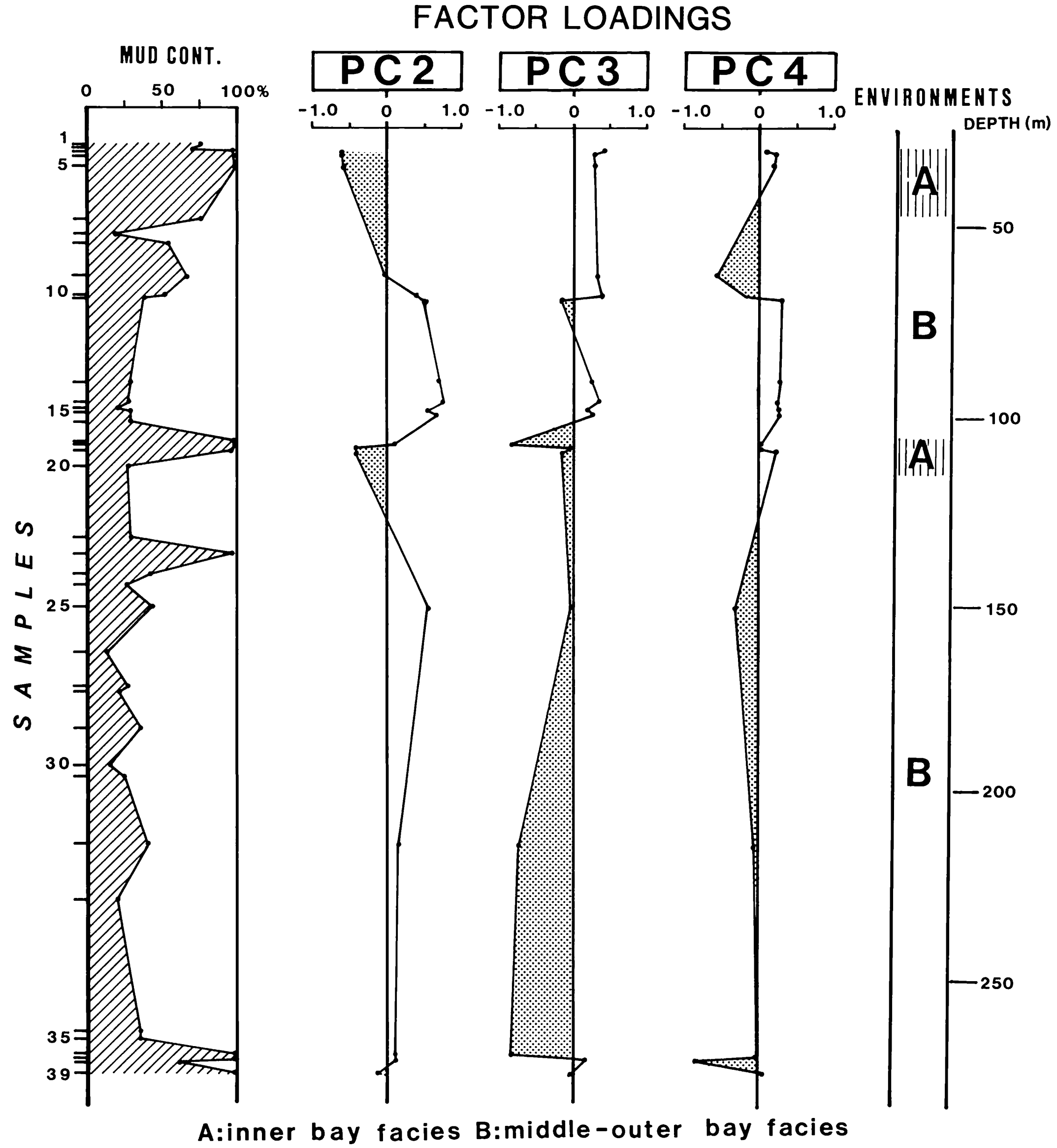


Figure 4. Stratigraphic distribution of factor loadings of principal components **2, 3**, and **4**, and suggested paleoenvironment.

Paleoenvironment

Although the main species representing the end-member assemblages are extinct or newly recognized taxa, the lithological character and the generic composition indicate the Matsue Formation has been deposited at shallow water depth. The paleobathymetry can be estimated by examining the bathymetric distribution of the present-day shallow water fauna with the following assumptions : the ecology of the taxa in question is close to that of the morphologically related living species ; the ecology of the known species is not changed significantly since the Miocene time.

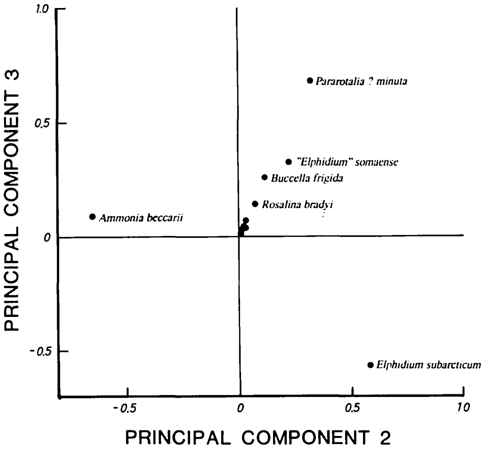


Figure 5. Plots of foraminiferal taxa on second and fourth principal component axes showing the end members of respective components in the Matsue Formation. The coordinates are factor scores.

The foraminiferal assemblages were compared to the present day faunas of the Japanese shallow water and/or bay areas in species composition and frequency (*e.g.*, Hokkaido region, Morishima and Chiji, 1952 ; Yoshida, 1954 ; northern Honshu region, Takayanagi, 1955 ; Uchio, 1962 ; Matoba, 1970 ; southwestern Honshu region, Ishiwada, 1958 ; Ikeya, 1977 ; Kato, 1986). In addition to these, the fauna reported from the littoral and lagoon areas of China (the Huanghai (Yellow) Sea and the Bohai Gulf) (Wang *et al.*, 1985a, b, c) is also comparable to that of the Matsue Formation in the predominance of *Ammonia* and elphidiid species. Referred to these faunal associations, the Matsue Formation is clearly suggested to have been deposited in hydrographically bay facies including brackish environment. The description concerning bottom water temperature is mostly incomplete in these studies, though the regions known their surface water temperature are characterized by having a high annual temperature range (usually in the range of *ca.* 15°-25°C) (Takayanagi, *op. cit.* ; Matoba, *op. cit.* ; Wang *et al.*, 1985b). Among the faunas of the above-mentioned regions, the fauna of northern Honshu region such as Matsukawaura lagoon (Takayanagi, *op. cit.*) and Matsushima Bay (Matoba, *op. cit.*) shows the closest similarity to that of the Matsue Formation. Particularly in Matsushima Bay, of 57 taxa selected for environmental discrimination of the bay, 11 taxa are comparable to those from the Matsue Formation (Matoba, *op. cit.*, fig. 30 ; Table 2 of this paper).

In order to elucidate the environmental changes of the Matsue Formation, the data selected from Matoba's results are incorporated in the analysis using principal component comparison (Tables 1 and 2). The first three components account for 97% of the variance. Figure 6 shows the taxa contributing to the end-member associations of the second and third PCs. The faunal trend described by the second PC represents the reciprocal variation in abundance between the *Ammonia beccarii* end-member and the *Pararotalia* ? *minuta, "Elphidium" somaense, Buccella frigida* and *Rosalina bradyi* end-member associations.

Examining the biotopes recognized by Matoba (1970) with the results of the respective factor loadings, the bathymetric distribution of the second PC shows a transition around the depth of 3 m between samples containing large proportions of the *Ammonia beccarii* association and the *P.* ? *minuta, "E". somaense, B. frigida* and *R. bradyi* association (Figure 7). According to Matoba's analysis, all the samples characterized by the former association are from the inner bay facies, whereas the latter association is from the middle to outer bay facies. In addition to the abundant occurrence of *Ammonia* species, the inner bay facies are also generally characterized by the occurrence of several agglutinated forms such as *Trochammina, Miliammina* and *Goesella.* The samples containing abundant *Ammonia* cf. *beccarii*, which are considered to indicate the inner bay facies, do not yield the agglutinated foraminifera except for the derived taxa. This difference may be a result of selective

Table 2. Main taxa from the Matsue Formation and morphologically similar taxa from Matsushima Bay indicated in right parentheses. Eleven taxa from Matsushima Bay are used for the analysis of principal component comparison.

Main species from the Matsue Formation		
1.	*Ammonia* cf. *beccarii* (Linné)	(I)
2.	*A.* sp. A	
3.	*Buccella frigida* (Cushman)	(II)
4.	*B.* cf. *kuromatsunaiensis* (Shirai)	(III)
5.	*Buliminella elegantissima* (d'Orbigny)	(IV)
6.	*Elphidiella praesomaensis*, n. sp.	(V)
7.	*Elphidium izumoense*, n. sp.	
8.	*E. matsuense*, n. sp.	
9.	*E. perforatum*, n. sp	(VI)
10.	*Murrayinella yakumoensis*, n. sp.	(VIII)
11.	*Pseudononion japonicum* Asano	(IX)
12.	*Quinqueloculina* cf. *fukushimaensis* Takayanagi	(X)
13.	*Rosalina bradyi* (Cushman)	(XI)
14.	*Trichohyalus* sp.	(VII)
15.	*Uvigerina* cf. *akitaensis* Asano	

Species from Matsushima Bay (Based on Matoba, 1970)	
I.	*Ammonia beccarii* (Linné)
II.	*Buccella frigida* (Cushman)
III.	*B. makiyamae* Chiji
IV.	*Buliminella elegantissima* (d'Orbigny)
V.	*"Elphidium" somaense* Takayanagi
VI.	*E. subarcticum* Cushman
VII.	*Glabratella milletti* (Wright)
VIII.	*Pararotalia* ? *minuta* (Takayanagi)
IX.	*Pseudononion japonicum* Asano
X.	*Quinqueloculina fukushimaensis* Takayanagi
XI.	*Rosalina bradyi* (Cushman)

preservation, through which weakly cemented agglutinated taxa are easily disintegrated.

The third PC, which is defined by *Elphidium subarcticum* and *Pararotalia* ? *minuta* as each end-member, reveals the trend of bottom water character represented by chlorinity and water temperature from the inner bay to outer bay facies. Samples having higher positive factor loadings are obtained from the area of higher chlorinity and those with higher negative factor loadings show a trend related to the temperature and chlorinity (see also Matoba's figs. 16, 17, 55 and 59).

The above distribution pattern of the foraminiferal taxa recognized in the modern fauna of Matsushima Bay, is correlated with those of the second and fourth principal components from the Matsue Formation (Figures 5, 6) excepting the third component

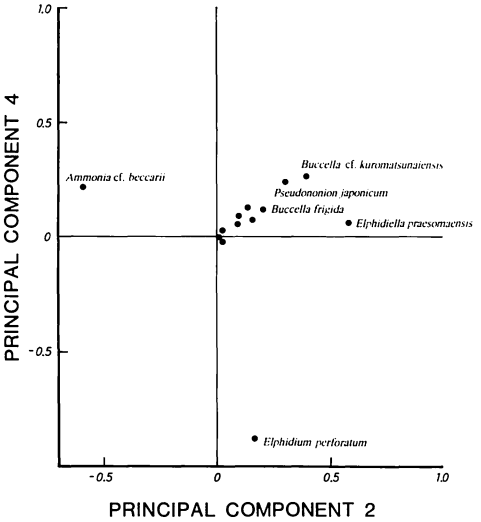


Figure 6. Plots of foraminiferal taxa from Matsushima Bay on the second and third principal component axes showing the similar distribution pattern to those of the Matsue Formation (Figure 5). The coordinates are factor scores.

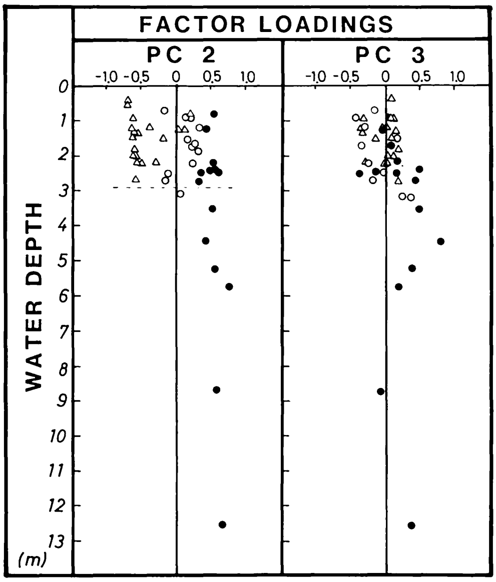


Figure 7. Depth distribution of samples classified into respective biotopes by Matoba (1970) showing depth related principal component 2 and principal component 3 explaining bottom water character. Triangle showing the sample from the inner bay facies. Circle showing the sample from the middle bay facies. Solid circle showing the sample from the outer bay facies.

where comparable species such as *Elphidium matsuense* are not found in Matsushima Bay. With respect to the second PC, the *Ammonia* cf. *beccarii* end-member assemblage and the *Elphidiella praesomaensis, Buccella* cf. *kuromatsunaiensis, Pseudononion japonicum, Buccella frigida* end-member assemblage of the Matsue Formation are respectively correlated with the *Ammonia beccarii* end-member and the *Pararotalia ? minuta, "Elphidium" somaense, Buccella frigida, Rosalina bradyi* end-member associations of Matsushima Bay (correlation coefficient $r=0.66$; $0.05<p<0.02$). The *Elphidium perforatum* end-member assemblage on fourth PC of the Matsue Formation is comparable to the *E. subarcticum* end-member on the third PC of Matsushima Bay ($r=0.67$; $0.05<p<0.02$). The principal component comparison reveals that the sediments were mostly of outer bay area facing an open shallow sea, but in two horizons, 30-35 m (represented by MT-3, 4, 5) and about 110 m, the inner bay facies was formed where the depths were supposedly less than 3 m (Figure 4). However, the middle to outer bay facies with the water of higher average chlorinity were developed in horizons such as 50-100 m and 145-275 m.

Concluding remarks

Aside from the foraminiferal fossils, some megafossils have been recorded from the Matsue Formation. Okubo (1975) reported on the occurrence of warm brackish water prawn fossils from 3.5 km south of this drilling site, and stated that the fossil bed might have been deposited in a brackish bay similar to the present-day environment of Nakanoumi or Lake Shinjiko. In addition, molluscan assemblages characterized by *Grycymeris cysyuuensis* from Nange, Kamihigashikawatsu-cho, located 3.5 km north of this site, have been considered as warm shallow water origin (Takayasu, 1981). In spite of uncertainty of their stratigraphic positions of these fossiliferous horizons, these results are almost consonant with the environment estimated from the foraminiferal study. Not all of the foraminiferal taxa obtained from this study, however, indicate a warm water environment. *Trichohyalus* sp., which is considered to be intimately related to cold water species as described in the remarks of the species, reveals an influence of cold water extending into the littoral or bay areas of the San'in region during the deposition of the Matsue Formation. *Buccella frigida* and *Buliminella elegantissima* are known as having a wide geographic distribution in cold to temperate-shallow seas. The southern limits of the co-occurrence of *B. frigida* and *B. elegantissima* in the North West Pacific are in the northern part of the East China Sea (Wang *et al.*, 1985c). The most common occurrences of these species are known from the shallow seas (<20-50 m in depth) in the northern sea of Japan, the Okhotsk Sea, and the Bering Sea (Fursenko *et al.*, 1979). Aside from the question what environmental factor does control the distribution of *B. frigida* and *B. elegantissima*, they are suggested to be related to cold water. Furthermore, the new species as *Elphidium perforatum* and the specimens compared to *Buccella kuromatsunaiensis* are thought to be morphologically related to cold water species.

Referred to the Matoba's inner bay facies, as discussed earlier, the *Ammonia* cf. *beccarii* end-member assemblage is supposed to have flourished in the brackish-water and is recognized in the uppermost and lowermost upper horizon of the core. Others are of shallow open-sea or outer bay environment. This feature indicates that the sedimentary basin became shallower during the deposition of the upper horizon with two fluctuations. Basement shallowing was resulted from an upheaval of the central ridge of the Shimane Peninsula as already stated by Nomura (1986a) and represents the last stage of tectonic movement in the San'in region (Yamauchi and Yoshitani, 1982; Kano and Nakano, 1986; Nomura, 1986a).

Based on these results, paleo-Matsue Bay is considered a warm shallow sea with cold water intrusions during the depositional stage of the Matsue Formation in northern Shimane Prefecture.

Systematic notes on species

Ammonia cf. *beccarii* (Linné)

Figures 10-1a, b

Cf. *Nautilus beccarii* Linné, 1758, *Syst. Nat.*, 10, p. 710.

Of forms referred to *Ammonia* cf. *beccarii*, one having a small number of chambers in the final whorl and with or without a small umbilical plug is similar to the figured specimens as *Ammonia beccarii* forma 2 by Matoba (1971, p. 48, pl. 5, figs. 10a-c, 11a-c, 12a-c), the other, which have 9-12 chambers in the final whorl, limbate sutures and umbilical plug falls within a range of young *A. tochigiensis* (=*Rotalia tochigiensis* Uchio, 1951).

Bolivina sp. A

Figure 10-3

Small-sized specimens are rarely found in sample MT-2.

Buccella frigida (Cushman)

Figures 10-8a–c, 11

Pulvinulina frigida Cushman, 1922, *Canad. Biol., Contr.*, no. 9 p. 12.

Buccella frigida (Cushman). Andersen, 1952, *Washington Acad. Sci., Jour.*, vol. 42, no. 5, p. 144, figs. 4a-6c.

This species occurs in close association with *Elphidiella praesomaensis*, *Buliminella elegantissima* and *Elphidium izumoense* in this formation and is common in the lower part of the upper horizon.

Buccella cf. *kuromatsunaiensis* Shirai

Figures 10-7a, b

Cf. *Buccella kuromatsunaiensis* Shirai, 1960, *Jour., Hokkaido Univ., Fac. Sci. ser. 4, Geol. Mineral.*, vol. 10, no. 3, p. 540-541, pl. 2, figs. 2a-c.

The specimens identified here are comparable to *Buccella kuromatsunaiensis* from the Pleistocene deposits (originally described as the Pliocene) of Kuromatsunai, southern Hokkaido, in having an average thickness/maximum diameter ratio of 0.52 and very slightly raised walls near the umbilicus. However, the specimens from the Matsue Formation consist of 7-9 chambers in the last whorl and have more inflated ventral chambers in comparison with *B. kuromatsunaiensis*. Ventral feature of this species is somewhat similar to those of *Buccella tanaii* and *Buccella makiyamae* Chiji, but the latter species have the strongly convex dorsal test.

The Matsue specimens are noted to have not supplementary apertures on the posterosutural margin of each chamber on the ventral side. The presence of the supplymentary apertures is one of the diagnostics of the genus *Buccella*, though the species is tentatively allocated to this genus.

B. cf. *kuromatsunaiensis* occurs abundantly in several horizons of the boring core and is one of the main constituents of the assemblage.

Buliminella elegantissima (d'Orbigny)

Figures 9-5a, b

Bulimina elegantissima d'Orbigny, 1839, *Voy. Amer. Merid., Foraminiferes*, vol. 5, pt. 5, p. 51, pl. 7, figs. 13, 14.

Buliminella elegantissima (d'Orbigny). Matoba, 1970, *Sci. Rep., Tohoku Univ., 2nd ser. (Geol.)*, vol. 42, no. 1, p. 50, pl. 3, fig. 24.

Around the seas of Japan, modern *Buliminella elegantissima* occurs commonly in the cold to temperate and shallow water regions (*e.g.*, Nomura, 1982). Ishiwada (1964) reported the *Buccella frigida*-*Buliminella elegantissima* assemblage from shallow water off Kushiro, Hokkaido, as a subarctic coastal assemblage. Recently, Oki (1989) suggested that *B. elegantissima* is originally a cold water species and the modern species living in the shallow seas off southwestern Japan might be adapted to warm water as a relict species. Besides the seas around the Japanese Islands, this species is found in the East China Sea and the South China Sea (Wang *et al.*, 1985c).

Buliminella elegantissima from the Matsue Formation occurs in the upper part of the lower horizon and the upper horizon, being in association with *Elphidiella praesomaensis*.

Cribrostomoides sp.

Like that of *Plectina*, poorly preserved specimens are found in the sample MT-14. The specimens are judged as reworked from the underlying formation, where *Cribrostomoides* cf. *crassimargo* is the main constituent in the Furue Formation (Nomura, 1986b).

Pseudononion japonicum Asano

Figures 9-1a, b, 2a–c

Pseudononion japonicum Asano, 1936, *Jour., Geol. Soc. Japan,* vol. 43, no. 512, p. 347, text-figs. a-c.

Pseudononion japonicum Asano. Saunders and Müller-Merz, 1982, *Jour. Foram. Res.*, vol. 12, no. 3, p. 262, pl. 1, figs. 1-3.

Compared with the original figures of Asano, the Matsue specimens have a thicker test ; the ratio of test thickness to length (T/L) is 4 in the original description, whereas the present specimens show an average ratio of 2.3. However, this ratio is almost equal to the topotype specimens redescribed by Saunders and Müller-Merz (1980).

SEM photographs show the smooth test surface with grooved sutures near umbilicus filled with small pustules and do not show the furrowed nature of test surface caused by slight inflation of chambers, which are usually recognized in typical *Pseudononion japonicum.*

Pseudononion japonicum is common in the Pliocene to Recent deposits of Japan whereas the Miocene forms have not been hitherto illustrated.

Plectina sp.

Figure 9-10

A broken incomplete specimen is found in sample MT-14. The specimen is also compressed due to fossilization. This feature is very close to specimens from the underlying Furue Formation, suggesting that this specimen has been derived from the Furue Formation.

Quinqueloculina cf. *fukushimaensis* Takayanagi

Figures 10-6a, b

Cf. *Quinqueloculina fukushimaensis* Takayanagi, 1955, *Contr., Inst. Geol. Pal., Tohoku Univ.*, no. 45, p. 51, figs. 26a-c.

Although *Quinqueloculina fukushimaensis* was originally described as having the wall cemented with very fine sand grains, the walls of holotype are covered with minute pits. Several comparable specimens from the Matsue Formation show such a granular appearance caused by light reflection on minutely pitted wall surface.

Rosalina bradyi (Cushman)

Figures 10-9a – c

Discorbis globuralis var. *bradyi* Cushman, 1915, *U. S. Nat. Mus., Bull.*, no. 71, pt. 5, p. 12, pl. 8, figs. 1a-c.
Discopulvinulina bradyi (Cushman). Asano, 1951, *Illust. Cat. Japan. Tert. Small. Foram.*, p. 4, text-figs. 25, 26
Rosalina bradyi (Cushman). Matoba, 1970, *Sci. Rep., Tohoku Univ., 2nd ser.* (*Geol.*), v. 42, no. 1, p. 60, pl. 4, figs. 8a-c.

This shallow-water species is rarely found in the upper part of the lower horizon and the upper horizon.

Trichohyalus sp.

Figures 10-10a, b, 12a – c

The mature specimens are characterized by having a large trochoid test consisting of a very strongly convex dorsal side and a flat ventral side, indistinct apertural foramen, flushed sutures, and ventral knobs (Figures 10-12a – c). The test of younger specimens shows a centrally situated aperture with radial striations (Figures 10-10a, b), whereas the dissected test without last few chambers reveals the trochospiral chamber arrangement and interiomarginal apertural foramen with fine striations on apertural face.

The walls of this form is thick and optically radial in texture. These diagnostics seem to be somewhat differentiated from the definition of the genus *Trichohyalus* ; nevertheless, the present form is tentatively assigned to this genus, following the description of Voloshinova *et al.* (1970).

Voloshinova *et al.* (1970) recorded similar form to the present one from the Pliocene deposits of Sakhalin as *Trichohyalus bartletti*, which has been known as cold water species. Similar form, *Glabratella ornatissima* (Cushman), is also reported by Erskian and Lipps (1987) from the Recent coastal zone of northern California.

Uvigerina cf. *akitaensis* Asano

Figures 9-11

Cf. *Uvigerina akitaensis* Asano, 1950, *Illust. Cat. Japan. Tert. Small. Foram.*, pt. 2, p. 28, figs. 60-62.

The small specimens showing somewhat eroded test surface are rarely found in the upper horizon. In their lobulate character of the periphery, these specimens are compared to *Uvigerina akitaensis*.

Description of new species

Order Foraminiferida Eichwald, 1830
Suborder Rotaliina Delage
and Herouard, 1896
Superfamily Glabratellacea Loeblich
and Tappan, 1964
Family Glabratellidae Loeblich
and Tappan, 1964
Genus *Murrayinella* Farias, 1977

Murrayinella yakumoensis Nomura, n. sp.

Figures 10-2a, b, 4a, b, 5a, b

Diagnosis.—Plano-convex test with numerous short spines. Periphery rounded, but not inflated. Ventral sutures depressed and filled with granular shell materials near the umbilicus.

Description.—Test small, generally plano-convex, dorsal side flat to slightly convex; peripheral margin rounded and lobulated, but narrower in the earlier formed portion; chambers distinct, inflated, five to six in last whorl, more rounded in the final one; sutures slightly limbate on dorsal side but ventrally depressed; chambers tend to separate near umbilicus, but generally obscured by hispid small spines; wall rough, with numerous short spines, and coarsely perforated; aperture obscure, an elongate, low arched opening at the based of septum about midway of ventral side; wall translucent, radial in texture.

Type and materials.—Holotype, DESS 88001, Figures 10-2a, b, from sample MT-13 of boring core, Matsue Formation, late Middle Miocene; paratype, DESS 88002, Figures 10-4a, b from the same sample; paratype, DESS 88003, Figures 10-5a, b, from the same sample.

Size and measurements.—Holotype, maximum diameter 0.32 mm, thickness 0.19 mm; 24 paratypes, maximum diameter 0.19-0.32 mm (av., 0.22 mm), thickness 0.09-0.19 mm (av., 0.13 mm).

Remarks.—This new species resembles *Rotalia* ? *minuta* Takayanagi (= *Pararotalia* ? *minuta* of Matoba, 1970 = *Murrayinella minuta* of Takayanagi and Hasegawa, 1987) in its test size and surface hispidity. According to Matoba (1970), *Pararotalia* ? *minuta* has nearly flat dorsal and strongly convex ventral sides and almost acute periphery with pustulous fringe except for the last few chambers of some specimens. Therefore, *Murrayinella yakumoensis* is distinguished from *P.* ? *minuta* by having a rounded periphery without pustulous fringe and coarse perforation.

This new species resembles *M. murrayi* (= *Rotalia murrayi* Heron-Allen and Earland), but differs from it in the less globular chambers and not deeply depressed sutures as well as the covering of pustulous materials on the umbilicus.

Superfamily Rotaliacea Schultze, 1854
Family Elphidiidae Schultze, 1854
Subfamily Elphidiinae Saidova, 1981
Genus *Elphidium* de Montfort, 1808

Elphidium izumoense Nomura, n. sp.

Figures 9-3a, b, 4a, b; 11-11, 12.

Diagnosis.—Compressed test with nearly flat umbilicus. Umbilicus with indistinct boss-like structure. Chambers fusing in a ring around the umbilicus.

Description.—Test compressed, nearly circular, not lobulate in side view; periphery rounded, nearly parallel in edge view; umbilical region flat, with indistinct boss-like structure and covered with less developed granular shell materials; chambers distinct, not inflated, 11 in the last whorl, fusing in a ring around the umbilicus; sutures distinct, grooved, but indistinct by forming a sutural canal around the umbilicus, without retral process ; wall smooth, very finely perforate, optically granular in texture ; aperture indistinct by the presence of granular shell materials ; previous apertures rounded, two or three openings at the base of the inner margin of the last-formed chamber.

Type and materials.—Holotype, DESS 88004, Figures 9-4a—c, from sample MT-7 of boring core, Matsue Formation, late Middle Miocene ; paratype, DESS 88005, Figures 9-3a, b, from the same sample.

Size and measurements.—Holotype, maximum diameter 0.22 mm, thickness 0.09 mm ; 20 paratypes, maximum diameter 0.21-0.35 mm (av., 0.26 mm), thickness 0.09-0.14 mm (av., 0.11 mm).

Remarks.—In lacking retral process or fossetts and the development of umbilical flaps, the external feature of this new species apparently coincides with the generic diagnoses of Paleogene *Protelphidium* Haynes redescribed by Banner and Culver (1978). However, in the possession of the intercameral lacunae and sutural canals around the umbilicus which intercommunicate with the umbilical spiral canals (Figures 11-11, 12), the present new species is assigned to the genus *Elphidium*.

In appearance, umbilical structure of this species resembles that of *Astrononion*. However, interiomarginal aperture is not a narrow slit but a row of small openings, which indicates this taxon is not assignable to *Astrononion*.

Elphidium izumoense, n. sp. is distinguished from *Elphidium simplex* Cushman by the development of ring-like structure around the umbilicus.

Elphidium matsuense Nomura, n. sp.

Figures 9-6a, b, 7a—c ; 11-5—7

Diagnosis.—Test smooth, except for slightly depressed umbilicus with granular shell materials. Sutures near the umbilicus depressed, without sutural pores. Sutural canals only formed in the umbilicus. Aperture consisting of a row of small rounded openings.

Description.—Test compressed, almost completely involute, bilaterally symmetrical ; peripheral margin rounded, not lobulate ; umbilical region slightly depressed, with granular shell materials, which extend to apertural area ; chambers distinct, not inflated, increasing gradually in size as added, 7 to 8 chambers in the last whorl ; sutures flush with surface excepting final one and umbilicus, where canals are formed by a umbilical flap-like structure, curved toward the periphery, without retral process or sutural bridges ; wall smooth, very finely perforate, polished, originally optically granular in texture ; aperture interiomarginal, a row of about four rounded openings at the base of apertural face, which is more or less hidden by tuberculated shell materials on the final chamber.

Type and materials.—Holotype, DESS 88006, Figures 9-7a—c, from samples Mt-17 of boring core, Matsue Formation, late Middle Miocene ; Paratypes, DESS 88007, Figures 9-6a, b. from the same sample.

Size and measurements.—Holotype, maximum diameter 0.38 mm, thickness 0.16 mm ; 27 paratypes, maximum diameter 0.16-0.54 mm (av., 0.34 mm), thickness 0.08-0.21 mm (av., 0.15 mm).

Remarks.— This new species may be assigned to the genus *Haynesina* by the feature of intercameral lacunae and umbilical tuberculation. However, the intercameral lacunae change to sutural canals around the umbilicus and do not intercommunicate with the latero-umbilical supplementary apertures as redefined in the *Haynesina* (Banner and Culver, 1978), but only internally communicate with umbilical spiral canals (Figures 11-5, 6). Usually the latero-umbilical supplementary apertures are not clearly observable in this species (Figure 11-7).

In addition to these features, the wall of

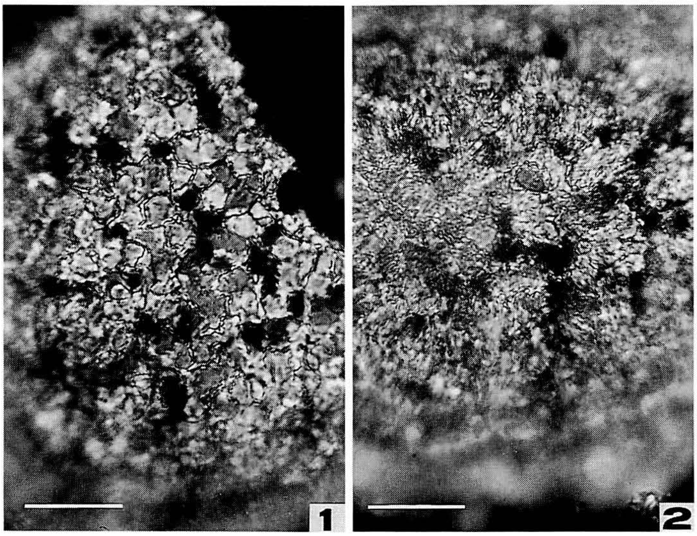


Figure 8. Two different optical wall characters of *Elphidium matsuense*. **1** shows a typical granular texture, whereas **2** depicted by the previous chamber wall is similar to an indistinctly radial texture. Crossed nicols. Scale: 50 μm.

this species is commonly optically granular in texture but in previous chamber with layered walls it shows an intermediate texture between granular and radial (Figure 8).

This species differs from *Astrononion umbilicatulum* Uchio in the shape of aperture and the absence of rounded openings associated with an umbilical flap.

Elphidium perforatum Nomura, n. sp.

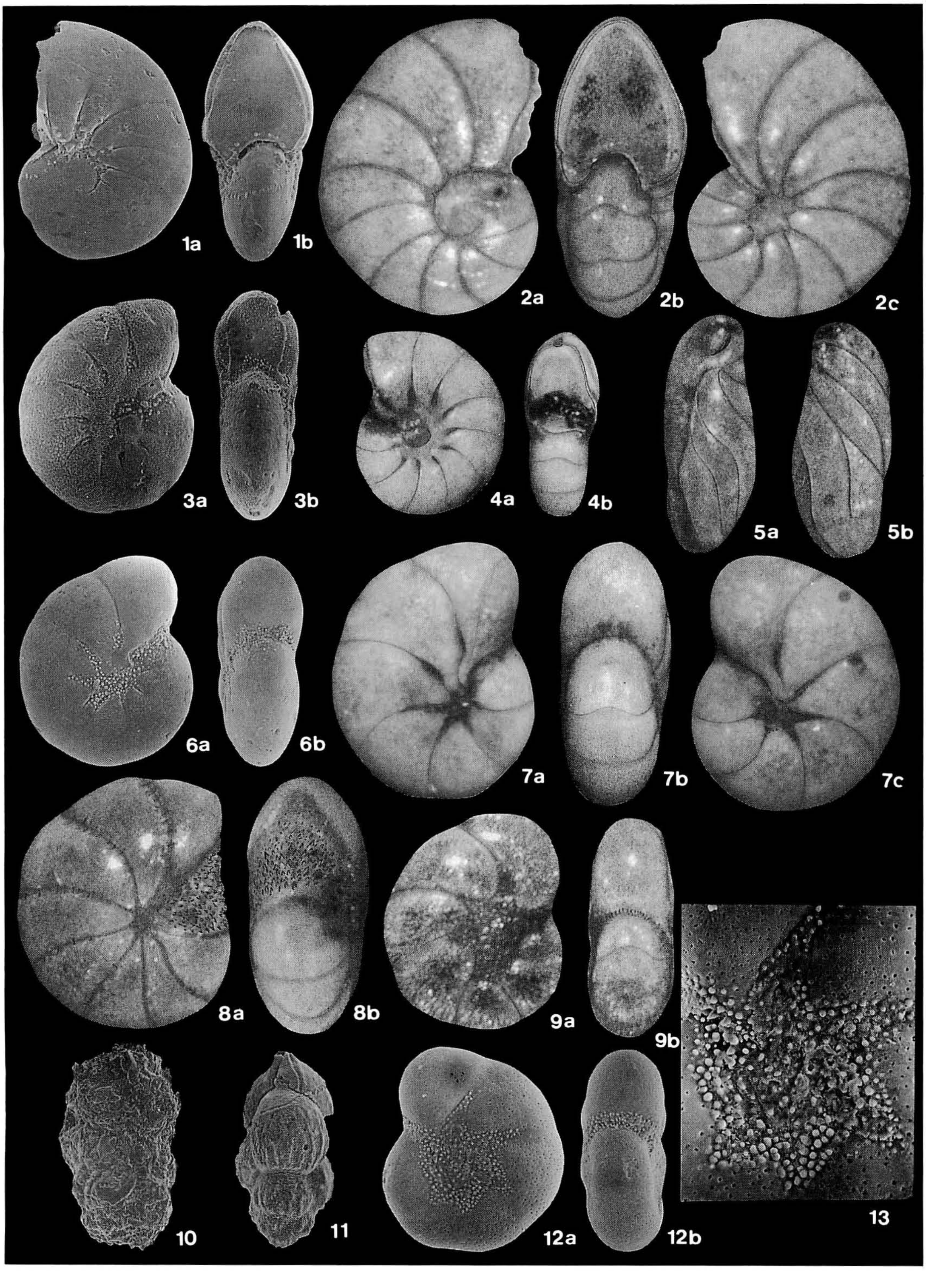
Figures 9-9a, b, 12a, b, 13; 11-1–4

Diagnosis.—Test with coarse perforation. Umbilicus covered with granular shell materials. Sutures limbate, without sutural pores. Sutural canals only formed in the umbilicus. Apertural openings indistinct.

Description.—Test compressed, subcircular in side view; periphery rounded and slightly lobulated; umbilical region slightly depressed or almost flat, covered with granular shell material extending partly to the base of apertural face; chambers seven to eight in the last whorl; sutures limbate, very slightly if at all depressed, without retral process and sutural pores; wall usually transparent, with distinct pore-lining; aperture of multiple openings at the base of apertural face of the last formed chamber, but usually indistinct by the presence of granular shell materials.

Type and materials.—Holotype, DESS 88008, Figures 9-9a, b, from sample MT-10 of boring core, Matsue Formation, late Middle Miocene; paratype, DESS 88009, Figures 9-12a, b, 13, from the same sample.

→ **Figure 9.** **1, 2**, *Pseudononion japonicum* Asano. **1a, b**; SEM photo, MT-13, ×94. **2a, b**; optical photo, MT-13, ×112. **3, 4**, *Elphidium izumoense* Nomura, n. sp. **3a, b**; SEM photo, MT-13, ×94. **4a, b**; holotype, optical photo, MT-13, ×112. **5.** *Buliminella elegantissima* (d'Orbigny). optical photo, MT-13, ×112. **6, 7**, *Elphidium matsuense* Nomura, n. sp. **6a, b**; SEM photo, MT-17, ×81. **7a-c**; holotype, optical photo, MT-17, ×112. **8**, *Elphidiella praesomaensis* Nomura, n. sp. optical photo, holotype, MT-13, ×112. **9, 12, 13,** *Elphidium perforatum* Nomura, n. sp. **9a, b**; optical photo, holotype, MT-10, ×112. **12a**, b; SEM photo, MT-10, ×105. **13**; SEM photo showing pustule on umbilical portion, ×240. **10,** *Plectina* sp. SEM photo, MT-14, ×53. **11,** *Uvigerina* cf. *akitaensis* Asano. SEM photo, MT-10, ×120.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12b
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Size and measurements.—Holotype, maximum diameter 0.32 mm, thickness 0.13 mm; 24 paratypes, maximum diameter 0.15-0.32 mm (av., 0.21 mm), thickness 0.09-0.14 mm (av., 0.12 mm).

Remarks.—This new species is similar to *Elphidium subarcticum* Cushman in having the sutural and umbilical spiral canals as well as the umbilical tuberculation, but differs in the absence of sutural pores and retral process, and by having coarse perforation. In the presence of the umbilical tuberculation, this species is further closely related to the arctic and boreal species such as *Cribroelphidium granatum* (Gudina) depicted by Gudina and Levtchuk (1989) and *Perfectnonion obscurus* (Voloshinova) reported by Voloshinova *et al.*, (1970) from the Pliocene of Sakhalin. However, *E. perforatum* can be distinguished from *C. granatum* by having a limited distribution of the tuberculation on the apertural face as well as the umbilical region and the absence of the sutural pores. It is also distinguished from *P. obscurus* by having fewer chambers in the last whorl and slightly depressed sutures around the umbilicus. As far as the figured holotype and paratype are concerned, *Elphidium nakanokawaense* Shirai (1960) from the Pleistocene deposits (originally described as the Pliocene) of Kuromatsunai, southern Hokkaido, is another species similar to this new one. Examined the specimens from near the type locality, however, it is pointed out that *E. nakanokawaense* is not closely related to *E. perforatum*, but rather related to *E. subarcticum* in the development of the tuberculation in the umbilical and the sutural regions and in the possession of the minute sutural pores.

The retral process has been recognized as the diagnostic feature of the genus *Elphidium*. Hansen and Lykke-Andersen (1975, p. 20) stated that all degrees of development of retral processes exist and stressed that retral process is a poor character for distinguishing the *Elphidium* group from similar groups. Based on their observations, this new species is here assigned to the genus *Elphidium*.

As far as known species from Japan and neighboring areas are examined, it seems that *E. perforatum* is related to arctic or boreal water.

Elphidiella praesomaensis Nomura, n. sp.

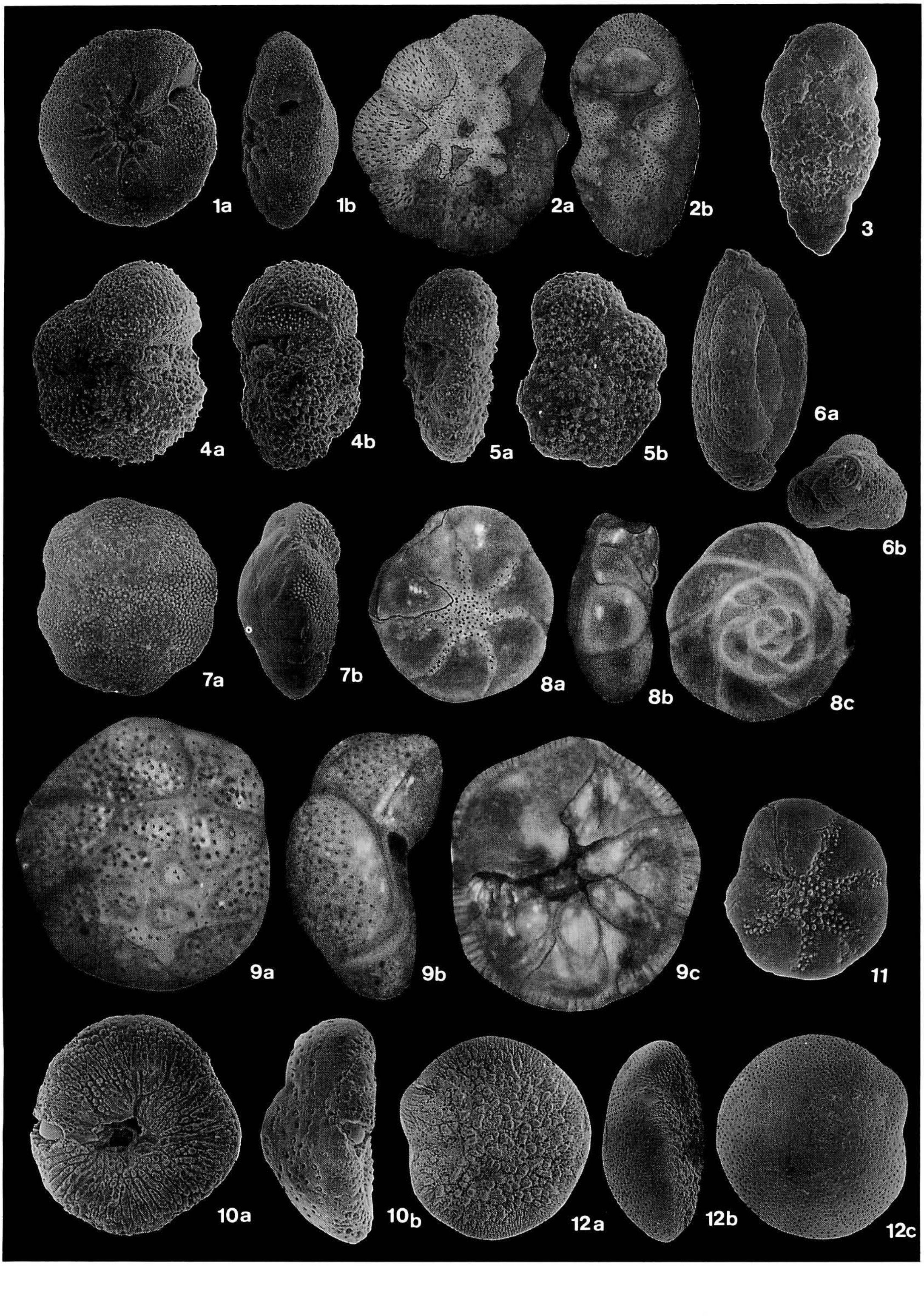
Figures 9-8a, b; 11-8–10

Diagnosis.—Test with rounded periphery. Apertural face decorated with numerous tuberculations. Sutures flushed with surface, with weak double row of small pores internally connected with subsutural canals.

Description.—Test medium, nearly circular in side view and elongate oval in edge view; periphery rounded, not lobulate; umbilical region slightly depressed; chambers distinct, increasing gradually in size as added, 8 to 9 chambers in the last coil; sutures gently curved toward periphery, almost flush with surface, with very weak double rows of small pores, which often indistinct; wall smooth, very finely perforate, optically granular in texture; aperture consists of several rounded interiomarginal openings, usually covered with numerous tuberculations.

Type and materials.—Holotype, DESS 88008, Figures 9-8a, b, from sample MT-13

→ **Figure 10.** **1**, *Ammonia* cf. *beccarii* (Linné). SEM photo, MT-3, ×94. **2, 4, 5**, *Murrayinella yakumoensis* Nomura, n. sp. **2a, b**; holotype, optical photo, MT-13, ×112. **4a, b**; SEM photo, MT-13, × 105. **5a, b**; SEM photo, MT-13, ×137. **3**, *Bolivina* sp. A. SEM photo, MT-2, ×194. **6**, *Quinqueloculina* cf. *fukushimaensis* Takayanagi. SEM photo, MT-15, ×94. **7**, *Buccella* cf. *kuromatsunaiensis* (Uchio). SEM photo, MT-13, ×120. **8, 11**, *Buccella frigida* (Cushman). **8a-c**; Optical photo, MT-10, ×112. **11**; SEM photo, MT-10, ×137. **9**, *Rosalina bradyi* (Cushman). Optical photo, MT-14, ×112. **10, 12**, *Trichohyalus* sp. **10a, b**; SEM photo, juvenile specimen, MT-14, ×106. **12a, b**; SEM photo, MT-14, × 38.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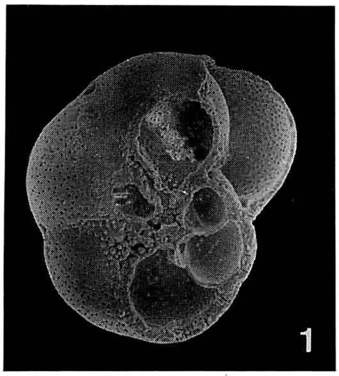
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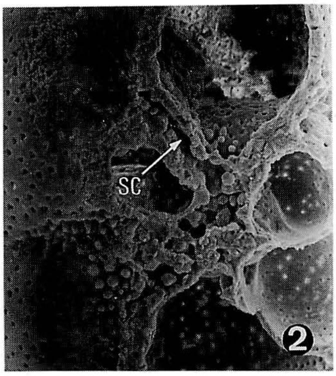
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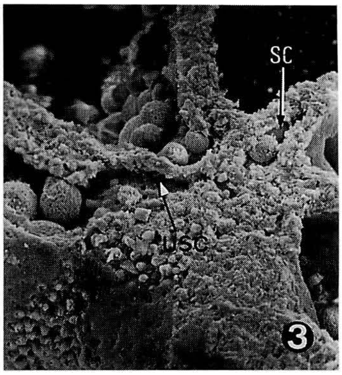
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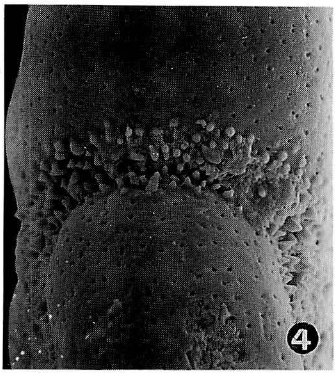
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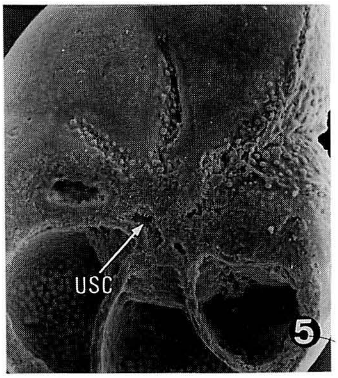
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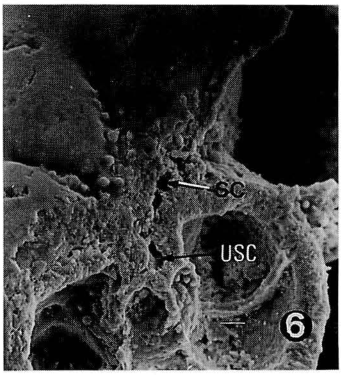
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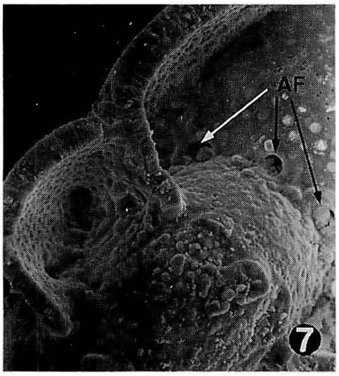
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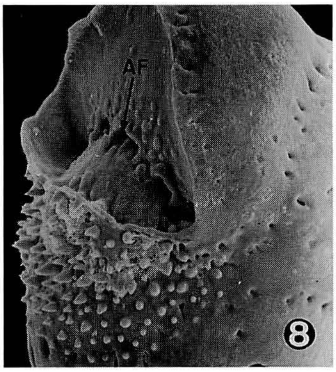
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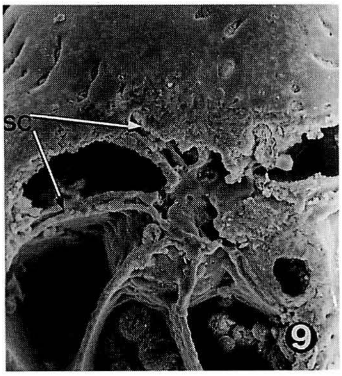
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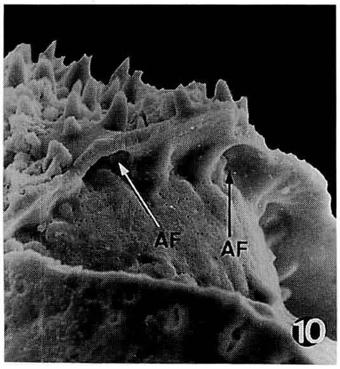
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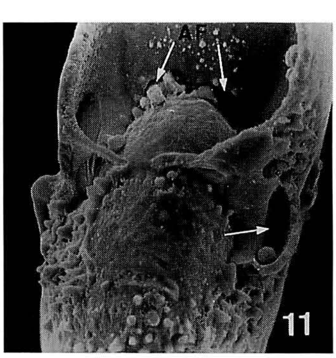
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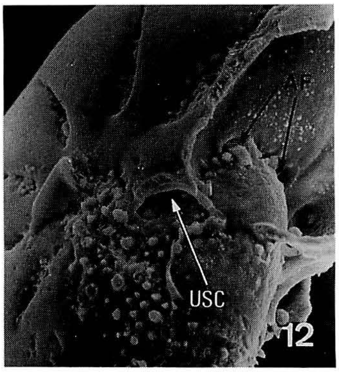
11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USC
12

of boring core, Matsue Formation, late Middle Miocene.

Size and measurements.—Holotype, maximum diameter 0.35 mm, thickness 0.18 mm; 20 paratypes, maximum diameter 0.21-0.38 mm (av., 0.27 mm), thickness 0.12-0.20 mm (av., 0.15 mm).

Remarks.—*Elphidiella praesomaensis* shows the double rows of sutural pores internally connected with subsutural canals (Figure 11-9), which are not so typical but most characteristic feature for the genus.

In appearance, this species is similar to *Elphidiella momiyamensis* Uchio (1951) occurring commonly from the early Middle Miocene deposits of Japan. However, topotypes of *E. momiyamensis* are characterized by having large and robust tests with usually 10-12 chambers. These diagnostics of *E. momiyamensis* are differentiated from those of this new species.

Despite of differently allocated generic position, this species is closely related to the present day species *Elphidium somaense* described by Takayanagi (1955) from the shallow bay area of Matsukawaura, Fukushima Prefecture, in its chamber arrangement and somewhat depressed umbilicus. Moreover, *Elphidiella praesomaensis* is characterized by having numerous small tuberculations around the aperture (Figure 11-8, 10), which is similar to those of the holotype as well as the subsequently figured specimen by Matoba (1970, p. 53; pl. 7, figs. 11a, b, 12a, b: *"Elphidium" somaense*), though no mention of them is made in the original description and remarks. Nevertheless, *Elphidiella praesomaensis* is differentiated from *E. somaense* in its greater test size and double rows of sutural pores mentioned above, suggesting a chronological differentiation between them.

Acknowledgments

I express my gratitude to Prof. Y. Takayanagi and Dr. S. Hasegawa, both of Tohoku University, and Prof. Y. Matoba of Akita University, for their critical comments on this manuscript.

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← **Figure 11.** **1-4**, *Elphidium perforatum* Nomura, n. sp. **1**; dissected specimen, ×125. **2**; enlargement of no. 1 showing sutural canals (SC), ×250. **3**; internal structure showing umbilical spiral canal (USC) of penultimate chamber, ×300. **4**; external structure showing apertural pustules, ×350. **5-7**, *Elphidium matsuense* Nomura, n. sp. **5**; dissected specimen showing umbilical spiral canals (USC), ×150. **6**; internal structure showing sutural canals (SC) and umbilical spiral canal (USC), ×300. **7**; internal structure showing previous apertural foramen, ×300. **8-10**, *Elphidiella praesomaensis* Nomura, n. sp. **8**; specimen without final chamber showing external apertural pustules and penultimate apertural foramen (AF), ×250. **9**; internal structure showing subsutural canals, ×250. **10**; internally viewed final aperture of no. 8, ×250. **11, 12**, *Elphidium izumoense* Nomura, n. sp. **11**; specimen without final and penultimate chambers showing internal apertural foramen and openings of umbilical spiral canal (USC). ×400. **12**; obliquely viewed no. **11** showing umbilical wall. ×350.

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Matsue 松江, Furue 古江, Fujina 布志名, Wakurayama 和久羅山, Teratsu 寺津, Kawatsu 川津, Kuroda 黒田, Yada 矢田, Asakumi-cho 朝酌町, Nange 南家, Kamihigashikawatsu-cho 上東川津町

島根県松江層の中期中新世後期の有孔虫：松江市街を中心とした低地帯には，中期中新世後期の浅海成層よりなる松江層が分布する。松江層はこれまで山陰地域の中新統最上部層として標準的に扱われてきたにもかかわらず，古環境の復元に十分な資料が蓄積されていなかった。今回，水源調査によって得られた1ボーリング試料により38タクサの底生有孔虫化石を認めることができたので古環境解析を行った。産出した有孔虫は *Ammonia* cf. *beccarii*, *Elphidium izumoense*, n. sp., *Elphidium matsuense*, n. sp., *Buliminella elegantissima*, *Buccella* cf. *kuromatsunaiensis*, *Elphidiella praesomaensis*, n. sp., *Elphidium perforatum*, n. sp., *Pseudononion japonicum*, *Trichohyalus* sp. 等を特徴種としている。層位的分布では上部に *A.* cf. *beccarii* 群集が，下部と上部の一部で *E. perforatum* 群集，*E. praesomaensis* 群集，*E. matsuense* 群集が発達する。このような群集組成は，類似種の量的な比較をする限り東北地方太平洋岸の松川浦や松島湾の現生有孔虫群と組成内容が極めて似ていることで注目される。そのため後者 Matoba（1970）のリストより選んだ11タクサについて主成分比較を行った結果，松江層の下部層準は湾口内外の堆積環境を示し，上部は水深が3m程度の内湾的環境へと変化していったと考えられる。従来松江層は貝化石群集や魚類-エビ化石より温暖な堆積環境が強調されていたのに対し，今回検討した有孔虫群集は，暖流系ばかりでなく寒冷水塊の影響も受けていたことを示す。　野村律夫

Appendix. Occurrences of foraminileral taxa from the Matsue Formation.

Stratigraphic horizon	Upper																		
Foraminiferal Taxa/Samples	MT-1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Median Depth of Sample (m)	29.5	30.5	31.6	32.3	35.5	49.5	53.5	56.0	64.3	69.5	70.5	93.4	98.5	99.5	100.4	103.8	108.4	109.5	110.5
(Agglutinated tests)																			
Cribrostomoides sp.														1					
Plectina sp.														1					
Proteonia compressa	1																		
Textularia sp.										1									
(Porcelaneous tests)																			
Quinqueloculina polygona													2		2				
Q. cf. *fukushimaensis*												3			1				
(Calcareous hyaline tests)																			
Ammonia cf. *beccarii*	7		445	146	201	37			28	37							21	127	91
A. spp.			1		1											1			
Bolivia sp. A		3																	
B. sp.														1		1			
Brizalina sp.																			
Buccella frigida									5	24	21	1	1	3	34				
B. cf. *fniglda* calida															1				
B. cf. *kuromatsunaiensis*									3	26	3	75	175	16	23	7			
B. sp.												1	1						
Buliminella elegantissima										22	10	22	62	1	6	7			
Elphidiella praesomaensis									11	43	9	44	274	21	18	9			
Elphidium cf. *excavatum*																	1	1	
E. izumoense							26	7	11	7	1	2	23		2				
E. matsuense			15	9	25	12	3		11	11	22	14	1	4	3	4	221	71	63
E. perforatum	4		14	2	5		46	8	38	54		2	8	2	5	24	13	33	2
Epistominella pulchella										1									
Fissurina cucurbitasema										1		1	2			1			
Gavelinella sp.									1										
Guttulina pacifica																2			
G. sp.										1									
Islandiella sp.		1										1							
Murrayinella yakumoensis									1	10	2	23	34	5	2	9			
Nonion sp.										2			2						
Pseudononion japonicum							5			20	48	12	82	7	22	18			
Rosalina bradyi														10		2			
R. sp.															1	1			
Trichohyalus sp.													5	41	7				
Trifarina sp.											1								
Uvigerina cf. *akitaensis*									1	4									
U. sp.											2								
Miscellaneous (agglutinated)										1		1	1	1					
Miscellaneous (calareous)																			
Total counted	12	4	475	157	232	49	80	15	110	265	119	202	673	114	127	86	256	232	156
Amount of sample (g)	80	80	34	80	80	80	80	80	80	80	80	39	80	80	80	80	80	80	80

Stratigraphic horizon	Lower																			
Foraminiferal Taxa/Samples	MT-20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Median Depth of Sample (m)	115.0	133.6	138.6	144.3	146.7	152.6	165.5	173.4	175.3	185.4	194.7	197.5	215.7	230.4	265.4	266.5	270.5	272.5	273.5	276.5
(Agglutinated tests)																				
Cribrostomoides sp.																				
Plectina sp.																				
Proteonina compressa																				
Textularia sp.																				
(Porcelaneous tests)																				
Quinqueloculina polygona																				
Q. cf. *fukushimaensis*																				
(Calcareous-hyaline tests)																				
Ammonia cf. *becarii*	3		1		13					3								18		81
A. spp.				1		5						3								
Bolivina deccusata																				
B. sp.						1														
Brizalina sp.		2										1								
Buccella frigida						1						1				1				
B. cf. *frigida calida*																				
B. cf. *kuromatsunaiensis*				6	1	1														
B. sp.														1						
Buliminella elegantissima				5	11	16			4	19			4							
EElphidiella praesomaensis					16	178			1	24			1							14
Elphidium cf. *exavatum*										2										
E. izumoense													17	2	10	38	2			235
E. matsuense	1		1	1		83	1	4	53				92		1		97			59
E. perforatum		3		1		114			33				24		8	24	12	170	40	1
Episotminella pulchella					1															
Fissurins cucubitasema																				
Gavelinella sp.																				
Guttulina pacifica																				
G. sp.																				
Islandiella sp.																				
Murrayinella yakumoensis					4	4				6										
Nonion sp.																				
Pseudononion japonicum		2		1		12				3		2	11							

Foraminiferal Taxa/Samples	MT-20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
Median Depth of Sample (m)	115.0	133.6	138.6	146.7	152.6	165.5	173.4	175.3	185.4	194.7	194.7	197.5	230.4	230.4	265.4	266.5	270.5	272.5	273.5	276.5
Rosalina bradyi					4															
R. sp.																				
Trichohyalus sp.																				
Trifarina sp.																				
Uvigerina cf. *akitaensis*																				
U. sp.						1														
Miscellaneous (agglutinated)				1																
Miscellaneous (calcareous)											3									
Total counted	4	7	2	16	50	416	1	4	91	57	3	7	149	3	19	63	111	188	40	390
Amount of sample (g)	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	39

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900. NOTES ON A CRETACEOUS BIVALVE *INOCERAMUS* (*PLATYCERAMUS*) *MANTELLI* DE MERCEY FROM JAPAN*

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Abstract. Based on a number of specimens of *Inoceramus* (*Platyceramus*) *mantelli* de Mercey, 1877, from Hokkaido several quantitative characters were examined biometrically. The specimens of *I.* (*P.*) *mantelli* from Japan have been hitherto ascribed to *I.* (*P.*) *yubariensis* Nagao et Matsumoto, 1940. From the precise comparison between the specimens from Europe and Japan, the morphological difference is so slight that specific distinction does not seem necessary. Thus the specific name *I.* (*P.*) *yubariensis* Nagao et Matsumoto falls in a junior synonym of *I.* (*P.*) *mantelli* de Mercey. Stratigraphically *I.* (*P.*) *mantelli* from Europe and eastern contiguous regions ranges throughout the Coniacian, whereas the range of this species in Japan is from the Upper Coniacian to the Santonian. The ancestry of *I.* (*P.*) *mantelli* is as yet uncertain, but this species may be the common ancestor of various species of *Inoceramus* (*Platyceramus*) from the Santonian and Campanian.

Key words. *Inoceramus* (*Platyceramus*) *mantelli*, *yubariensis*, synonym, Upper Coniacian, Santonian.

Introduction

Inoceramus mantelli de Mercey, 1877 occurs commonly in the Coniacian of Europe and contiguous regions of Asia, but this species has been undescribed in Japan.

On the other hand, *I. incertus* var. *yubariensis* was established by Nagao and Matsumoto (1940) on the basis of a single well-preserved specimen, HK5960 (Figures 2-1a, b, c, 2a, b) from the Upper Cretaceous of Kamihobetsu, south central Hokkaido. Subsequently, Matsumoto and Noda (1968) separated *I. yubarensis* [sic] from *I. incertus* as an independent species. Since then, *I. yubarensis* [sic] has been listed in several papers without giving a revised definition and clear extent of variation.

This paper is to clarify the systematic relationship between *I. mantelli* and *I. yubariensis*. For this purpose we made field works together with T. Matsumoto in the type area of Hobetsu, and Noda (M.N.), with T. Matsumoto (T.M.) and others, in the Ikushumbets (Mikasa) area. Meanwhile, Toshimitsu (S.T.) obtained a considerable number of specimens during his field work in the Haboro area. In addition, A. Inoma's collection from the Kotanbetsu area, kept in Kyushu University was provided for this study by

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courtesy of T. Matsumoto. To make clear the extent of variation and to settle the systematic position, a statistic method has been applied for these specimens. Furthermore, we discuss the phylogenetic relationship between *I.* (*P.*) *mantelli* and allied species.

Method

To make clear the extent of variation of *I. yubariensis* [= *I.* (*P.*) *mantelli*] from Hokkaido, a biometric method is applied for some selected characters.

The basic linear measurements and angles are shown in Figure 1. A calipers of JIS standard, 200 mm in measurable extent and 1/20 mm in accuracy and a contact goniometer were used for measurements of length and angle respectvely. A flexible guage was also applied for shell convexity. The measurements were made three times for the same part and the mean was adopted. On the basis of measurements, the mean value, standard deviation, population standard deviation and Pearson's coefficient of variation of the selected characters were calculated.

The individual relative growth of shell length vs. shell height and that of shell breadth vs. shell height were examined. These are demonstrated by reduced major axes on logarithmic graph paper and expressed by power functions [$l = \beta h^{\alpha}$, $b = \beta h^{\alpha}$]

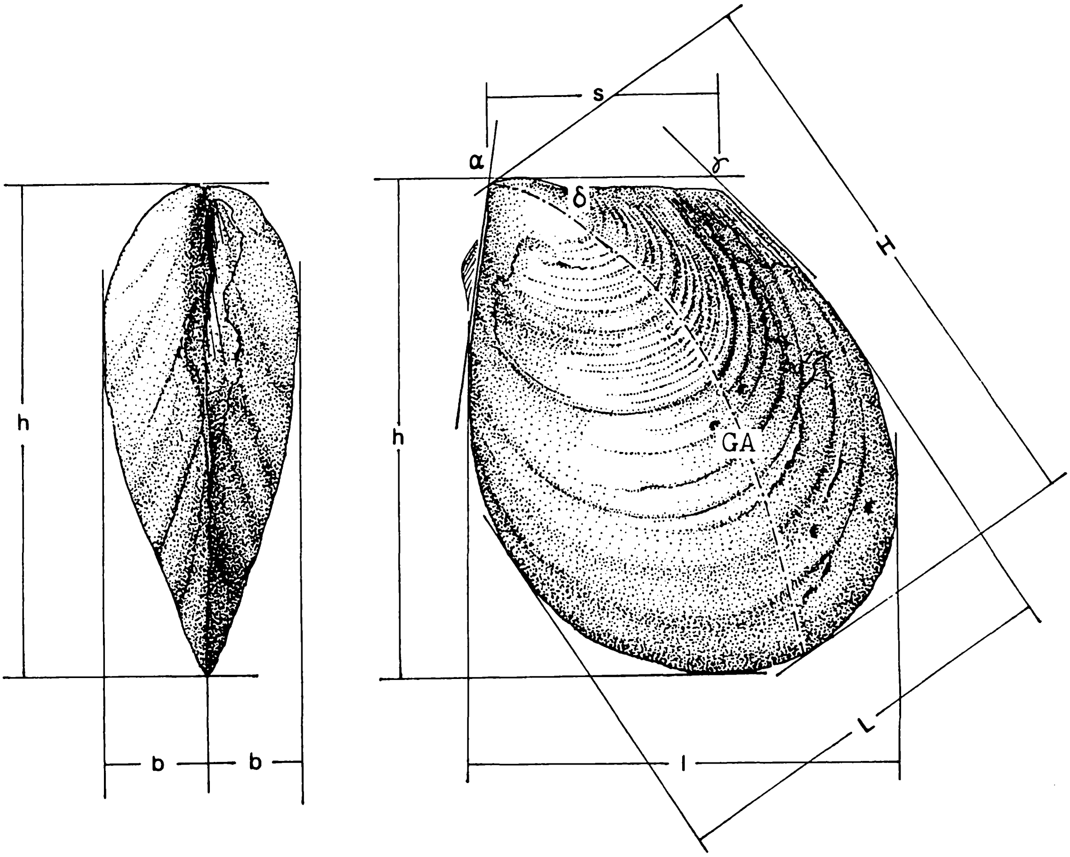


Figure 1. Basic morphology for measurements. h : shell height, l : shell length, b : shell breadth, s : length of hinge line, H : maximum linear dimension from umbo to ventral extremity, L : Maximum linear dimension perpendicular to H, GA : growth axis, α : anterior hinge angle, β : beak angle, angle of umbonal inflation, γ : posterior hinge angle, δ : obliquity, angle between hinge line and H.

and the correlation coefficient is calculated for each of them. Isometric or allometric relationship is evaluated by means of the K-test.

The ontogenetic change of l/h vs. H, that of b/h vs. H and also that of obliquity (δ) are shown in the same way as Seitz's (1961) and Tröger's (1967) for the comparison with allied species.

For evaluation of the morphological differences between *Mytiloides incertus* and *I.* (*P.*) *yubariensis*, and *I.* (*P.*) *mantelli* from Europe and *I.* (*P.*) *yubariensis*, the Student's t-test was adopted. If the F-value was significant, the t-value was calculated by the Welch's method.

For the procedure of statistics, readers may refer to Hayami (1969), Hayami and Matsukuma (1971), Tanabe (1973) and Noda (1975).

Palaeontological description

Family Inoceramidae Zittel, 1881
Genus *Inoceramus* Sowerby, 1814
Subgenus *Platyceramus* Seitz, 1961

Type species.—*Inoceramus mantelli* de Mercey was designated by Seitz (1961).

Remarks.—*Platyceramus* was originally proposed by Heinz (1932) as an independent genus of Inoceramidae and he designated *I. mantelli* de Mercey as the type species, but it is invalid under the Code of I.C.Z.N., because of no generic diagnosis. Seitz (1961) gave the diagnosis for *Platyceramus* as a subgenus of *Inoceramus* (s.l.) and designated *I. mantelli* as the type species. Since then, *Platyceramus* obtained the validity. Thus the authorship of *Platyceramus* should be ascribed to Seitz under the Art. 50 of I.C.Z.N. For the subgeneric diagnosis and the additional notes, readers may refer to Seitz (1961) and Noda (1979, 1983b, p. 202). But Vokes (1967, 1980) has regarded *Platyceramus* as being invalid, and Cox (1969) has included *Platyceramus* to *Inoceramus* (s.s.) as a junior synonym.

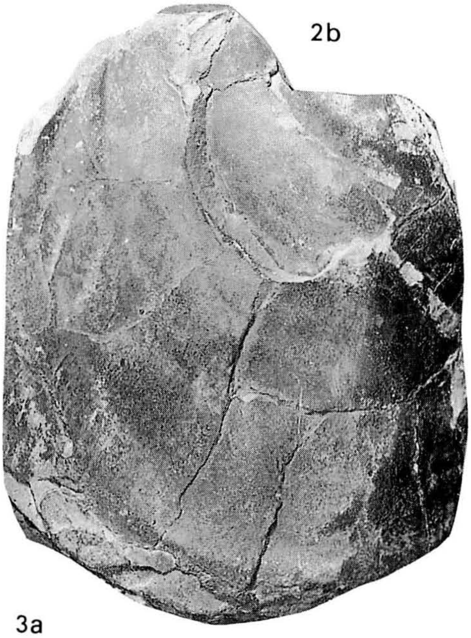
Inoceramus (*Platyceramus*) *mantelli*
de Mercey, 1877

Figures 2–11

1877 *Inoceramus Mantelli* de Mercey, p. 324, pls. 1, 2.
1878 *Inoceramus Mantelli*, Barrois, p. 478.
1879 *Inoceramus Mantelli*, Barrois, p. 454, pl. 4, figs. 1, 2.
1929 *Inoceramus circularis* Schlüter var. *oblonga* Heine, p. 54, 55.
1929 *Inoceramus circularis* Schlüter var. *undata* Heine, p. 55, 56, pl. 5, fig. 24.
1932 *Inoceramus mantelli* Mercey; Heinz, p. 10.
1934 *Inoceramus mantelli* Mercey (Barrois); Heinz, p. 32.
1940 *Inoceramus incertus* Jimbo var. *yubariensis* Nagao et Matsumoto, p. 11-13, pl. 5, fig. 1.
non 1954 *Inoceramus mantelli* de Mercey; Voûte, p. 149, 150, 153.
1962 *Inoceramus* (*Platyceramus*) *mantelli mantelli* Mercey (Barrois); Seitz, p. 360-363, pl. 10, figs. 1, 2; pl. 11, figs. 1, 2, 6; pl. 12, fig. 3.
1962 *Inoceramus* (*Platyceramus*) *mantelli undatus* Heine; Seitz, p. 363, 364, pl. 12, fig. 6.
1962 *Inoceramus* (*Platyceramus*) *mantelli subrhenanus* Seitz, p. 366, 367, pl. 11, figs. 3, 4; pl. 12, fig. 1.
1962 *Inoceramus* (*Platyceramus*) *mantelli angustus* Seitz, p. 367-369, pl. 12, figs. 2, 5, 7; pl. 13, fig. 1.
non 1962 *Inoceramus* (*Platyceramus*) *mantelli* (?) *rhenanus* (Heinz; Seitz, p. 365, 366, pl. 11, fig. 5. cf.) *I.* (*Cordiceramus*), n. sp. (in process of study)
1965 *Inoceramus* (*Platyceramus*) *mantelli beyenburgi* Seitz, p. 96.
1968 *Inoceramus yubarensis* [sic] Nagao et Matsumoto; Matsumoto and Noda, p. 320.
non 1976 *Inoceramus* (*Platyceramus*) *mantelli subrhenanus* Seitz; Szăsz, p. 210, pl. 14. cf. *I.* (*P.*), n. sp. A (in process of study)
1976 *Inoceramus yubarensis* [sic] Nagao et Matsumoto; Noda and Matsumoto, sheet 267, p. 1, listed (*in Japanese*).
1977 *Inoceramus waltersdorfensis yubariensis* Nagao et Matsumoto; Kauffman, p. 182, 183.
1983 *Inoceramus* (*Platyceramus*) *yubarensis* [sic] Nagao et Matsumoto; Noda, p. 213, 214, text-figs. 11, 12.
1985 *Inoceramus mantelli beyenburgi* Seitz; Szˇasz, p. 171, pl. 33, fig. 3; pl. 34, fig. 2; pl. 40, fig. 1.

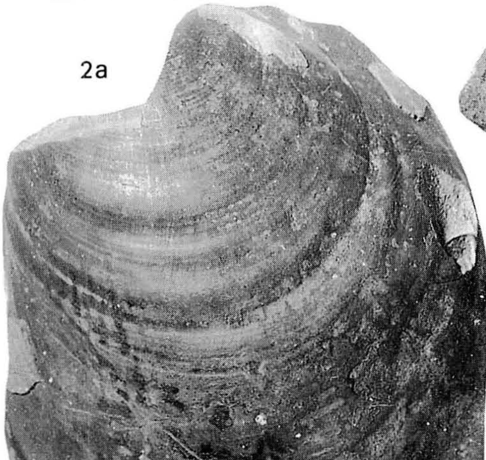

1a

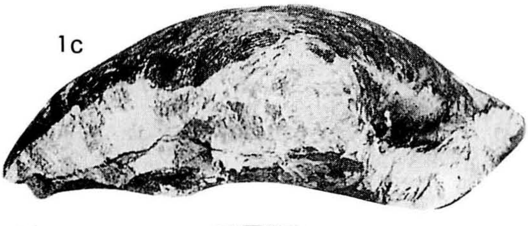

1b


2b


4


3a


2a


1c


3b

non 1986 *Inoceramus* (*Platyceramus*) *yubariensis* Nagao et Matsumoto (pars); Noda, p. 363, listed. *I.* (*P.*), n. sp. A (in process of study)
1986a *Inoceramus* (*Platyceramus*) *mantelli mantelli* (Barrois); Lõpez, p. 22-25, pl. 1, figs. 3a, b.
1986a. *Inoceramus* (*Platyceramus*) *mantelli subrhenanus* Seitz: Lõpez, p. 25-27, pl. 1, fig. 4.
non 1986a *Inoceramus* (*Platyceramus*) *mantelli* ? *rhenanus* Heinz; Lõpez, p. 27, 28, pl. 1, fig. 5.
1986b *Inoceramus* (*Platyceramus*) *mantelli mantelli* (Barrois); Lõpez, p. 236, 237, pl. 1, fig. 2.
1986b *Inoceramus* (*Platyceramus*) *mantelli subrhenanus* Seitz; Lõpez, p. 236, 237, pl. 1, fig. 3.
non 1986b *Inoceramus* (*Platyceramus*) *mantelli* ? *rhenanus* Heinz, Lõpez, p. 236, 237, pl. 1, fig. 4.

Lectotype.—A specimen figured by Barrois (1879, pl. 4, fig. 1=Seitz, 1962, pl. 10, fig. 1) was designated by Seitz (1962). For details of the designation of the lectotype, readers may refer to Seitz (1962, p. 355 and 356).

Remarks.—The validity of the lectotype designated by Seitz (1962) is somewhat questionable. The lectotype should be selected from among the de Mercey's original specimens (1877) under the Code of Art. 74 of I.C.Z.N., but Seitz designated the type specimen from among the Barrois ones (1879). If Barrois used the de Mercey's original specimens for his figures, it is reasonable, but Seitz does not make any mention of this. Therefore, it is now outside of our capacity for to comment on the validity of the lectotype. Lõpez (1986a) followed Seitz's designation and Szăsz (1985) did not refer to the lectotype. We follow, at now, tentatively after Seitz.

Material.—In addition to the illustrated specimens from abroad by literature, the following 32 specimens from Hokkaido are concerned with this study, of which 25 specimens are used for measurements and statistics (BV: both valves, L: left valve, R: right valve). HK5960 (BV) (holotype of *I.* (*P.*) *yubariensis*), loc. H3019, coll. Otatume (1932); GK.H8250 (R), loc. RH2441; GK.H8251 (R), loc. RH5047c8; GK.H8252 (BV), loc. RH4046p; GK.H8253 (BV), loc. RH 2148a; GK.H8254 (R), loc. RH2411d; GK.H8255 (L), loc. RH1271a; GK.H8277A (L), loc. RH7242b, coll. Uchida and Toshimitsu; GK.H8277B (L), loc. RH7242b, coll. Uchida and Toshimitsu; GK.H8323 (L), loc. H3019; GK.H8324 (L), loc. Ik 1117b, coll. Matsumoto; GK.H8325 (R), loc. R371 (RH1275 of S.T.), coll. Nishida and Okada; GK.H10128 (R), loc. IA2119, coll. A. Inoma; GK.H10129 (R), loc. IA2133, coll. A. Inoma; JG.H2796 (R), loc. Ik1506r, coll. Matsumoto and Muramoto; JG.H2902 (R), loc. Ik2707p; JG.H2906 (R), loc. Ik1535, coll. Matsumoto and Muramoto; JG.H2910 (R), loc. Ik1533a, coll. Matsumoto and Muramoto; JG.H2917 (R), loc. Ik1537, coll. Matsumoto and Muramoto; JG.H2918 (R), loc. Ik2708, coll. Uchida; JG.H2912 (BV), loc. Ik5561p; JG.H2793 (L), loc. IK561p; JG.H2916 (L), loc. Ik5617p; JG.H2921 (L), loc. H2027c; JG.H2922 (R), loc. H2027c; JG.H2923 (R), loc. Ik8387p; JG.H2924 (R), loc. Ik8304p; JG.H2988 (R), loc. Ik8053p; JG.H3002 (BV), loc. Ik8390r; JG.H3003 (R), loc. IK8390p; JG.H3004 (BV), loc. Ik8060p and JG.H3005 (R), loc. Ik8064p.

The above specimens were mostly collected by us, unless otherwise stated.

Repositories: GK: Dept. of Geology, Kyushu University, Fukuoka, HK: Dept. of Geology and Mineralogy, Hokkaido University, Sapporo, JG: Jonan Geological Association, Oita.

For localities, readers may refer to the Appendix : Locality Guide.

Description.—Shell medium to large, equivalve, inequilateral, higher than long, with axis of growth broadly concave towards the anterior. Valve gently and uniformly convex, anterior part steep to the commissure

←— **Figure 2.** *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. **1-a—c.** HK5960, illustrated in Nagao and Matsumoto (1940), from Loc. H3019. **2a, b.** HK5960, same specimen, at present the umbonal part missing. **3a, b.** GK.H8277B, from Loc. RH7241a. **4.** GK.H8277A, from Loc. RH7241a. (all figures in natural size)

Figure 3. *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. GK.H8323, natural size, from Loc. H3019. left valve showing anterior ear.

Figure 4. *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. GK.H8323, same specimen of Figure 3. natural size **1c** : external mould of left valve showing the delicate ornament of anterior ear.

plane and posterior one gradually flattened, passing into the wing-like area without sharp boundary. Anterior ear present and clearly demarcated from the main part of shell. Umbo terminal or subterminal and slightly prominent. Anterior margin long, straight or slightly concave; ventral margin moderately rounded, passing gradually to broadly arcuate and then nearly straight posterior one. Hinge line about a half of shell length, with some variability. Concentric ribs typically low, broad and weak but sometimes irregular in breadth and intensity. Minor rings generally fine and weak but occasionally somewhat coarse and distinct.

Observation.—HK5960 (Figures 2-la, b, c; 2-2a, b) well shows the major ribs and minor rings. Its umbonal portion is now missing. It is articulated but the right valve is secondarily squashed. The cross section of the anterior ear is observed in the left valve. GK.H8323 well preserves the anterior ear, whose surface ornamentation is distinctly impressed on the external mould (Figures 3, 4a—c). GK.H8252 (Figures 5-la—e) and GK.H8253 (Figures 6-5a—c) are closed articulated specimens. They show evidently the original equivalveness, although are slightly dislocated along the plane of commissure. The hinge structure is clearly visible and the anterior ear is preserved in GK.H8252 (Figure 8-l), GK.H8277B (Figures 2-3a, b) and JG.H2998 (Figure 6-l). The outer shell layer is well preserved in JG.H2922 (Figure 6-8) and partially remains in JG.H2924 (Figure 5-2), GK.H8252, GK.H8253 and GK.H10128, and the inner shell layer remains in JG.H291O, JG.H2921 (Figure 6-7), JG.H2923 (Figure 5-3) and GK.H8277B (Figures 2-3a, b). The concentric major ribs and minor rings are well shown in HK596O, GK.H8252, GK.H8253, JG.H 2921, 2922, 2923 and 2924. In JG.H2923 the major ribs are comparatively regular in strength near the umbo and broaden gradually with growth, though very irregular in JG.H2921, and the minor lirae are clearly visible in early stage of growth in both specimens. Occasionally small pits of hemispheric pearl are impressed on the internal mould (JG.H2998, Figure 6-1).

Biometry.—The measurements of selected characters, *i.e.*, h, l, b, s, H, L, α, β, γ, δ, $\delta_{H=60\,mm}$, l/h, $l/h_{H=60\,mm}$, L/H, $L/H_{H=60\,mm}$ and s/l, are shown in Table 1. The statistics for these characters are in Table 2. As is clear from Table 2, the Pearson's coefficient of variation are generally small for these characters, but for $b/h_{H=60\,mm}$ and s/l.

The individual relative growth of shell length (l) vs. shell height (h) and shell breadth (b) vs. shell height (h) in the two well-preserved specimens are demonstrated in Figure 9. The growth indices, Y-intercept of the reduced major axes and the coefficient of correlation for every specimen were calculated. According to Hayami and Matsukuma (1971, p. 150, 151), the reduced major axes in all the examined bivariate characters are within the scope of negative monophasic allometry. The ontogenetic changes of l/h, b/h and shell obliquity (δ) are demonstrated in Figures 10A, B and C, respectively. As is clear from Figures 10A and B, the simple ratio of l/h decreases gradually with growth in each individual, whereas the simple ratio b/h is nearly constant throughout the growth. The ontogenetic change of the angle (δ) between hinge line and the growth axis enlarges gradually with growth, as shown Figure 10C. In other words, the obliquity decreases with growth. The profiles of five selected specimens in two directions are illustrated in Figure 11.

Specific assignment

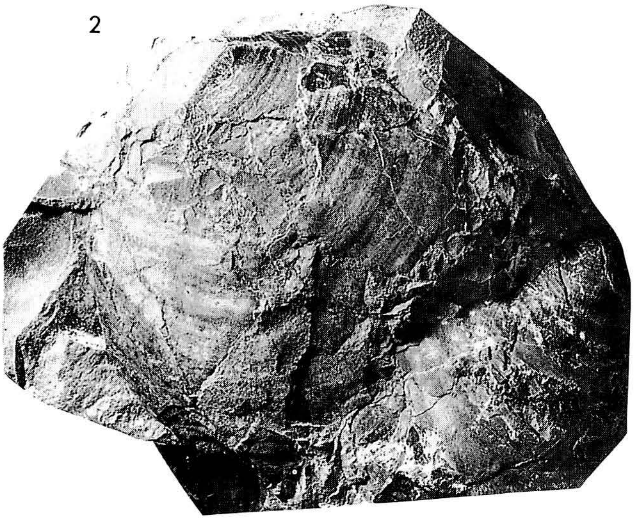
Seitz (1962, p. 355, 356) discussed the establishment of *I. mantelli* de Mercey (Barrois) in

→ **Figure 5.** *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. **1a—e.** GK.H8252, Loc. RH4046p. **2.** JG.H2924, Loc. Ik8304p. **3.** JG.H2923, Loc. Ik8387, "*undatus* type" (Heine, 1929, p. 55; Seitz, 1962, p. 363) (all figures in natural size)

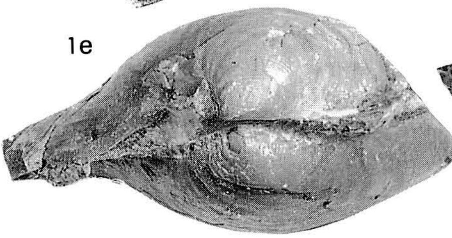
900. *Inoceramus* (*Platyceramus*) *mantelli*

1a

2



1e



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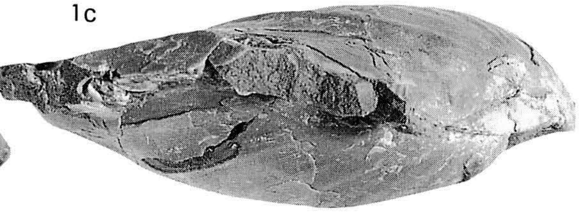

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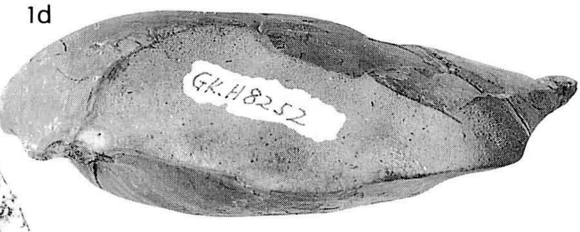

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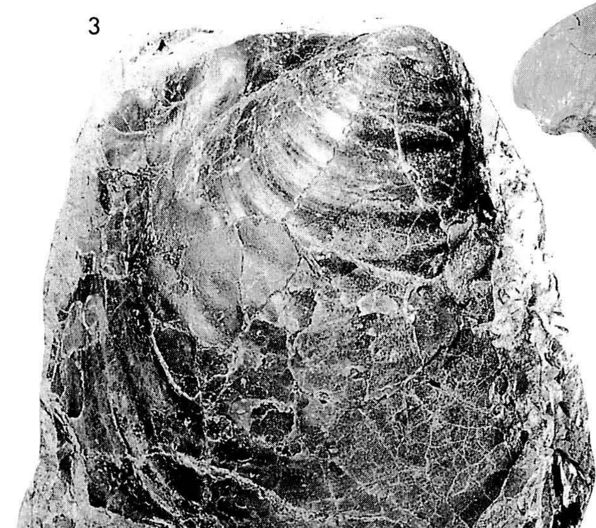


1b

detail. On the other hand, *I.* (s.l.) *yubariensis* was established by Nagao and Matsumoto (1940), originally as a variety of *Inoceramus incertus* Jimbo (=*Mytiloides incertus* in a revised sense). Matsumoto and Noda (1968) ranked it as an independent species for its much taller outline and separated occurrence in a higher stratigraphic position. In that paper the original name of "*yubariensis*" was erroneously spelled as "*yubarensis*". Subsequently, Noda (1984) examined statistically a number of specimens of *M. incertus* from the type locality (Ik2011-2014), as representing a fossil population. Accordingly the extent of variation of the measurable characters was elucidated quantitatively. On this occasion, we examine the morphological difference between *M. incertus* and the so-called *I.* (*P.*) *yubariensis* by means of the Student's *t*-test. Before the *t*-test, the *F*-test was attempted. The results are shown in Table 3. The significant difference between the two species is confirmed in the characters of α, γ, and 1/h, and the obliquity is nearly constant in *M. incertus* throughout the growth (Noda, 1984, p. 462, text-fig. 6A), whereas it decreases gradually in "*I.* (*P.*) *yubariensis*" (Figure 10C). From the above comparison, the two species are clearly discriminated morphologically.

Matsumoto (1986, personal communication) has suggested us that *I.* (*P.*) *yubariensis* may be specifically identical with *I.* (*P.*) *mantelli* de Mercey. Evidently *I.* (*P.*) *yubariensis* closely resembles *I.* (*P.*) *mantelli* from the Coniacian of Europe, in many respects, *e. g.*, outline, ornamentation, mode of growth, hinge structure and existence of anterior ear. According to Sornay (1981, p. 420), *I.* (*P.*) *mantelli* occurs in the Lower Coniacian of northern France, partially associated with *I. schloenbachi* Fiege, and Sornay (1983) cited the result of Amedro *et al.* (1979) that *I.* (*P.*) *mantelli* appears already in the Upper Turonian of northern France.

Seitz (1962) recorded the occurrence of *I.* (*P.*) *mantelli* in the Lower and Middle Coniacian of Germany, although the stage and substage boundaries in Germany at that date (before Seibertz, 1979) were set at higher level than those of the international scale.

Szăsz and Ion (1984) defined the Middle Coniacian of Rumania as the Assemblage Zone of *I.* (*P.*) *mantelli* in parallel with the Ammonite Zone of *Peroniceras tridorsatum* (Schlüter). Lõpez (1986a, b) reported *I. (P.) mantelli* from the Upper Coniacian of the St. Corneri area of Spain.

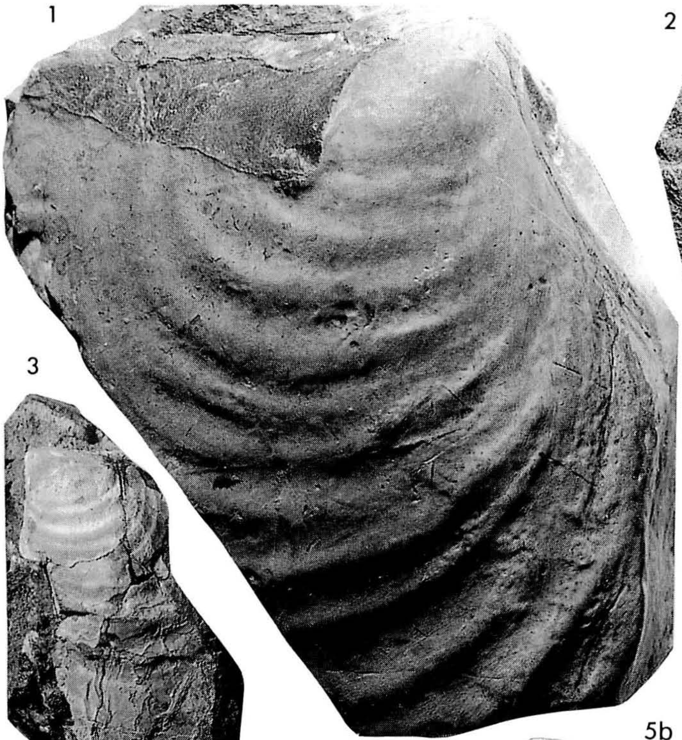
Seitz (1962) divided the specimens of *I.* (*P.*) *mantelli* obtained from the schaft II of Preussen Mine and other areas of West Germany into five subspecies, *e. g., I.* (*P.*) *mantelli mantelli* Mercey (Barrois), *I.* (*P.*) *mantelli undatus* Heine, *I.* (*P.*) *mantelli* (?) *rhenanus* Heinz, *I.* (*P.*) *mantelli subrhenanus* Seitz and *I.* (*P.*) *mantelli angustus* Seitz [=*I. circularis* Schlüter var. *oblonga* Heine, 1929, =*I.* (*P.*) *mantelli beyenburgi* Seitz, 1965]. Szăsz (1976, 1985) and Lõpez (1986a, b) followed Seitz's subspecific distinction. However, it is biologically unnatural that various subspecies of one species occur in the synchronous stratigraphic unit of a limited area, unless their habitats were originally different.

On the other hand, Sornay (1986, in a letter to Matsumoto) pointed out some questions about Seitz's assignment of the specimens of A408, the holotype of *I.* (*P.*) *mantelli* (?) *rhenanus* Heinz (Seitz, 1962, pl. 2, fig. 5) and the specimen of *I.* (*P.*) *mantelli subrhenanus* Seitz (Szăsz, 1976, pl. 14) to the species *I.* (*P.*) *mantelli*. We agree with his suggestion. The specimen of A408 is probably discriminated at specific level from *I.* (*P.*) *mantelli* because of its acutely pointed beak,

→ **Figure 6.** *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. **1.** JG.H2998, natural size, Loc. Ik8053, showing anterior ear. **2.** JG.H2976, ×1.3, Loc. Ik1506r. **3.** GK.H8255, natural size, Loc. RH1271a. **4.** JG.H2907, ×1.4, Loc. Ik1536. **5a–c.** GK.H8253, natural size, Loc. RH2148a2. **6.** GK.H8254, natural size, Loc. RH2411d. **7.** JG.H2921, ×1.3, Loc. H2027. **8.** JG.H2922, natural size, Loc. 2027.

900. *Inoceramus* (*Platyceramus*) *mantelli*

1



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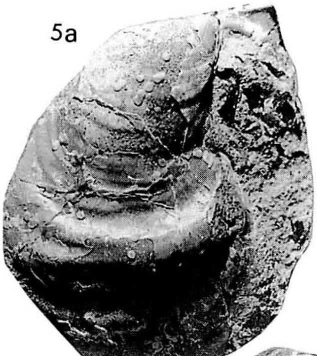
5a



5c

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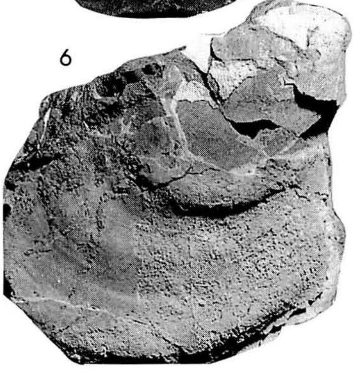

7

small beak angle and angularly bent concentric undulation. The Szăsz's specimen from the Vasilatu Formation of the Brezoi Basin (South Carpathian area, Rumania) is also discriminated from the typical form of *I.* (*P.*) *mantelli subrhenanus* Seitz, so far as we observed his photograph, in its small beak angle and the ontogenetic change of obliquity. Similar specimens to Szăsz's occur in the Upper Coniacian of Hokkaido ; these will be described in a separate paper by one of the authors (M. N.). The identification of the specimen N⁰-35009 of Lŏpez (1986a, pl. 1, fig. 5 ; 1986b, pl. 1, fig. 4) with *I.* (*P.*) *mantelli* (s.l.) is also doubtful, because of its small beak angle, considerably inflated shell and almost invariable obliquity throughout the growth.

Although the subspecific discrimination by Seitz (1962) is unreasonable under the modern biological concept, it suggested a large extent of variation in a species of *I.* (*P.*) *mantelli* in its outline and surface ornamentation *i.e.*, intensity, breadth and curvature.

At the suggestion of Sornay (1986, personal communication through Matsumoto), the measurements on the photographs of several specimens of *I.* (*P.*) *mantelli* by Seitz (1962) are shown in Tables 4 and 5. To make clear the morphological difference between the two forms from Japan and Europe, *F*-test and *t*-test have been applied for some selected characters. The *t*-values, as shown in Table 6, are not significant about all the examined characters except for the simple ratio s/l.

I. (*P.*) *mantelli* is also recorded in the Upper Coniacian (in the bipertite scheme of the USSR) of the platform of East Europe, Caucasus and the western region of Central Asia (Moskvin *et al*. ed., 1986, p. 201, 282 ; 1987, p. 175). Although the Upper Coniacian bipartite in the Russian scheme may overlap with the upper part of the Middle Coniacian of the international scheme, the range of *I.* (*P.*) *mantelli* in Europe and contiguous regions is partially

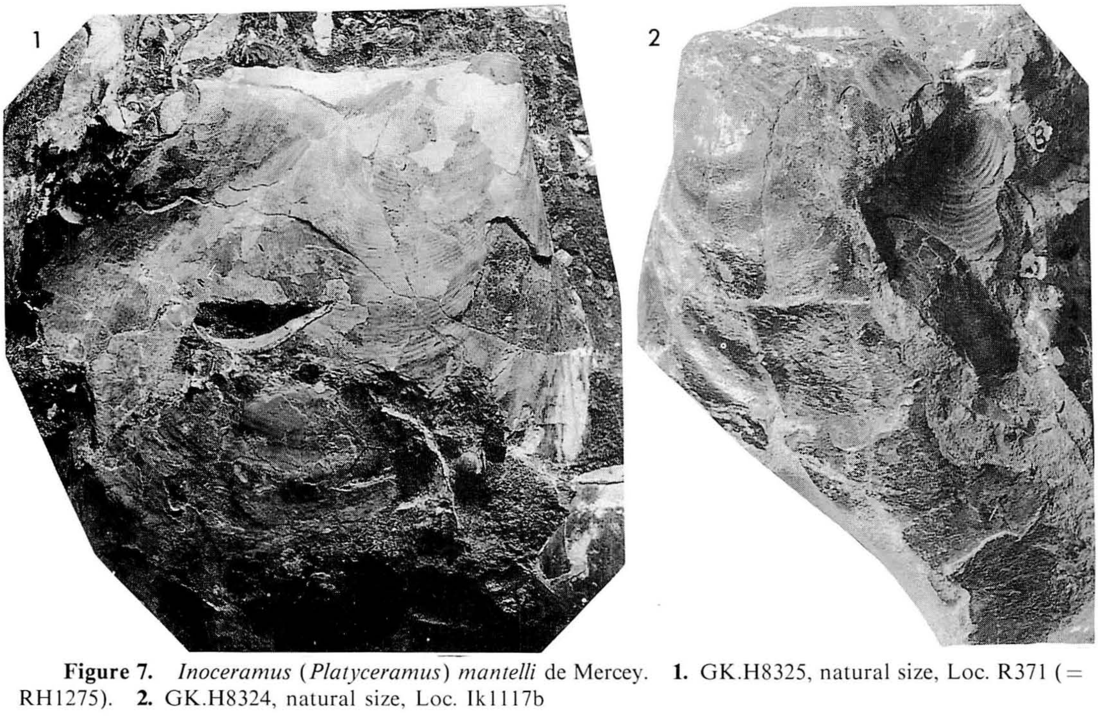

Figure 7. *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. **1.** GK.H8325, natural size, Loc. R371 (= RH1275). **2.** GK.H8324, natural size, Loc. Ik1117b

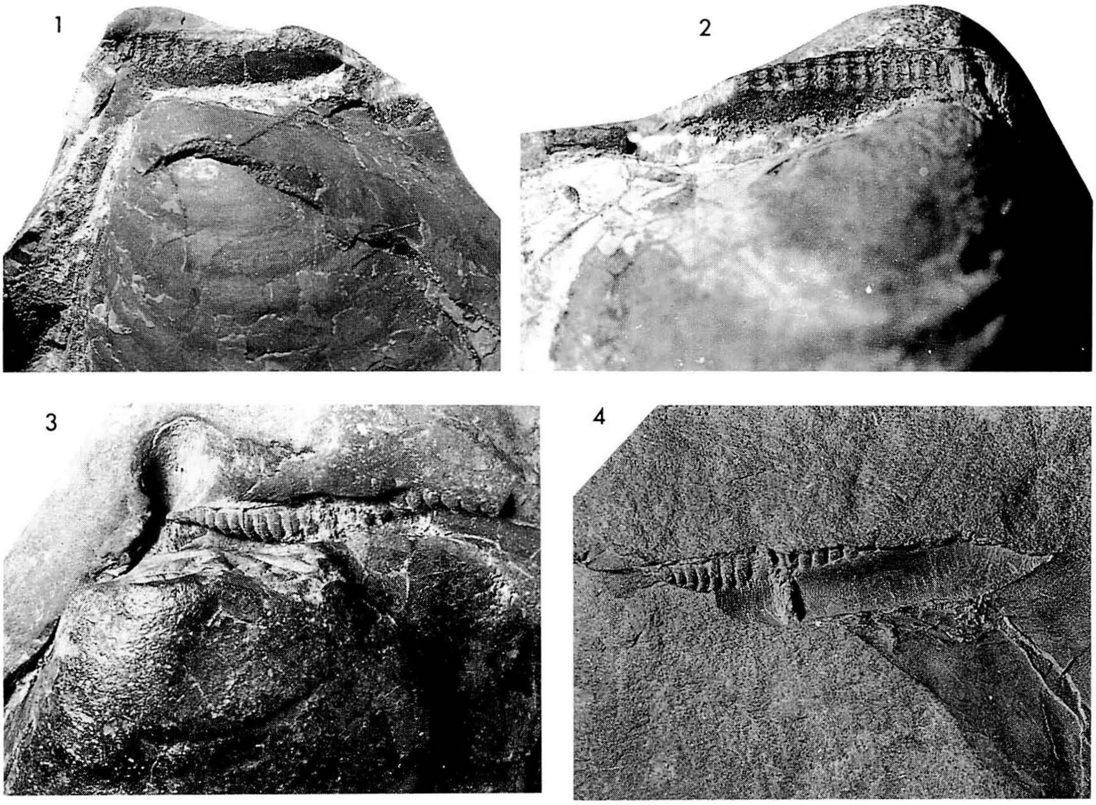

Figure 8. Ligament structure **1.** *Inoceramus* (*Platyceramus*) *mantelli* de Mercey. GK.H8252 **2.** *Inoceramus* (*Platyceramus*) cf. *rhomboides* Seitz. JG.H2899, Loc. Kt6, Onkono-sawa (Sanada coll., 1980). **3.** *Inoceramus* (*Inoceramus*) *cuvierii* Sowerby. JG.H2983, Loc. H2065p, Nutapomanai, Hobetsu, area, internal mould. **4.** *Inoceramus* (s. l.) *amakusensis* Nagao et Matsumoto. JG.H2984, Loc. HI102, Hinoshima, Amakusa, Kyushu, internal mould.

overlaps that of *I.* (*P.*) *yubariensis* in Hokkaido. In fact, the former occurs throughout the Coniacian Stage, with some delay eastwards, whereas the latter occurs in the Upper Coniacian and Santonian.

To sum up, the morphological difference between the samples of *I.* (*P.*) *yubariensis* from Japan and that of *I.* (*P.*) *mantelli* from Europe is so slight that they are certainly of identical species ; the former falls in a junior synonym of the latter.

Comparison

I. (*P.*) *expansus* Baily, 1855 (p. 462, pl. 13, fig. 5) from the probable Santonian of South Africa, has a broad anterior ear, but differs from *I.* (*P.*) *mantelli* in its large ratio of l/h, L/H and the large anterior hinge angle.

I. (*P.*) *cycloides ahsenensis* Seitz, 1961 from the Santonian of the Rhur area, West Germany, somewhat resembles *I.* (*P.*) *mantelli* in its tall outline with gentle convexity and the ontogenetic change of obliquity, but the former is discriminated from the latter in its considerably convex anterior margin, narrowly arcuate ventral margin, predominant and regular concentric ribs and absence of anterior ear.

I. (*P.*) *collignoni* Sornay, 1964, from the Coniacian of Madagascar is also similar to *I.* (*P.*) *mantelli subrhenanus* Seitz, 1962 and *I.*

Table 1. Measurements of *Inoceramus* (*Platyceramus*)

specimen	valve	h	l	b	s	H	L	α	γ	δ	$\delta_{H=60mm}$	l/h
HK 5960	L.	92.0	70.0	19.0	40.0	95.0	72.0	107°	123°	70°	54°	0.76
JC. H 2793	R.	109.3	89.0	22.1	—	113.2	89.0	112°	113°	75°	58°	0.81
JC. H 2796	R.	48.6	40.5	9.6	19.0	50.4	43.6	117°	110°	68°	—	0.83
JC. H 2902	R.	60.4	50.4	12.4	22.9	68.7	58.0	100°	126°	63°	58°	0.83
JC. H 2906	R.	37.6	29.6	7.8	16.2	39.7	31.8	96°	111°	63°	—	0.76
JC. H 2910	R.	48.0	40.6	—	21.0	50.5	44.9	111°	128°	62°	—	0.85
JC. H 2912	R.	60.5	58.6	13.0	26.7	62.0	54.8	109°	116°	60°	60°	0.97
JC. H 2916	L.	56.7	47.4	16.5	23.0	65.8	50.3	108°	130°	60°	58°	0.84
JC. H 2917	R.	50.0	39.0	9.9	22.0	54.8	46.7	97°	126°	63°	—	0.78
JG. H 2918	R.	61.0	55.2	12.0	23.0	68.2	53.4	97°	125°	63°	60°	0.90
JG. H 2921	L.	33.1	30.6	5.5	16.4	38.2	26.5	91°	127°	56°	—	0.92
JC. H 2922	R.	44.8	45.3	6.4	16.4	56.2	42.9	102°	123°	47°	—	1.01
JG. H 2923	R.	90.6	70.0	19.0	39.2	93.0	71.0	104°	113°	72°	56°	0.77
JC. H 2998	R.	65.1	66.3	14.0	30.2	73.7	60.2	105°	143°	54°	50°	1.02
JG. H 3002	L.	86.6	83.0	12.3	37.0	94.0	82.7	116°	122°	64°	57°	0.96
	R.	77.6	70.0	13.4	41.7	77.6	75.2	108°	128°	60°	53°	0.90
JG. H 3003	R.	41.5	44.7	8.5	19.8	46.9	41.6	114°	—	59°	—	1.08
JG. H 3004	L.	88.8	89.6	13.0	28.1	98.3	80.8	130°	140°	57°	53°	1.01
JG. H 3005	R.	94.5	94.5	18.6	45.5	101.0	97.7	119°	139°	63°	58°	1.00
GK. H 8250	R.	47.6	40.4	11.0	21.7	54.3	45.8	101°	—	64°	—	0.85
GK. H 8251	R.	44.3	37.7	9.3	20.3	48.5	39.0	102°	127°	65°	—	0.85
GK. H 8252	L.	56.7	50.0	9.3	27.2	64.6	53.0	103°	111°	66°	65°	0.88
	R.	65.2	—	15.4	—	72.3	—	111°	—	65°	62°	—
GK. H 10128	L.	26.5	21.4	6.5	12.3	29.6	23.1	96°	115°	52°	—	0.81
GK. H 10130	L.	57.0	50.0	14.0	23.0	64.0	43.0	90°	135°	58°	57°	0.88
GK. H 10131	L.	30.0	28.0	—	16.0	34.0	28.0	90°	128°	60°	—	0.93
GK. H	L.	108.6	91.8	20.0	57.0	112.6	96.0	104°	120°	64°	56°	0.85

reference :

$\delta_{H=60mm}$: angle between hinge line and H at the growth stage of 60 mm in H, l/h : simple ratio of l vs. h, $l/h_{H=60mm}$: simple ratio of l vs. h at the growth stage of 60 mm in H, b/h : simple ratio of b vs. h, $b/h_{H=60mm}$: simple ratio of b vs. h at the growth stage of 60 mm in H, L/H : simple ratio

(*P.*) *mantelli beyenburgi* Seitz, 1965 [=*I.* (*P.*) *mantelli angustus* Seitz, 1962] as Sornay (1964) already pointed out. But it differs from the two subspecies in its more inflated shell, weak major concentric ornamentation, absence of anterior ear and almost constant obliquity throughout the growth.

I. (*P.*) *cycloides colossus* Sornay, 1969 from the Lower Campanian of tripartite scheme of Madagascar may be analogous to *I.* (*P.*) *mantelli* in its tall outline, but the former is clearly distinct from the latter in its convex antero-dorsal margin, regular concentric ornament and their curvature, which is narrowly bent at the ventral extremity, and the almost invariable obliquity throughout the growth.

I. (*P.*) *paramantelli* Sornay, 1969 from the Upper Santonian of tripartite scheme to the Lower Campanian of Madagascar is clearly *mantelli* from Hokkaido. linear dimension in mm.

$l/h_{H=60mm}$	b/h	$b/h_{H=60mm}$	L/H	$L/H_{H=60mm}$	s/l	remarks
0.98	0.21	0.21	0.76	0.84	0.57	anterior wing
0.96	0.20	0.20	0.79	0.97	—	hinge part imperfect
—	0.20	—	0.87	—	0.47	smaller than 60 mm in H
0.83	0.21	0.20	0.84	0.84	0.45	
—	0.20	—	0.80	—	0.59	smaller than 60 mm in H
—	—	—	0.89	—	0.52	somewhat crushed
0.97	0.21	0.21	0.88	0.88	0.46	anterior wing
0.85	0.29	0.29	0.76	0.77	0.49	
—	0.20	—	0.86	—	0.56	smaller than 60 mm in H
0.90	0.20	0.20	0.78	0.80	0.42	
—	0.17	—	0.69	—	0.53	smaller than 60 mm in H
—	0.14	—	0.76	—	0.36	smaller than 60 mm in H
0.82	0.21	0.20	0.76	0.78	0.56	
1.09	0.22	0.21	0.82	0.83	0.46	
1.02	0.14	0.17	0.88	0.90	0.45	
1.02	0.17	0.18	0.97	1.00	0.60	
—	0.20	—	0.89	—	0.44	smaller than 60 mm in H
1.03	0.15	0.15	0.82	0.81	—	hinge part imperfect
1.01	0.20	0.22	0.97	0.80	0.48	
—	0.23	—	0.84	—	0.54	smaller than 60 mm in H
—	0.21	—	0.80	—	0.54	smaller than 60 mm in H
0.88	0.16	0.17	0.82	0.82	0.55	
—	0.24	—	—	—	—	imperfect, anterior wing
—	0.25	—	0.78	—	0.57	smaller than 60 mm in H
—	0.25	—	0.67	—	0.46	smaller than 60 mm in H
—	—	—	0.82	—	0.57	somewhat cruthed
0.96	0.18	0.26	0.85	0.76	0.62	anterior wing

of L vs. H, $L/H_{H=60mm}$: simple ratio of L vs. H at the growti stage of 60 mm in H, s/l : simple ratio of s vs. l, L. : left valve, R. : right valve.
For others readers may refer to Figure 1.

distinguished from *I.* (*P.*) *mantelli*, regardless of the derivation of the specific name, in its long outline, comparatively short anterodorsal margin, large ratio of s/l and considerably oblique growth axis, though the development of the anterior ear in the specimen no. 1611 (Sornay, 1969, pl. F, fig. 5) is similar to that of the specimen GK.H8323 (Figure 4-c).

I. (*P.*) *miyahisai* Noda (1983a, p. 103, 111, 112, pls. 2, 5) from the Middle Campanian of western Shikoku also resembles *I.* (*P.*) *mantelli* in its tall outline with gentle convexity but differs in its convex anterior margin, predominant major ribs and the absence of the anterior ear. Its stratigraphic position is also much higher than that of *I.* (*P.*) *mantelli*.

Discussion of phylogeny

"*Inoceramus* (*Platyceramus*) *yubariensis*"

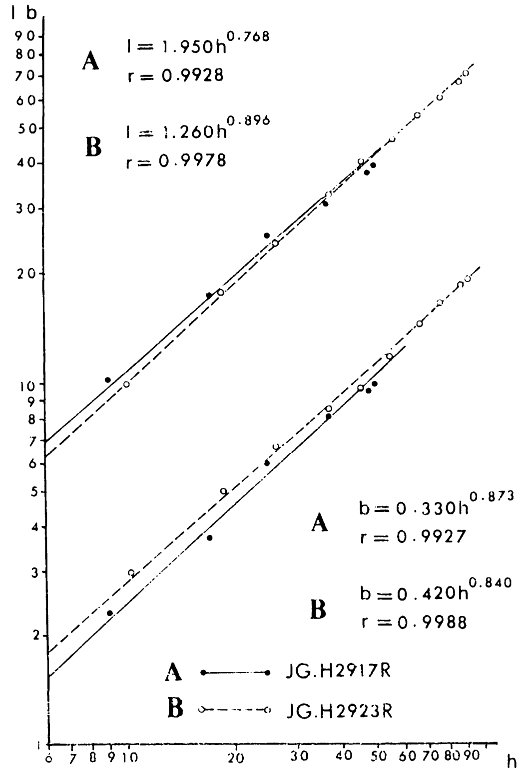

Figure 9. Diagram showing the individual relative growth between l vs. h and b vs. h (in mm) for selected specimens of *Inoceramus* (*Platyceramus*) *mantelli*.

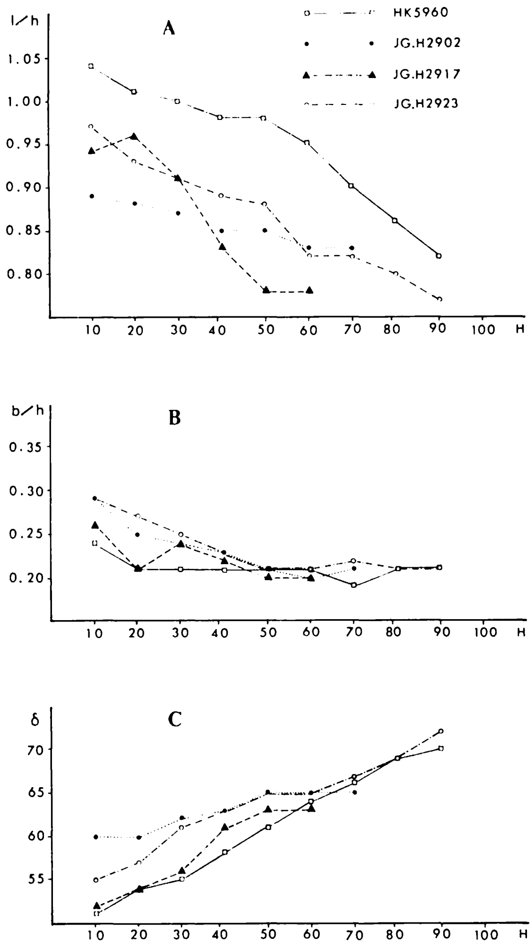

Figure 10. Diagram showing the ontogenetic change of selected characters. **A** : simple ratio l/h, **B** : simple ratio b/h, **C** : obliquity.

was originally assigned to a variety of *Mytiloides incertus* (Jimbo, 1894) from the Upper Turonian. The two species of *I.* (*P.*) *yubariensis* [$=$*I.* (*P.*) *mantelli*] and *M. incertus* are apparently similar to each other in a gently and uniformly convex shell and inconspicuous concentric ribs with distinct minor rings. Matsumoto and Noda (1968) tentatively assigned *M. teraokai* (Matsumoto et Noda, 1968) to *Platyceramus*, but this has been corrected since Matsumoto *et al.* (1982, p. 64). *M. teraokai* indeed resembles *Platyceramus* in outline and surface ornamentation. Particularly, the existence of an anterior ear in *M. teraokai* and *I.* (*P.*) *mantellai* suggests close phylogenetic relationship.

M. incertus, a senior synonym of *M. fiegei fiegei* (Tröger, 1967) (see Noda, 1984), is common in the Upper Turonian of various regions of the world. Its stratigraphic position is generally lower than *I.* (*P.*) *mantelli.* In our opinion, the resemblance between *M. incertus* and "*I.* (*P.*) *yubariensis*" in Japan is well harmonious with that between "*M. fiegei fiegei*" and *I.* (*P.*) *mantelli* in Europe. However, the value of l/h in *I.* (*P.*) *mantelli* becomes smaller with growth. In other words, the outline becomes gradually higher, whereas the value of l/h in *M. incertus* is almost constance throughout the growth. Moreover, the hinge structure is clearly dis-

Table 2. Biometric characters of *Inoceramus* (*Platyceramus*) *mantelli* from Hokkaido.

	α	γ	$\delta_{H=60mm}$	$l/h_{H=60mm}$	$b/h_{H=60mm}$	$L/H_{H=60mm}$	s/l
N	27	24	16	14	14	14	24
m	105.2	124.1	57.2	0.951	0.205	0.843	0.511
s	9.46	9.36	3.67	0.0830	0.0359	0.0718	0.0657
σ	9.28	9.17	3.56	0.0800	0.0346	0.0692	0.0644
v	8.99	7.54	6.42	8.73	17.51	8.52	12.86

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

tinct between *Platyceramus* and *Mytiloides*, that is, the ligament pits of *M. labiatus* are finer and smaller than those of *Platyceramus*, as illustrated by Sornay (1966, p. 63, fig. 26), and those of *M. teraokai* are also of *Mytiloides* type (Matsumoto and Noda, 1968, p. 322, text-fig. 2). The difference of the ligament structure should be regarded as a taxonomic criterion above the specific level. From the above discussion, it is questionable to link *Platyceramus* to *Mytiloides*.

Kauffman (1977) regarded "*I.* (*P.*) *yubariensis*" as a subspecies of *I. waltersdorfensis* Andert, 1911 from the highest Turonian to the Lower Coniacian of the Euramerican and Caribbean regions, and pointed out "*I.* (*P.*) *yubariensis*" is possibly descended from *I. waltersdorfensis*. Tröger (1967, p. 118, 119) clearly described subspecific distinction between *I. waltersdorfensis waltersdorfensis* Andert and *I. waltersdorfensis hannovrensis* Heinz, 1932, saying that two subspecies are hardly discriminated in the juvenile stage, but that the shell convexity increases gradually in the former and the concentric rings are broadened with growth in the latter. As shown in Figure 11, the shell convexity of *I.* (*P.*) *mantelli* from Hokkaido is comparable with that of *I. waltersdorfensis hannovrensis* illustrated by Tröger (1967, p. 120, fig. 31). In fact, *I. waltersdorfensis hannovrensis* resembles roughly *I.* (*P.*) *mantelli* from Hokkaido in outline, shell convexity and surface ornamentation, but more presice examination of ligament structure, presence or absence of anterior ear and ontogenetic change of form ratios on a number of well preserved specimens, is necessary to make clear the phylogenetic relationship between the two species.

Kauffman (1977) also mentioned that "*I.* (*P.*) *yubariensis*" may be incorporated in an early form of *I.* (*Cremnoceramus*) *inconstans* Woods (1911, also see Andert, 1934, pl. 3, fig. 1). The specimen (A. Nr. 35) of *I.* (*Cr.*) *inconstans* Woods em. Andert from the Uppermost Turonian (in the Scheme of Seibertz, 1979) resembles the "holotype of *I.* (*P.*) *yubariensis*" (HK5960, this paper, Figures 2-1a, b, c ; 2-2a, b) in general outline and surface ornamentation, but the specimen HK5960 is characterized by the existence of anterior ear (the section of anterior ear is visible in Figures 2-1b, c). In our opinion, it is still insufficient to link phylogenetically *Platyceramus* to *Cremnoceramus*.

To sum up, the ancestry of *I.* (*P.*) *mantelli* is as yet uncertain.

On the other hand, *I.* (*P.*) *mantelli* may be the common or ultimate ancestor of various species of *I.* (*Platyceramus*) from the Santonian and Campanian Stages. In connection with the restudy of the so-called *I. japonicus* Nagao et Matsumoto, 1940, Noda (1983b) showed an idea of parallel development of *I.* (*P.*) *ezoensis* Yokoyama, 1890 and *I.* (*P.*) *mantelli* [*I.* (*P.*) *yubariensis* at that date] from some common ancestor, giving

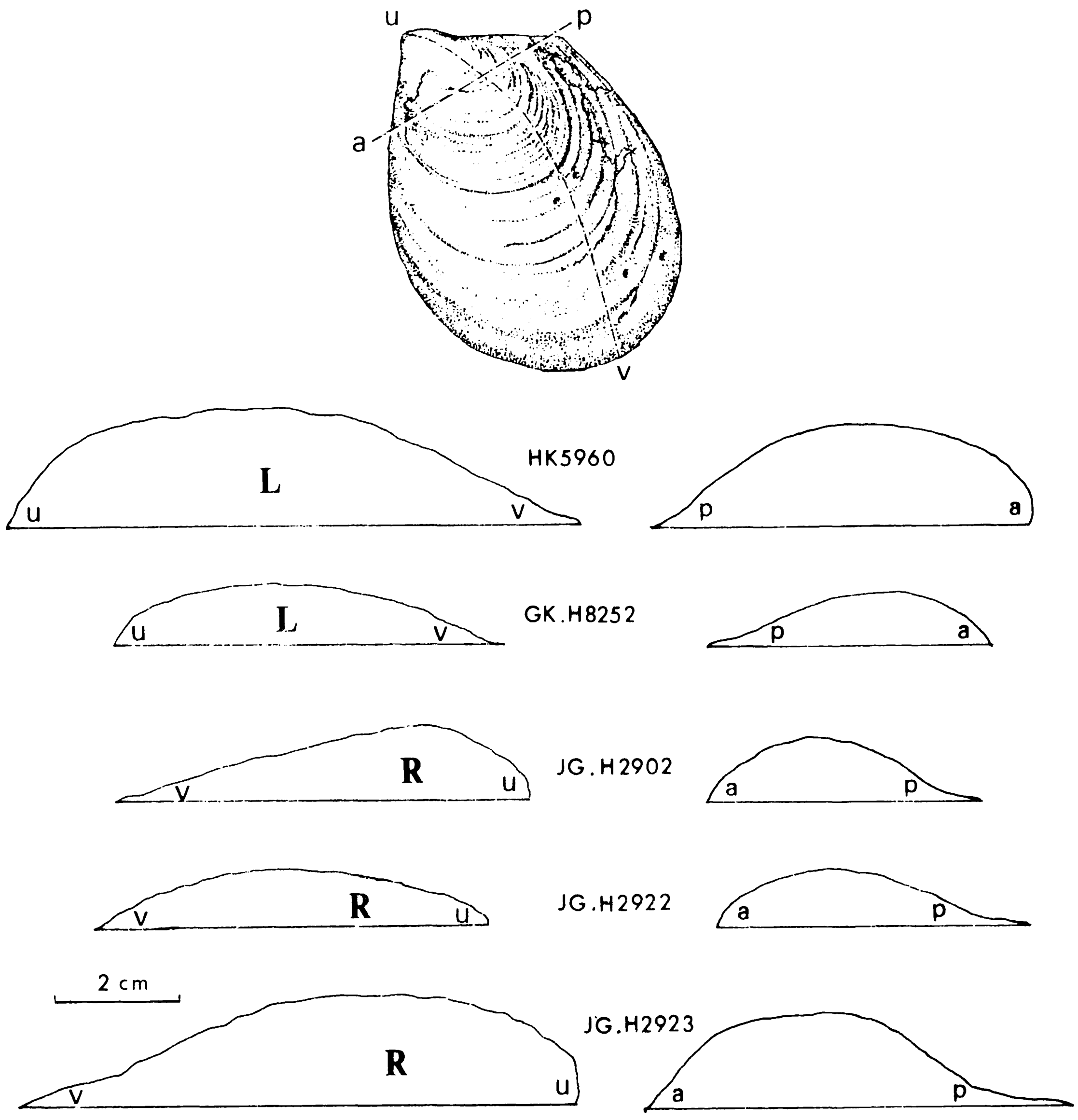

Figure 11. Profiles of five selected specimens in two directions.

rise to *I.* (*P.*) *japonicus* and *I.* (*P.*) *higoensis* Noda, 1983 respectively in later stages of evolution. Besides a clearer redescription of *I.* (*P.*) *ezoensis* is necessary, as Matsumoto *et al.* (1982) pointed out. Recently Matsumoto presented a question in our free discussion what species was rised from *I.* (*P.*) *mantelli* in Europe, if the species *I.* (*P.*) *higoensis* was derived from that species in Japan.

I. (*P.*) *higoensis* was originally included in the scope of *I. japonicus* Nagao et Matsumoto, 1940 as forma α, for its characteristic ornamentation with divergent ribs superposed on the concentric sculpture, but it is discriminated from the typical form (γ) and another one (β) in its tall outline, short hinge line and the ontogenetic change of obliquity as shown in Noda (1983, p. 213, text-fig. 11).

Table 3. F-test and Student's t-test of the selected characters of *Inoceramus* (*Platyceramus*) *mantelli* [= *I.* (*P.*) *yubariensis*] and *Mytiloides incertus* (Jimbo)

		α	γ	$l/h_{H=60mm}$	$L/H_{H=60mm}$	s/l
A	N	27	24	14	14	24
	m	105.2	124.1	0.951	0.843	0.511
	s	9.46	9.36	0.0830	0.0718	0.0657
F value		2.1116	4.1403	1.4661	1.2652	1.0369
significance		●	●	○	○	○
t value		2.806	4.678	2.473	0.361	0.672
significance		●	●	●	○	○
B	N	30	17	15	30	23
	m	113.3	147.0	1.036	0.860	0.498
	s	6.51	4.60	0.1005	0.0808	0.0669

reference :

A : *Inoceramus* (*Platyceramus*) *mantelli* [= *Inoceramus* (*P.*) *yubariensis*], B : *Mytiloides incertus*,

● : significant, ○ : not signficant.

For others readers may refer to Tables 1 and 2.

Table 4. Measurements of *Inoceramus* (*Platyceramus*) *mantelli* from West Germany. linear dimension in mm.

specimens	valve	h	l	s	H	L	α	γ	δ	$\delta_{H=60mm}$	l/h	$l/h_{H=60mm}$	L/H	$L/H_{H=60mm}$	s/l
lectotype	R.	52	64	34	70	52	117°	143°	45°	42°	1.23	1.26	0.74	0.71	0.53
paratype	L.	81	96	56	110	79	117°	131°	56°	50°	1.19	1.43	0.72	0.75	0.58
B667	R.	134	128	76	140	137	140°	112°	76°	62°	0.96	1.22	0.98	1.00	0.59
B668	R.	317	249	152	368	235	90°	132°	57°	40°	0.79	0.84	0.64	0.72	0.61
B6106	R.	97	80	31	97	78	110°	120°	71°	64°	0.82	0.79	0.80	0.72	0.39
Ko473	L.	84	78	50	101	78	102°	115°	58°	48°	0.93	1.17	0.77	0.90	0.64
Ko478	L.	136	106	68	144	114	110°	114°	70°	50°	0.78	0.82	0.79	0.92	0.64
S291WB	L.	141	112	51	144	108	110°	111°	74°	58°	0.79	1.10	0.75	0.90	0.46
S294WB	R.	80	70	40	90	72	100°	113°	60°	56°	0.88	0.85	0.80	0.75	0.57
S296WB	L.	67	57	37	77	63	120°	136°	70°	65°	0.85	0.78	0.82	0.77	0.65
S297WB	R.	82	79	46	94	77	100°	130°	60°	53°	0.96	1.00	0.82	0.76	0.58
S337WB	L.	212	192	100	244	196	123°	128°	65°	54°	0.91	1.00	0.80	0.84	0.52

In that paper, Noda referred briefly to the stock of *I.* (*P.*) *undulatoplicatus* Roemer connecting with *I.* (*P.*) *rhomboides* Seitz, 1961 and *I.* (*P.*) *cycloides* Wegner, 1905. Seitz (1961) described three subspecies in *I.* (*P.*) *undulatoplicatus* [*I.* (*Cladoceramus*) *undulatoplicatus* in Seitz's sense] *e.g.*, *I.* (*P.*) *undulatoplicatus undulatoplicatus*, *I.* (*P.*) *undulatoplicatus michaeli* Heinz, 1928 and *I.* (*P.*) *undulatoplicatus* subsp. indet., of which the specimens of subspecies indet., *i.e.*, Ko. 135, S335WB and Hg, 49, are indeed similar to *I.* (*P.*) *mantelli* in their concave anterior margin, large anterior hinge angle (α), short hinge line and the ontogenetic change of obliquity except for development of divergent plicae, and the stratigraphic position of the subspecies is somewhat higher than that of *I.* (*P.*) *mantelli*.

Furthermore, the specimen no. 685 of *I.* (*P.*) aff. *undulatoplicatus michaeli* Heinz (Sornay, 1964, p. 175, fig. 7) from the Middle

Table 5. Biometric characters of *Inoceramus* (*Platyceramus*) *mantelli* from West Germany.

	α	γ	$\delta_{H=60mm}$	$l/h_{H=60mm}$	$L/H_{H=60mm}$	s/l
N	12	12	12	12	12	12
m	111.6	123.8	53.5	1.022	0.812	0.563
s	13.15	10.87	8.04	0.2147	0.0967	0.0777
σ	12.59	10.41	7.70	0.2056	0.0925	0.0744
v	11.78	8.78	15.03	21.01	11.91	13.80

Table 6. *F*-test and Student's *t*-test of the selected characters of *Inoceramus* (*P.*) *mantelli* from Hokkaido and West Germany.

		α	γ	$\delta_{H=60mm}$	$l/h_{H=60mm}$	$L/H_{H=60mm}$	s/l
A	N	27	24	16	14	14	24
	m	105.2	124.1	57.2	0.915	0.843	0.511
	s	9.46	9.36	3.67	0.0830	0.0718	0.0657
F value		1.9323	1.3487	4.7994	6.6913	1.8138	1.3987
significance		○	○	●	●	○	○
t value		1.725	0.086	1.483	1.077	0.937	2.107
significance		○	○	○	○	○	●
B	N	12	12	12	12	12	12
	m	111.6	123.8	53.5	1.022	0.812	0.563
	s	13.15	10.87	8.04	0.2147	0.0967	0.0777

reference :
A : sample from Hokkaido, B : sample from West Germany, ● : significant, ○ : not significant.
For others readers may refer to Tables 1 and 2.

Santonian of the Ampamba-Antsirasira region of Madagascar also resembles *I.* (*P.*) *mantelli* in the characters mentioned above. These facts may suggest some phylogenetic relationship between the two species.

Conclusion

1. From the results of biometric examination, *Inoceramus* (*Platyceramus*) *mantelli* de Mercey, 1877 from Japan, including the holotype and topotype of *I.* (*P.*) *yubariensis* Nagao et Matsumoto, 1940, shows a small extent of variation in the examined characters, *i. e.*, α, γ, δ, l/h and L/H.
2. The individual relative growth of shell length vs. shell height and that of shell breadth vs. shell height show negative allometry. The simple ratio of l/h and shell obliquity decrease gradually with growth, while simple ratio b/h is relatively constant throughout the growth or slightly decreases.
3. The morphological differences between the form of *I.* (*P.*) *mantelli* from Japan and that of *I.* (*P.*) *mantelli* from Europe and eastern contiguous regions is so slight that they can be regarded as specifically identical. Stratigraphically the former ranges from the Upper Coniacian upwards to the Santonian and the latter throughout the Coniacian. Although there is some delay in the occurrence of the Japanese form, *I.* (*P.*) *yubariensis*

Nagao et Matsumoto, 1940 is evidently a junior synonym of *I.* (*P.*) *mantelli* de Mercey, 1877.

4. The ancestry of *I.* (*P.*) *mantelli* is uncertain. *Mytiloides incertus* (Jimbo) from the Upper Turonian of Japan, Europe and elsewhere looks somewhat similar to *I.* (*P.*) *mantelli*, but the true phylogenetic relationship between *Inoceramus* (*Platyceramus*) and *Mytiloides* or *Cremnoceramus* has yet to be worked out by examining the fundamental characters, *e.g.*, hinge and shell structures.

5. *I.* (*P.*) *mantelli* may be a common or ultimate ancestor of various species of *Inoceramus* (*Platyceramus*) from the Santonian and Campanian.

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APPENDIX : **Locality guide**

Arranged in the order from A to D in the index map of Figure 12.

Loc. H3019. The type locality of *Inoceramus* (*Platyceramus*) *yubariensis* Nagao et Matsumoto,

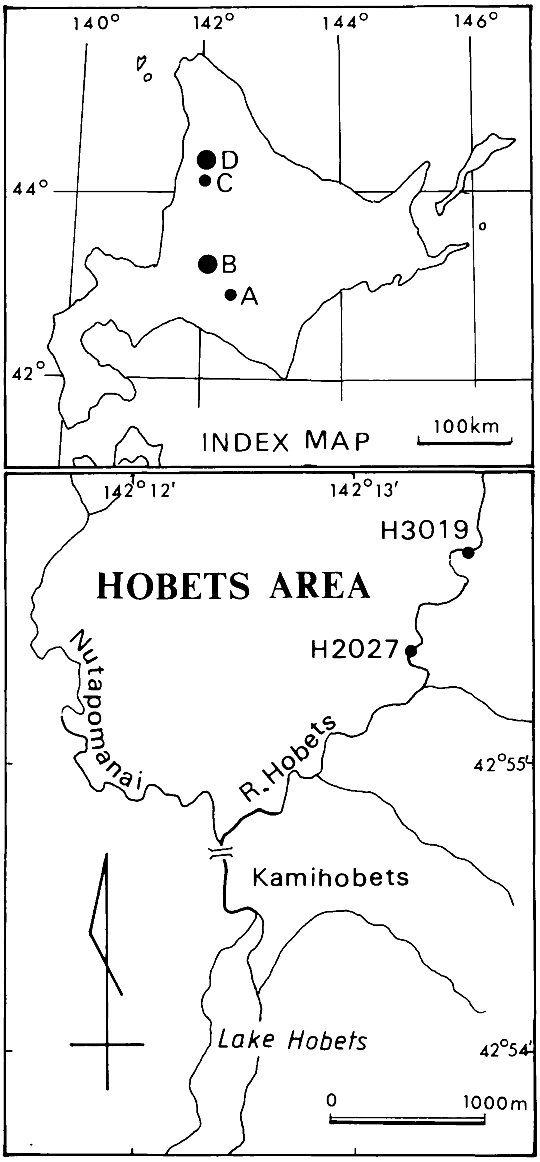

Figure 12. Above : Index map of Hokkaido, showing the studied areas, A : Hobetsu area, B : Ikushumbets area, C : Kotanbetsu area, D : Haboro area. Below : Locality map of Kamihobetsu.

1940. Topographic map of the Osawa Quad. (1 : 25000), Long. 142°12′30″E, Lat. 42°55′44″N. A cliff on the left bank of the main course of the R. Hobetsu, Kamihobetsu (0sawa), Hobetsu area, southern central Hokkaido (Figures 12, 13). Zone of *Inoceramus* (s.l.) *amakusensis*, upper part of the Upper Yezo Group, Santonian.

Loc. H2027c. Topographic map ditto, Long. 142°12′ 12″E, Lat. 42°55′20″N. A cliff on the right bank of the main course of R. Hobetsu, about 750 m downstream from loc. H3019, probably same horizon as the loc. H3019 (Figure 12).

Locs. Ik1506r, 1533a and 1535. Topographic map of the Katsurazawa-ko Quad. (1 : 25000), Long. 142° 3″04″E-142°03′07″E, Lat. 43°13′10″N-43°13′06″N. The road cutting along the R. Ikushumbets, Ikushumbets area, central Hokkaido. Lower part of the Member IIId, Zone of *I.* (s.l.) *amakusensis*, Santonian (Figure 14).

Loc. Ik1537. Topographic map ditto, Long. 142°3′ 32″E, Lat. 43°12′42″N. A cliff on the left bank of the R. Ikushumbets, about 500 m downstream from the confluence of the Hidarimata-zawa. Upper part of the Member IIIc, Zone of *I.* (*Cremnoceramus*) *mihoensis*. Upper Coniacian.

Locs. Ik5561p and 5617p. Topographic map ditto, Long. 142°04′02″E-142°04′06″E, Lat. 43°12′25″N-43° 12′31″N. Pebbles in the Hidarimata-zawa, a tributary of the R. Ikushumbets, in the sequence of the Zone of *I.* (*Cr.*) *mihoensis* and Zone of *I.* (s.l.) *amakusensis*, stratigraphic position precisely unknown (Figure 14).

Loc. Ik8304p. Topographic map ditto, Long. 142° 06′36″E, Lat. 43°11′28″N. A pebble on the forestry roadside along the Okuhidarimata-zawa, a tributary of the R. Ikushumbets, probably originated from the Member IIIc. Upper part of the Middle Coniacian (Figure 14).

Locs. Ik8387p and 8390r. Topographic map ditto, Long. 142°05′57″E, Lat. 43°10′16″N-43°10′14″N. Pebbles in the upper reaches near the terminal of the forestry road along the Yubarigoe-zawa, a tributary of the Okuhidarimata-zawa. Stratigraphic position exactly unknown (Figure 14).

Locs. Ik8053p and 8060p. Topographic map ditto, Long. 142°00′56″E-142°01′12″E, Lat. 43°11′24″N-43°11′30″N. Pebbles in the Hiromine-zawa, a tributary of the Kikumezawa, Ikushumbets area, probably in the sequence of the Member IIIc of the Upper Yezo Group (Figure 14).

Loc. Ik8064. Topographic map ditto, Long. 142°00′ 47″E, Lat. 43°11′24″N. A stream floor of the Hiromine-zawa, about 150 m upstream from the confluence with a little branch. Stratigraphic position : IIIc or IIId, exactly unknown (Figure 14).

Loc. Ik1117b. Topographic map of the Mikasa Quad. (1 : 25000), Long. 141°59′52″E, Lat. 43°13′06″ N. A cliff on the right slope of the Banno-sawa, a tributary of the R. Ikushumbets, above the key bed of tuffaceous sandstone, basal part of the Zone of *I.* (s.l.) *amakusensis* (see Matsumoto, 1965, fig. 2. for the location ; now under the water of the artificial lake of Katsura-zawa dam) (Figure 14).

Locs. Ik2707 and 2708. Topographic map of Ikushumbets Quad. (1 : 25000), Long. 141°59′22″E, Lat. 43°17′52″N. A cliff on the left bank of the upper reaches of the Pombetsgono-sawa (= Takino-sawa or Takiyoshi-zawa), a tributary of the R. Pombets, Ikushumbets area, upper part of the Member IIIc of the Upper Yezo Group. The stratigraphic position of Loc. Ik2707 is about 3 m above of Ik2708. Upper Coniacian. For details readers may refer to Matsumoto and Noda (1985, p. 265, text-fig. 1). For the stratigraphic succession in the Ikushumbets area

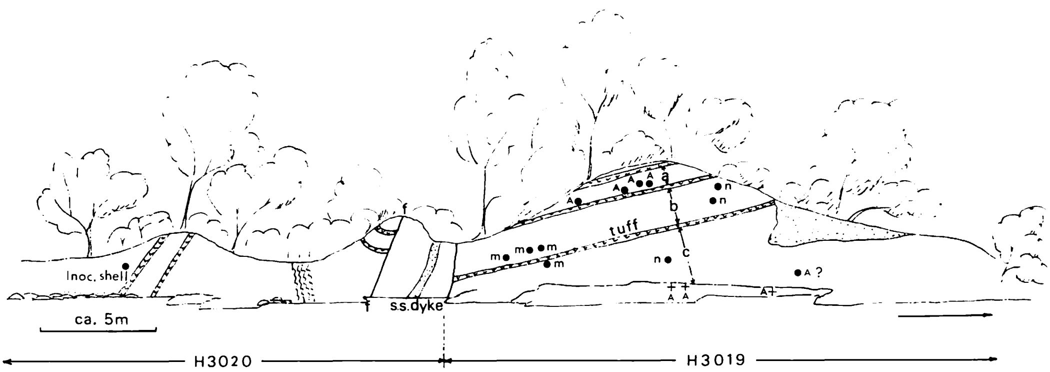

Figure 13. Sketch of the outcrop H3019 (in July 1988) (type locality of *I. yubariensis*). A : *Inoceramus* (s. l.) *amakusensis*, m. *Inoceramus* (*Platyceramus*) *mantelli*, n : *Sphenoceramus naumanni*, ● : in situ, + : fallen, a : 0.7m, b : 2.0m c : 2.7m

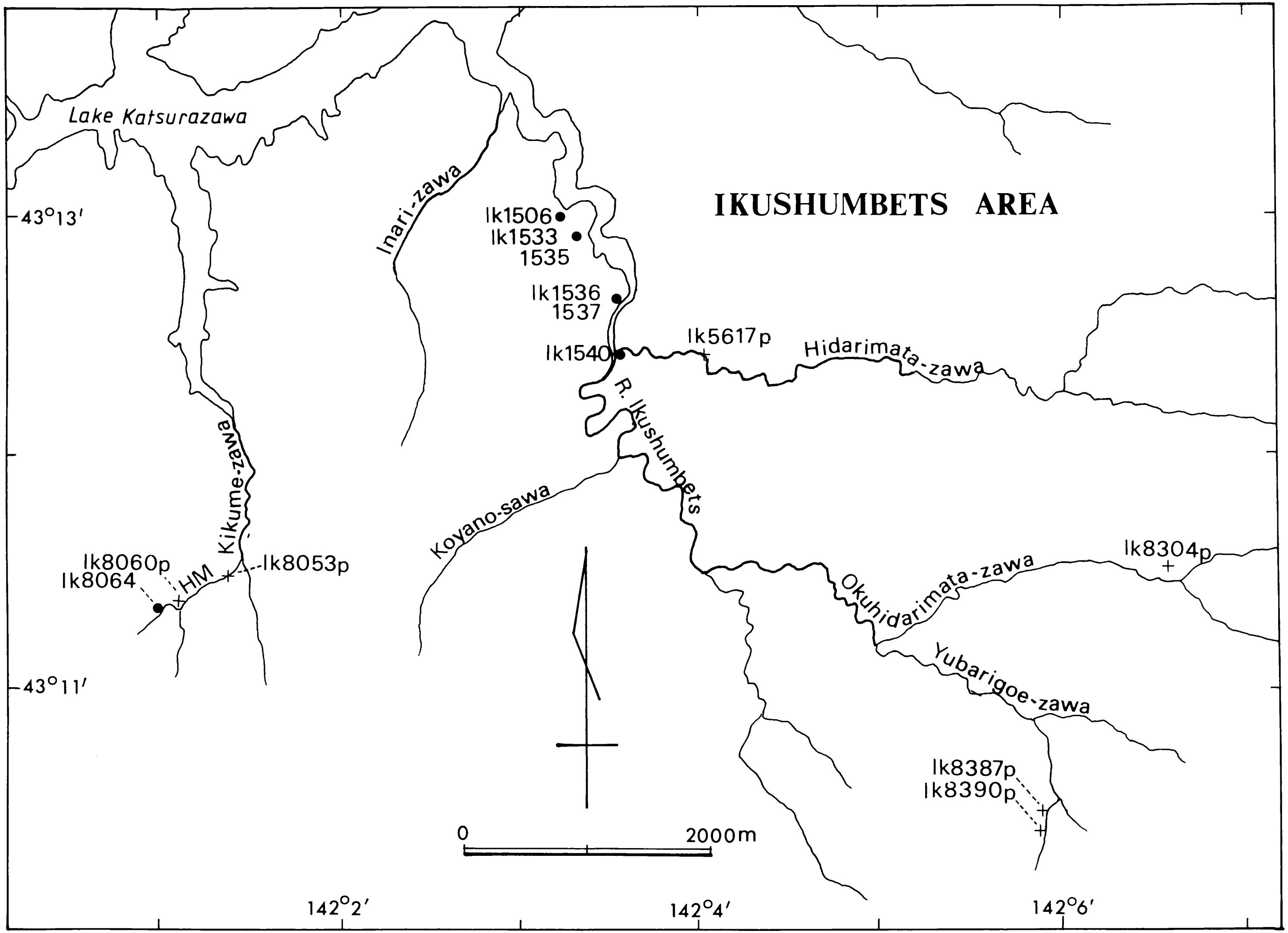

Figure 14. Locality map of the Ikushumbets area.

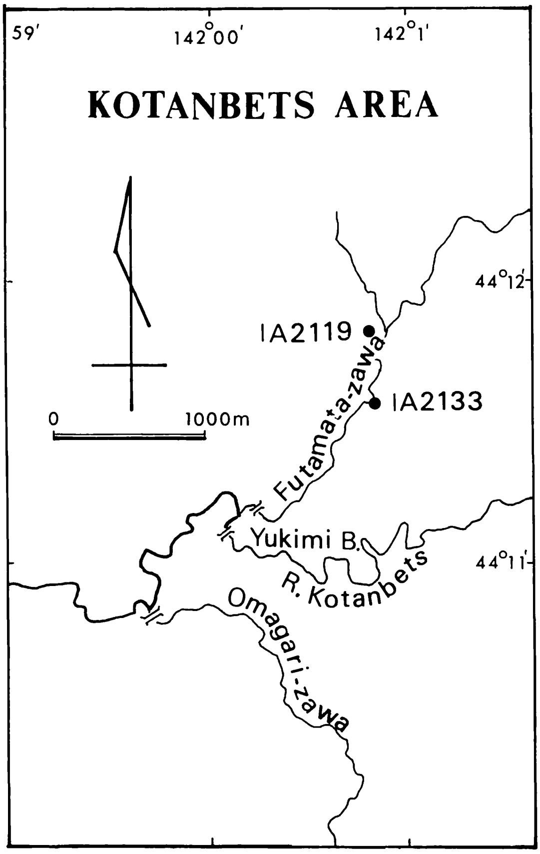

Figure 15. Locality map of the Kotanbetsu area.

readers refer to Matsumoto *et al.* (1978).

Loc. IA2119. Topographic map of the Kiritachi-toge Quad. (1 : 25000), Long. 142°00′50″E, Lat. 44°11′50″N. A cliff on the roadside of the National Highway, Route 239, about 2000 m northwards from Yukimi Bridge, Kotanbets area (Tomamae-machi, Tomamae-gun), northern Hokkaido (Figure 15).

Upper part of the Member Uy3 (Geological map of the Soeushinai Quad., 1 : 50000, 1965 (= Member F of Inoma, 1969) of the Upper Yezo Group. Upper Coniacian or Lower Santonian.

Loc. IA2133. Topographic map ditto, Long. 142°00′52″E, Lat. 44°11′25″N. A left bank of the Futamata-zawa about 1000 m upstream from the confluence with the R. Kotanbetsu. Lower part of the Member Uy4 (Hashimoto *et al.*, 1965) of the Upper Yezo Group. Lower Santonian (Figure 15).

The following localities with RH number, are all in the Haboro area. For the locations in detail and stratigraphy of this area, readers may refer to Toshimitsu (1985, 1988) and also Okada and Matsumoto (1969).

Loc. RH1287p. Topographic map of the Haborodake Quad. (1 : 25000), Long. 142°00′09″E, Lat. 44°17′09″N. Upper reaches of the R. Sakasa-gawa, a tributary of the R. Haboro, about 150 m upstream from the confluence with the Yutakazawa, (Haboro-machi, Tomamae-gun), in the sequence of the Lower Haborogawa Formation (Toshimitsu, 1985), but the stratigraphic position exactly unknown, presumably Upper Coniacian (Figure 16).

Loc. RH1271a. Topographic map of the Horobetsu-yama Quad. (1 : 25000), Long. 141°59′57″E, Lat. 44°16′44″N. A cliff on the right bank of the upper reaches of the R. Sakasagawa, about 800 m downstream from the confluence with the Yutaka-zawa. Sandy siltstone bed below the sandstone member of MHs3 of the Middle Haborogawa Formation of the Upper Yezo Group. Lower part of the Santonian (Figure 16).

Loc. RH1275 (= R371 of Okada and Matsumoto, 1969). Topographic map of the Haborodake Quad. (1 : 25000), Long. 142°00′09″E, Lat. 44°16′42″N. A cliff on the left bank about 300 m upper reaches from loc. RH1271. Sandy siltstone bed above the sandstone of MHs2 of the Middle Haborogawa Formation. Lower part of the Santonian (Figure 16).

Loc. RH1429a. Topographic map ditto, Long. 142°00′39″E, Lat. 44°17′10″N. A cliff on the right bank of the upper reaches of the Yutaka-zawa, about 1000 m upstream from the confluence with the R. Sakasagawa. Upper part of the Lower Haborogawa Formation of the Upper Yezo Group. Upper Coniacian (Figure 16).

Locs. RH2506 and 2148a2. Topographic map of the Horobetsuyama Quad. (1 : 25000), allocated along the R. Nakanofutamata-gawa, a tributary of the R. Haboro. Loc. RH2506 : Long. 141°58′50″E, Lat. 44°17′55″N. About 600 m downstream from the confluence with the Machiyoi-zawa. Sandy siltstone of the Middle Haborogawa Formation of the Upper Yezo Group, immediately below the sandstone bed of MHs3 at the top of the same member. Lower part of the Santonian.

Loc. 2148a2: Long. 141°59′40″E, Lat. 44°17′47″N. About 1000 m upstream from the confluence with the Machiyoi-zawa. Sandstone bed of MHsl of the Middle Haborogawa Formation, Upper most of the Upper Coniacian or basal part of the Lower Santonian (Figure 16).

Loc. RH2411d. Topographic map ditto, Long. 141°59′19″E, Lat. 44°18′05″N. A stream floor of the Machiyoi-zawa, about 700 m upstream from the confluence with the R. Nakanofutamata-gawa. Mudstone bed immediately below the sandstone bed MHs2 of the lower part of the Middle Haborogawa Formation. Middle part of the Santonian (Figure 16).

Loc. RH7106a. Topographic map ditto, Long. 141°

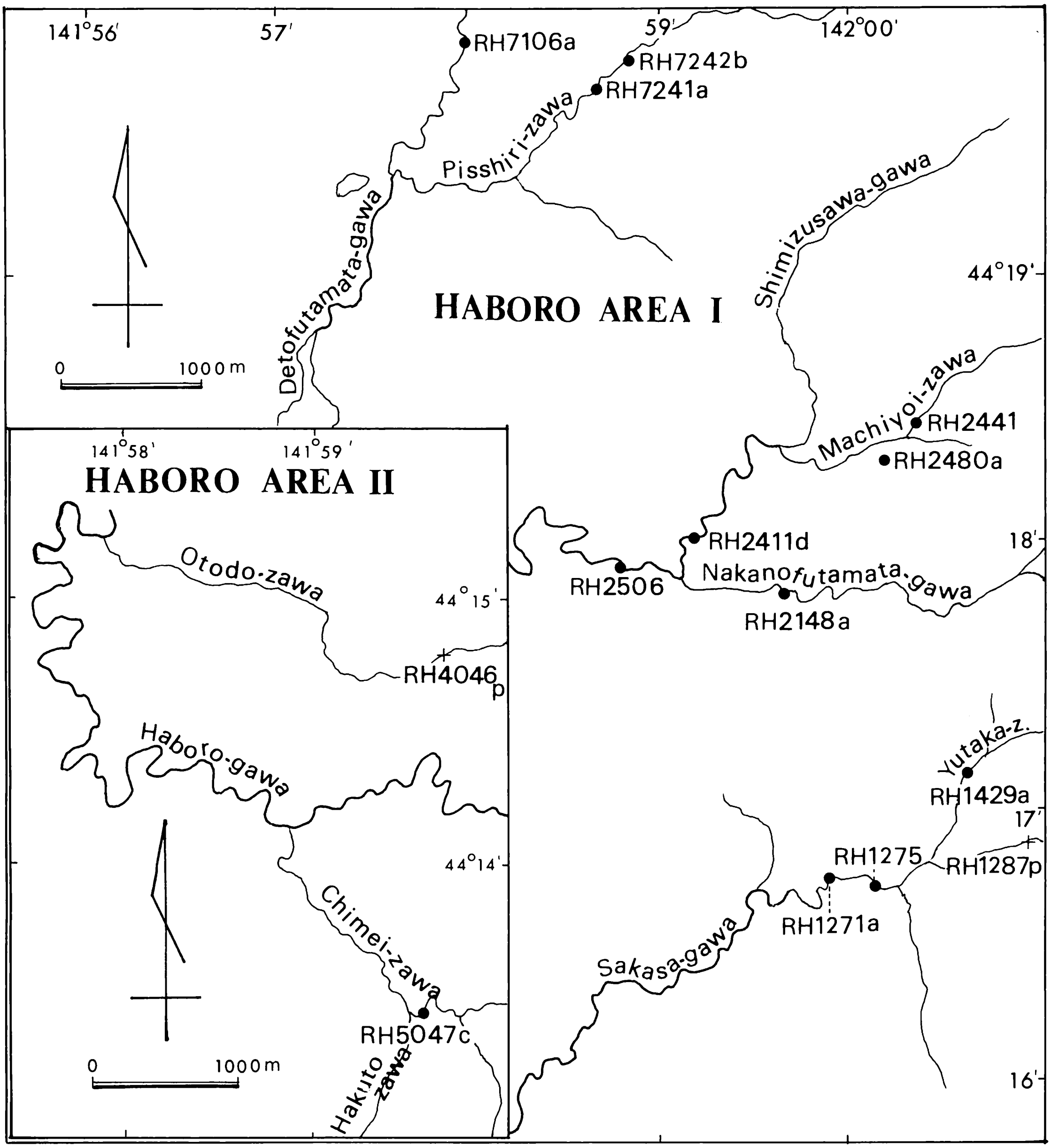

Figure 16. Locality map of the Haboro area.

58'00"E, Lat. 44°19'55"N. A left bank of the upper reaches of the Detofutamata-gawa, a tributary of the R. Haboro, about 1050m upstream from the confluence with the Pisshiri-zawa. Siltstone bed of the highest part of the MHs5 member at the top of the Middle Haborogawa Formation. Middle part of the Santonian (Figure 16).

Loc. RH7241a. Topographic map ditto, Long. 141°58'51"E, Lat. 44°19'49"N. A cliff on the left bank of the Pisshirizawa, about 2500 m upstream from the confluence with the Detofutamata-gawa. Sandstone bed of the lower part of the Upper Haborogawa Formation. Upper part of the Santonian (Figure 16).

Loc. RH2441. Topographic map of the Haborodake Quad. (1 : 25000), Long. 142°00'19"E, Lat. 44°18'25"

N. A cliff on the right bank of the Machiyoi-zawa, about 2500 m upstream from the loc. RH2411. Mudstone bed immediately below the sandstone member of the MHsl of the Middle Haborogawa Formation. Upper part of the Middle Coniacian (Figure 16).

Loc. RH2480. Topographic map ditto, Long. 142° 00′09″E, Lat. 44°18′18″N. A cliff on the forestry roadside along the Machiyoi-zawa, about 600 m southwestwards from the loc. RH2441. Mudstone bed immediately below the sandstone member of MHs2 of the Middle Haborogawa Formation. Lower part of the Santonian (Figure 16).

Loc. RH4046p. Topographic map of the Hakutozan Quad. (Kiritachi Quad.) (1 : 25000), Long. 141°59′ 39″E, Lat. 44°14′47″N. Pebble in the upper reaches of about 30 m upwards from the terminal of the forestry road along the Otodozawa, a tributary of the R. Haboro. In the sequence of siltstone bed of the middle part of the Upper Haborogawa Formation. Stratigraphic position exactly unknown.

Loc. RH5047c. Topographic map ditto, Long. 141° 59′34″E, Lat. 44°13′26″N. A river floor of the Chimei-zawa, a tributary of the R. Haboro, about 150 m upstream from the confluence with the Hakuto-zawa. Sandy siltstone bed immediately below the sandstone member UHsl of the lower part of the Upper Haborogawa Formation. Upper part of the Santonian.

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日本産白亜紀 *Inoceramus* (*Platyceramus*) *mantelli* de Mercey について：本論では北海道各地から産した *I.* (*P.*) *mantelli* de Mercey, 1877 の多くの標本についての観察に加えて生物測定学的見地からその特徴を検討してみた。その結果次のようなことが確認された。従来記載された種の特徴に加えていくつかの形質について変異の幅が明らかになった。日本から産した本種の標本はこれまで *I.* (*P.*) *yubariensis* Nagao et Matsumoto, 1940 として扱われてきたが，ヨーロッパのものと t 検定をも含めて詳細に比較した結果，その形態上の違いは種のレベルでは区別し難いことが明らかになった。従って，*I.* (*P.*) *yubariensis* の種名は *I.* (*P.*) *mantelli* の新参シノニムということになる。層序学的には本種はヨーロッパならびにその東方地域ではコニアシアン階の各層準から産しているが，日本では若干おくれてコニシアン上部からサントニアンにかけて産出する。本種の先祖型については今の所確認されていないが，本種はサントニアンやカンパニアン階の多くの *Inoceramus* (*Platyceramus*) の種に対して共通の，あるいは究極の先祖にあたると考えられる。

野田雅之・利光誠一。

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 158, pp. 513-534, 16 Figs., June 30, 1990

901. PARAMETERS FOR DESCRIPTION OF THE SHELL FORM OF THE GENUS *ANADARA* (MOLLUSCA ; BIVALVIA)*

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Abstract. Ontogenetic change in morphological features of *Anadara* shells is analyzed on the relationship between 4 proportions of portions of shell and shell size. These relational changes are interpreted in the framework of the shell coiling model ; ontogenetic change in the shape of cardinal area and teeth arrangement represents a change in revolution around the coiling axis, whereas ontogenetic change in the proportion of the anterior and posterior toothed hinge lengths represents a change in the shape of the commissure.

The taxonomic criteria of the genus *Anadara* are proposed based on similarities of the ontogenetic change in shell shape. The extremely variable population of *Anadara ninohensis* in the Kubota Formation (Middle Miocene, Fukushima Prefecture) has previously been classified into three species. Analysis of the ontogenetic variation shows that all Kubota specimens fall into the single variable species *Anadara* (*Anadara*) *hataii* Noda, and the other population from the Kadonosawa Formation (lower Middle Miocene, Iwate Prefecture) is placed in the subgenus *Scapharca*.

Key words. *Anadara*, ontogenetic change, shell coiling, shell form.

Introduction

The molluscan shell is a product of secretory activities operating throughout growth. The secreted shell is retained from stage to stage and the form becomes integrated at every stage. It must be emphasized that bivalve shells retain the same shape throughout growth is only an approximation to the truth. Many studies of the shell growth lines indicated a slight progressive change in shape as the valves grow. Molluscan forms, therefore, should be described "dynamically" in such a way that the description emphasizes the sequence of ontogenetic changes, and the description and classification of shells should be based on the constraints of growth.

Mathematical methods have been used in morphological studies of molluscs and other taxa (Thompson, 1942 ; Owen, 1953 ; Rudwick, 1959 ; Stasek, 1963 ; Raup and Michelson, 1965 ; Raup, 1966). In such studies, some equations are written that describe ontogenetic change in an idealized form. The advantage of these mathematical approach is that the factors of ontogenetic change in form can be appreciated through the equations within the framework of the coiling models.

Several sets of parameters have been suggested to describe differences and similarities between coiled forms. However, there have been few if any successful applications of this knowledge to the problems facing the description and classification of coiled forms. One reason is that the shell form has been represented by a logarithmic spiral in the models. However, many shells change in the mode of its spiral throughout ontogeny, so that they grow exactly in a non-logarithmic

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mode. This logarithmic growth assumption of the models, then, makes them difficult to use for the analysis of molluscan shells in nature.

The purpose of the present paper is to propose some taxonomic criteria of the genus *Anadara* based upon similarities in the ontogenetic sequence. The primary objective of this study is to publish the parameters for the description of ontogenetic change in the morphology of *Anadara* species. Similarities and differences in ontogenetic change will be examined in the taxonomic categories proposed in *Anadara* by Noda (1966). Finally, an attempt will be made to discriminate two species by using the similarities and differences of their ontogeny.

Definitions

The shape of the shell, and the shape and orientation of the taxodont teeth are useful morphological features for taxonomic discrimination in Arcidae (Reinhart, 1943). The shape of the shell is described by the degree of inflation of the shell, the position of the beak, and degree of the curvature of the anterior, posterior and ventral margins. The intervals of various parts of the shell measured in this study are defined here in order to describe the features of the shell.

Figure 1a shows the shape of the shell of the genus *Anadara* in interior view. TL is the length of the toothed portion of the hinge line. AM and PM are the heights of the anterior and posterior margins. The absolute size of the specimen is represented by the length of the toothed portion of the hinge line (TL). Figure 1b shows the shape of the cardinal area. CH is the height of the cardinal area.

The inflation of the *Anadara* shell is represented by the ratio between the height (CH) and length (TL) of the cardinal area. The degree of curvature of the anterior and posterior margins is represented by their heights (AM and PM).

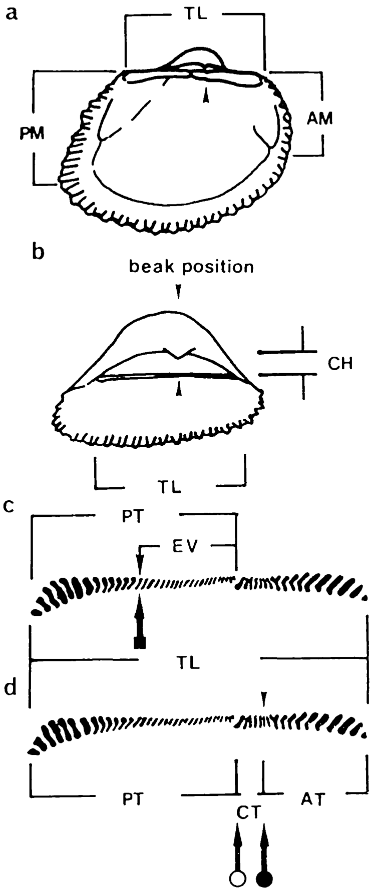


Figure 1. Linear dimensions measured for the analysis of ontogenetic change in shell form. **1a,** TL : length of the toothed portion of the hinge line. AM, PM : heights of the anterior and posterior margins of the commissure. **1b,** CH : height of the cardinal area. **1c,** EV : length of the divergent-toothed portion of the posterior teeth segment. **1d,** PT, CT, AT : lengths of the posterior, central and anterior segmental teeth series.

The hinge plate of *Anadara* species is straight or moderately arched and is located just below the cardinal area. The numerous taxodont teeth lie transverse to the hinge margin. Two major features of the hinge teeth are considered ; 1) the mode of arrangement, and 2) the ratio between the lengths of the parts of the toothed hinge anterior and posterior to the beak.

Figure 1c shows the arrangement of the

hinge teeth. The taxodont teeth of the genus *Anadara* were classified into three types by Reinhart (1943) based on their shape and their inclination to the hinge line: convergent teeth, divergent teeth, and v-shaped teeth. As shown in Figure 1c, the divergent teeth are at the center of hinge line, the convergent teeth at both extremities, and the v-shaped teeth between the other two types. EV is the length of the divergent-toothed portion of the posterior hinge line.

Noda (1966) classified the arrangement of taxodont teeth of the genus *Anadara* into three categories based on the combination of the tooth types of Reinhart (1943); he recognized the ventrally convergent type, the divergent type, and the divergent type with v-shaped teeth. These types of tooth arrangement are represented by using the ratio of the length of the divergent toothed portion to the length of the posterior segment of the hinge line (EV/PT).

Figure 1d shows the change in tooth size along the hinge line. The toothed portion of the hinge line can be divided into three segments by two points where the size of the teeth changes discontinuously. PT is the length of the posterior segment of the toothed portion of the hinge line, CT is the length of the central portion, and AT is the length of the anterior one.

The position of the beak is traditionally represented by the proportion between the lengths of the anterior and posterior parts of hinge line. The point that divides the central teeth segment from the anterior segment corresponds well to the position of the beak on the hinge line, especially in young shells (*ex*. specimen 1 in Figure 2). Therefore, the beak position is represented by using the proportion of the length of the anterior toothed segment to the length of the toothed portion of the hinge line (AT/TL) in this paper.

Material

The basic data used in this study comprise biometry of 3 subgenera and 15 species (Table 1). Populations of these species were selected for measurement by the following restrictions. Firstly, many specimens of one

Table 1. Stratigraphic distributions of the *Anadara* species studied here.

specific name			formations	age
Anadara	(*Anadara*)	*amicula elongata* Noda	Sasaoka, Omma	Pliocene, Pleistocene
A.	(*A.*)	*hataii* Noda	Kubota	Miocene
A.	(*A.*)	*hokkaidoensis* Noda	Chokubetsu, Okkoppezawa	Miocene
A.	(*Hataiarca*)	*kakehataensis* Hatai and Nisiyama	Kurosedani, Sunakozaka	Miocene
A.	(*H.*)	*kogachiensis* Noda	Haneji	Pleistocene
A.	(*H.*)	*subcrenata* (Lischke)	Recent, Narita	Recent, Pleistocene
A.	(*H.*)	*pseudosubcrenata* Ogasawara	Omma	Pleistocene
A.	(*Scapharca*)	cf. *satowi* (Dunker)	Omma	Pleistocene
A.	(*S.*)	*ommaensis* Otuka	Omma	Pleistocene
A.	(*S.*)	n. sp.	Koyu	Pliocene
A.	(*S.*)	*broughtonii* (Schrenck)	Recent, Narita	Recent, Pleistocene
A.	(*S.*)	*taiwanica* Noda	Tokazan	Pliocene
A.	(*S.*)	*makiyamai* Hatai and Nisiyama	Heiroku, Kurosedani	Miocene
A.	(*S.*)	*ninohensis* (Otuka)	Kadonosawa	Miocene
A.	(*S.*)	*tricenicosta* (Nyst)	Recent, Tokazan	Recent, Pliocene

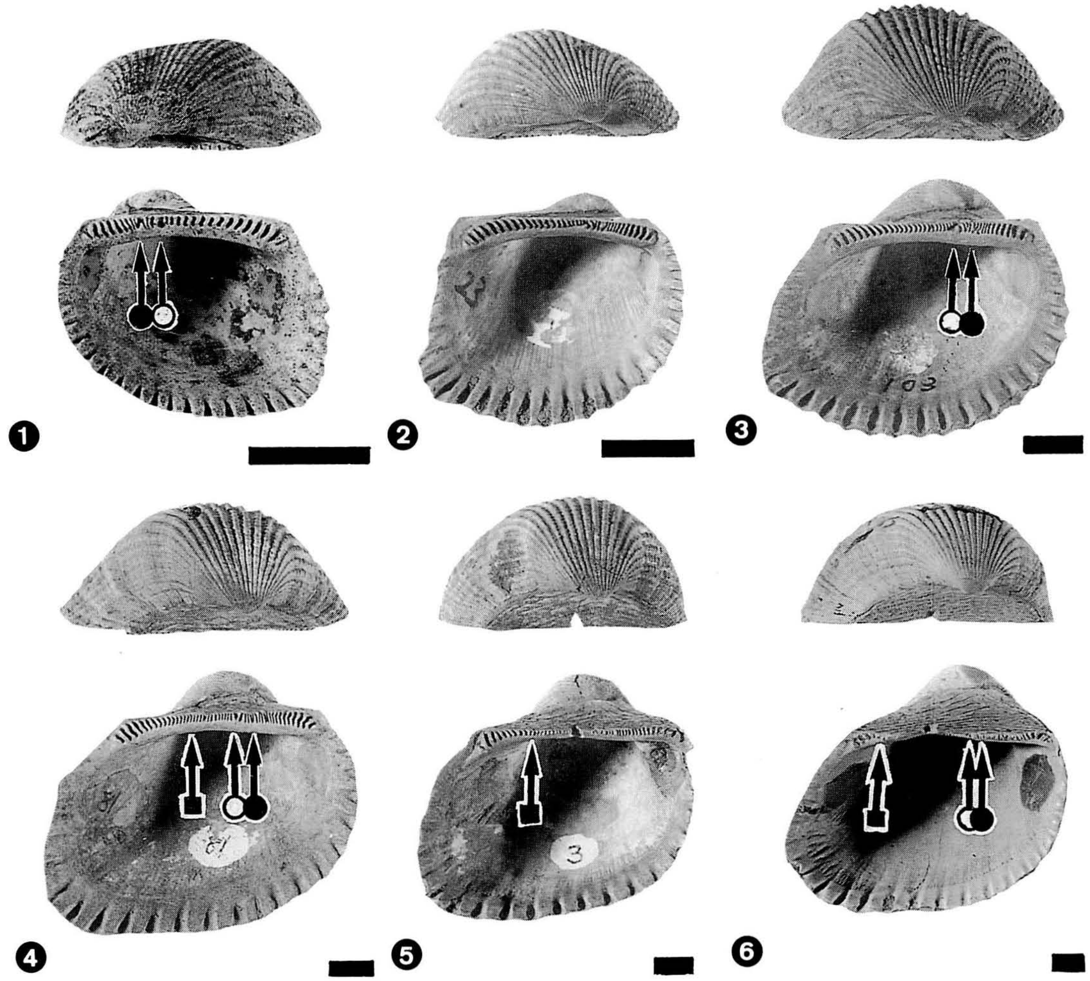


Figure 2. Ontogenetic variation of *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama from the Sunakozaka Formation in Toyama Prefecture. Scale bar = 5 mm. Symbols indicate the dimensions measured in the hinge teeth, as shown in Figure 1.

species must be available from one locality; the effects of geographical and evolutional variations were thereby minimized. Secondly, the number of specimens must be large enough to be treated statistically. Finally, the specimens must demonstrate considerable ontogenetic variation with shell size; the range of ontogenetic variation was maximized.

Ontogenetic change in the shape of shell

(a) Shape of the cardinal area

Figure 2 shows the shapes of the cardinal area of *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama at different growth stages. In juvenile shells, the cardinal area is a low triangular shape, but it becomes progressively taller as the shell grows. Such a change can be represented by the change in the ratio between the height (CH) and length (TL) of the cardinal area. This relationship

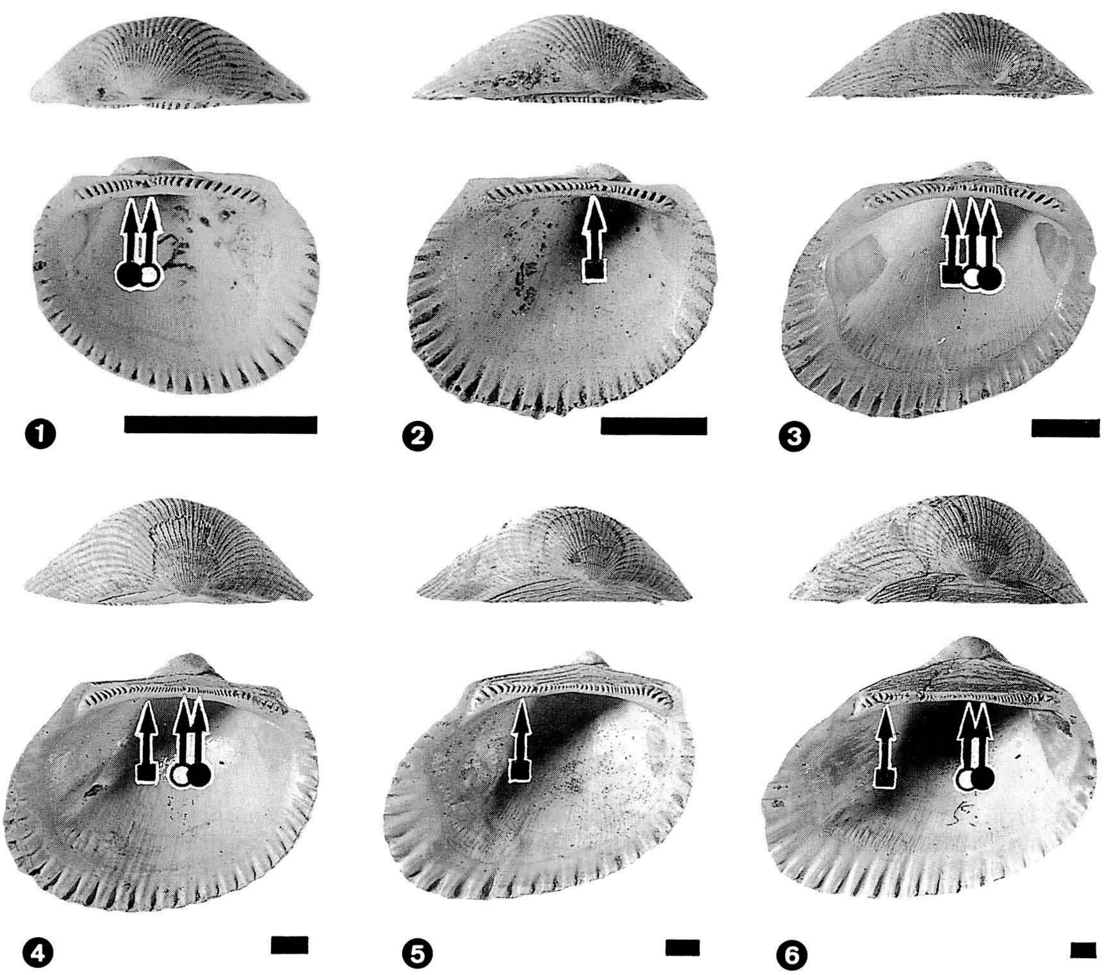


Figure 3. Ontogenetic variation of *Anadara* (*Anadara*) *amicula elongata* Noda from the Omma Formation in Ishikawa Prefecture. Symbols as in Figure 1.

is plotted in Figure 4a. The plotting of TL against the log of CH produced a linear array of points at TL < 23 mm, and a curved array at TL < 23 mm; the linear array of points suggests that the cardinal area grows in a logarithmic mode at TL > 23 mm. The mode of growth in the cardinal area is not constant throughout ontogeny, and for this species, it changes at a TL value of 23 mm.

Figure 3 shows the shapes of the cardinal area of *Anadara* (*Anadara*) *amicula elongata* Noda. The relationship between TL and log CH of this species is plotted in Figure 4b. The logarithmic growth of the cardinal area can be observed at TL values greater than 12 mm. For *A.* (*A.*) *amicula elongata*, the growth mode changes at a TL value of 12 mm.

These examples indicate that the cardinal area changes in its growth mode through ontogeny; that is, the cardinal area grows in non-logarithmic mode during the juvenile stage, and in logarithmic mode during the post-juvenile stage. Such change in growth mode is observed in other *Anadara* species (Table 2). Therefore, the value of TL at which the growth mode changes is a useful parameter for the description of ontogeny of

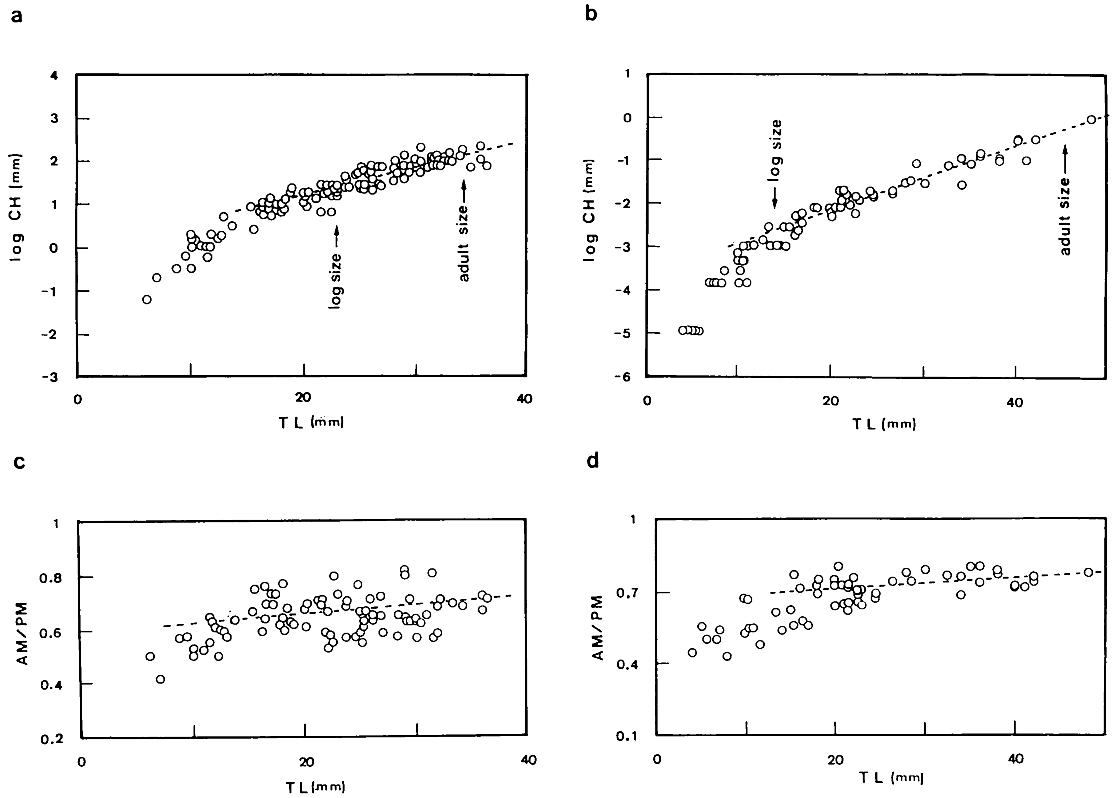


Figure 4. **a, b** : Distribution of ontogenetic variation with respect to the relationship between the height (CH) and length (TL) of the cardinal area. Logarithmic growth of the cardinal area, represented by broken line, occurs at greater than log sizes (when EV/PT=0). **c, d** : Ontogenetic change in the ratio between the heights of the anterior (AM) and posterior (PM) margins of the commissure. Broken lines represent linear change in mean value of the ratio in adult shells. **a, c** ; *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama. **b, d** ; *Anadara* (*Anadara*) *amicula elongata* Noda.

the cardinal area of *Anadara*, and the TL value at which the growth mode changes is named a log size.

(b) Shape of the commissure

Specific cases of variation in the shape of the commissure fall practically into two categories : either variation in the ratio between the height and length of the commissure, or variation in the ratio between the heights of the posterior and anterior parts of the commissure. The majority of ontogenetic changes in the shape of the commissure observed on *Anadara* species occur in the ratio between the heights of the posterior and anterior parts of the commissure (AM/PM).

Variation in the shape of the commissure for *Anadara* (*Hataiarca*) *kakehataensis* is illustrated in Figure 2. In the juvenile stage, the posterior margin is higher than the anterior margin ; the commissure has a distinctly inequilateral form. The commissure becomes progressively more equilateral as the shell grows. Such ontogenetic change can be represented by the change in the ratio between the heights of the anterior and posterior margins (AM/PM). The AM/PM and TL data were plotted as a scatter diagram in order to examine whether there is a correlation between them. Figure 4c shows the scatter diagram for *A.* (*H.*) *kakehataensis*. The correlation between AM/PM and TL is positive for this species ; that is, TL increases as AM/PM increases.

Ontogenetic change in hinge teeth

(a) Arrangement of the hinge teeth

Arkell (1930) reported that the arrangement of the hinge teeth of the Glycymerididae and Cucullaeidae was the divergent type with v-shaped teeth in adult shells, which changed progressively from the convergent type in juvenile shells as the shell grew. Such a change in the teeth arrangement can be observed also in the ontogey of *Anadara* species.

Figure 2 shows the arrangements of hinge teeth at a variety of growth stages in *Anadara* (*Hataiarca*) *kakehataensis*. In the juvenile stage, the arrangement is of the convergent type. The shape of the teeth is transformed into v-shaped teeth, and into divergent teeth along the central part of the hinge line, progressively further outward as the shell grows, so that by the adult stage, the arrangement of the teeth becomes the divergent type with v-shaped teeth. Change in the arrangement of teeth will be represented here by change in the ratio of the length of the divergent toothed portion to the length of the posterior toothed portion of the hinge line (EV/PT). If a shell has the convergent type of teeth arrangement, the value of EV/PT will be 0. As the arrangement changes from the convergent type to the divergent type with v-shaped teeth, the value of EV/PT increases progressively, and finally approaches the maximum value (EV/PT = 1). The shell size at which

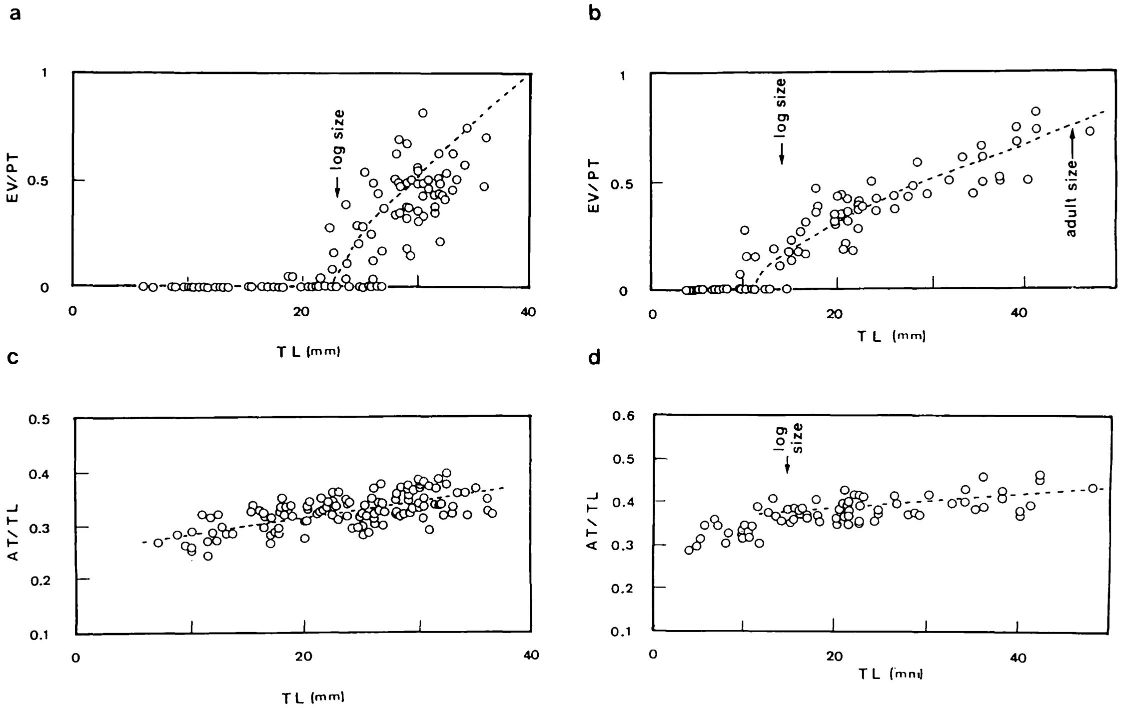


Figure 5. **a, b** ; Distribution of ontogenetic variation in teeth arrangement represented by change in the value of EV/PT. When EV/PT = 0, a shell has the convergent type teeth arrangement, and when EV/PT > 0, the divergent type with v-shaped teeth arrangement. **c, d** ; Growth change in the ratio of the length of the anterior teeth segment to the length of the toothed portion of the hinge line, which represents the migration of the beak position. **a, c** ; *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama. **b, d** ; *Anadara* (*Anadara*) *amicula elongata* Noda.

Table 2. Biometorical data for *Anadara* species studied here.

specific name	relative size	Log size (TL (0)) EV/PT=0			Adult size (TL (0.75)) EV/PT=0.75		
	TL (0) TL (0.75)%	TL (mm)	AT/TL	CH/TL	TL (mm)	AT/TL	CH/TL
Anadara (*Anadara*) *amicula elongata* Noda	27	12	.075	.36	45	.222	.42
A. (*A.*) *hataii* Noda	30	15	.066	.4	50	.22	.39-.43
A. (*A.*) *hokkaidoensis* Noda	31	14	.1	.4	45	.266	.45
A. (*Hataiarca*) *kakehataensis* Hatai and Nisiyama	63	23	.145	.31	35	.242	.35
A. (*H.*) *kogachiensis* Noda	71	32	.141	.38	45	.222	.4
A. (*H.*) *subcrenata* (Lischke)	51	23	.87	.31-.4	45	.188	.38-.42
A. (*H.*) *pseudosubcrenata* Ogasawara	51	18	.111	.29	35	.188	.38
A. (*Scapharca*) cf. *satowi* (Dunker)	60	30	.77	.33	50	.15	.4
A. (*S.*) *ommaensis* Otuka	50	22	.136	.28	44	.148	.37
A. (*S.*) n. sp.	48	16	.057	.27	33	.121	.28
A. (*S.*) *broughtonii* (Schrenck)	46	30	.05	.34	65	.154	.38
A. (*S.*) *taiwanica* Noda	56	25	.075	.32	45	.12	.35
A. (*S.*) *makiyamai* Hatai and Nisiyama	51	18	.14	.3	35	.186	.34
A. (*S.*) *ninohensis* (Otuka)	61	20	.1	.32	33	.152	.38
A. (*S.*) *tricenicosta* (Nyst)	52	30	.1	.31	58	.152	.36

TL (0)/TL (0.75): relative size, which is the ratio between the lengths of the tothed portion of the hinge line at EV/PT=0 and at EV/PT=0.75. TL: length of toothed portion of hinge line. AT/TL: ratio of the length of the anterior teeth segment to the length of the toothed portion of the hinge line. CH/TL: proportion of the height (CH) to the length (TL) of the cardinal area. EV/PT: ratio of the length of divergent-toothed portion of the posterior teeth segment to the length of the posterior teeth segment.

the arrangement changes to the divergent type with v-shaped teeth is named a critical size.

The relationship between EV/PT and TL in *A.* (*H.*) *kakehataensis* is plotted in Figure 5a. The value of EV/PT is constantly 0 at TL<23 mm. As TL becomes greater than 23 mm, the value of EV/PT progressively increases and approaches the maximum value (EV/PT=1). For this species, the critical size of EV/PT is TL=23 mm.

Figure 3 shows tooth arrangements of *A.* (*A.*) *amicula elongata*. The relationship between EV/PT and TL is illustrated in Figure 5b. For this species, the critical size for the change in EV/TL is TL=12 mm.

Ontogenetic change in the tooth arrangement can be observed in other *Anadara* species, and measured values of the critical size of the species are shown in Table 2.

(b) The ratio between the lengths of the hinge anterior and posterior to the beak

Figure 2 shows the ontogenetic variation in hinge teeth for *A.* (*H.*) *kakehataensis*. In the juvenile stage, the beak is located at the anterior fourth to third of the hinge length, but it shifts progressively during ontogeny so that by the adult stage, the beak is located near the center of the hinge line.

Figure 5c is a scatter diagram on which the AT/TL and TL data for all the specimens of *A.* (*H.*) *kakehataensis* are plotted. The relationship between AT/TL and TL is positive; that is, as TL increases, AT/TL increases. This ontogenetic change in the proportion of the lengths of the anterior and posterior portions of the hinge (*i.e.*, backward migration of the beak) occurs also in all other *Anadara* species.

Relationship between the ontogenetic changes in the shape of shell and in the features of hinge teeth

Ontogenetic changes in the shape of the shell and in the features of the hinge teeth are observed in *Anadara* species. The relationship between these two types of ontogenetic change is examined as follows.

(a) The relationship between the changes in cardinal area and in tooth arrangement

Figure 6 shows the relationship between EV/PT and CH/TL for *Anadara* (*Hataiarca*) *kakehataensis*. The plotting of EV/PT against the log of CH/TL produces a linear array of points at EV/PT>0. This linear relationship suggests that the value of EV/TL depends on the value of CH/TL at EV/PT>0; that is, the ontogenetic change in the shape of the cardinal area has the effect of transforming the arrangement of the hinge teeth. This dependency between these characters is shown also by comparing the values of the critical size of the arrangement of the hinge teeth with the log size of the shape of the cardinal area; for example, in *A.* (*H.*) *kakehataensis*, the critical size measured in ontogenetic change in EV/PT is 23 mm, which is equal to the log size of change in CH/TL. The critical and log sizes, which are defined on different ontogenetic features, are nearly equal in other *Anadara* species as well (Table 2).

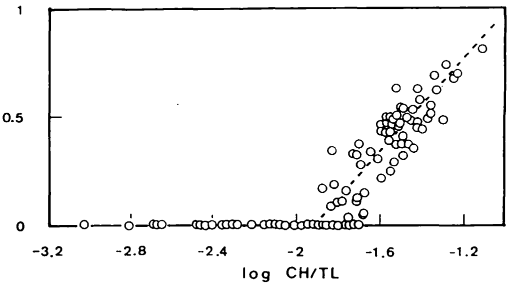


Figure 6. Relational change between the teeth arrangement (EV/PT) and the shape of the cardinal area (CH/TL) for *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama.

(b) The relationships between ontogenetic changes in the proportion of the commissural margins and the hinge line

A positive correlation exists between AM/PM and TL distribution (Figures 4c, d). This correlation thus produces a positive correlation between AM/PM and AT/TL. Figure 7a shows the correlation between them for *A.* (*H.*) *kakehataensis*, plotted as a scatter diagram. The positive correlation between AM/PM and AT/TL suggests that the ontogenetic change in the shape of the

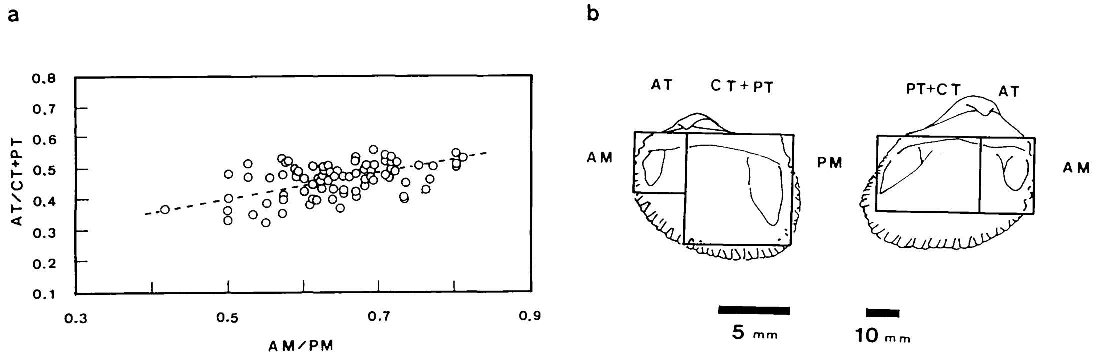


Figure 7. **a**; Linear relationship between ontogenetic changes in the ratio of the two ratios relating shapes of posterior and anterior parts of the shell (anterior to posterior hinge length, AT/CT+PT; heights of anterior and posterior commissural margins, AM/PM) for *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama. **b**; Model of ontogenetic change in the shape of the commissure.

commissure is shown by a change in the ratio between the squares of the anterior and posterior parts of the commissure (Figure 7b). Therefore, the ontogenetic change in the shape of the commissure can be represented by change in the ratio of the lengths of the portions of the hinge anterior and posterior to the beak (AT/TL).

Parameters for the description of *Anadara* shell morphology

In the light of the coiling shell model, the geometry of a shell can be described by the relationships between several parameters. Owen (1953) resolved the growth direction at any point on the shell margin into three components: 1) a radial component radiates from the umbo in the plane of the generating curve, 2) a transverse component expresses the transverse effect of the revolution of the plane of the generating curve, and 3) a tangential component of growth in the plane of the generating curve may be expressed by a "apivoting" of the generating curve within its plane. His model is useful to analyze the shell deformation that occurs during ontogeny. Raup and Michelson (1965) proposed a simple model for the description of a coiled shell by using four basic parameters. They are: 1) the shape of the generating curve (S), 2) the whorl expansion rate (W), 3) the position of the generating curve in relation to the coiling axis (D), and 4) the rate of whorl translation (T). The four parameters are classified into two categories; parameters for the description of shell coiling (D, W and T), and parameters for the description of the shape of the commissure (S). The simplicity of this model makes it easy to visualize shell forms through computer simulations. Computer-drawn pictures serve as a framework through which different forms may be compared.

Figures 1a, b show the intervals of *Anadara* shells measured here. These intervals are compared with the parameters of the two models, and the coiling shell model is used as a framework through which the ontogenetic changes in the shape of *Anadara* species may be appreciated. As noted above, the cardinal area and the commissure change in shape during ontogeny in *Anadara* species.

In a transverse section of an *Anadara* shell through the beak and the center of the ventral margin, the surface of the shell and the cardinal area are described by two spiral curves. One of them, the spiral curve of the cardinal area is considered here; the height of the cardinal area (CH) corresponds to the distance from the coiling axis to the generating curve (D) of Raup and Michelson's model, and to the integrated transverse components of Owen's model of the spiral curve of the cardinal area. The length of the toothed portion of the hinge line (TL) corresponds to the radius of the generating curve of Raup and Michelson's model. Therefore, the differentiated TL is the whorl expansion rate (W) of Raup and Michelson's model, and the differentiated TL is also equal to the radial component of Owen's model.

The CH-TL relationship, which represents the change in the shape of the cardinal area, can be compared with the D-W relationship of Raup and Michelson's model. A change in position on the D-W plane of Raup's (1966) morphological space expresses a change in the degree to which the shell becomes evolute. Similarly, for the *Anadara* shell, an increase in the value of CH/TL expresses an increase in the degree of shell inflation.

If the increasing rate of CH/TL increases constantly during ontogeny, the end of the cardinal area traces a logarithmic spiral curve, so that the shape of the spiral can be expressed simply by the increasing rate of a logarithmic spiral [$CH=\exp.(a*TL)$: $a=$ const.]. However, the rate of the increase of CH/TL is not constant for *Anadara* species; ontogenetic change of the cardinal area shows that non-logarithmic growth occurs in the juvenile stage and logarithmic growth occurs in the post-juvenile stage. The shell shape produced by non-logarithmic growth can be changed by changing the ratio between the lengths of the juvenile and adult stages, without changing the shell inflation; the proportion of the length of the juvenile stage to the length of the completed adult shell involves basic information on the shape of non-logarithmic growth. It is required in non-logarithmic growth that the scale of growth is defined in order to calculate the proportion of the lengths of growth stages. The value of EV/PT is a useful marker of shell growth, because EV/PT value increases depend on CH/TL value during logarithmic growth but not on absolute shell size. Therefore, the nature of shell coiling of *Anadara* species can be described by using sets of CH/TL and EV/PT values.

The shape of the commissure of *Anadara* species is described by using two ratios; AM/PM, the ratio of the heights of the anterior and posterior margins, and AT/TL, the ratio of the lengths of the anterior and the whole toothed portions of the hinge margin. Therefore, these two ratios correspond to the descriptive parameter for the shape of the generating curve (S) of Raup and Michelson's model.

The primary factor in deformation of the shape of the commissure is asymmetrical secretion about the antero-posterior axis of the margins. In Raup and Michelson's model, ontogenetic change in the shape of the commissure (S) would be represented by asymmetry of the magnitude of the expansion rate of the commissure (W) about the antero-posterior axis. In Owen's model, the gradient of the tangential component along the axis generated the ontogenetic change. The changes in AM/PM and AT/TL express the change in ratio of the squares of the anterior and posterior parts of the commissure plane. Therefore, the differentiated AM/PM and AT/TL over growth time corresponds to the ratio of W values at the anterior and posterior parts of the commissure, and to the gradient of the tangential component along the antero-posterior axis. Thus, ontogenetic change in the shape of the commissure of the *Anadara* shell can be represented by using AT/TL values.

Using these parameters, I took as an example a comparison between the shell shapes of *Anadara* (*Hataiarca*) *kakehataensis* and *Anadara* (*Anadara*) *amicula elongata* at the log size (EV/PT$=$0) and the adult size (EV/PT$=$0.75). At the log size (EV/PT$=$0); *A.* (*H.*) *kakehataensis* has TL$=$23 mm, AT/TL$=$0.145, CH/TL$=$0.31, and *A.* (*A.*) *amicula elongata* has TL$=$12 mm, AT/TL$=$0.075, CH/TL$=$0.36. At the adult size (EV/PT$=$0.75), *A.* (*H.*) *kakehataensis* has TL$=$35 mm, AT/TL$=$0.242, CH/TL$=$0.35, and *A.* (*A.*) *amicula elongata* has TL$=$45 mm, AT/TL$=$0.222, CH/TL$=$0.42. Comparison between sets of these values makes it clear that these species differ not only in absolute size, but also in shell geometry at the same growth stage (Table 2). The relative size is defined as the ratio of the TL value at the log size to the TL value at the adult size [TL(0)/TL(0.75)]. The relative size represents approximately the proportion of the length of the juvenile stage to the length of the completed adult shell. The value of the relative size for *A.* (*H.*) *kakehataensis* is 63%, while the value for *A.* (*A.*) *amicula elongata* is 27%; these values suggests that the shell shape of these species differs in shell coiling shape.

In summary, the basic elements of the shape of shell can be described by the set of parameters; EV/PT, AT/TL, CH/TL, TL and TL(0)/TL(0.75), where

EV/PT is the ratio of the length of the divergent toothed portion to the length of the posterior toothed portion of the hinge line, and represents the scale of the growth stage;

AT/TL is the ratio of the length of the anterior portion to the length of the toothed portion of the hinge line, which is a parameter for the description of the shape of the commissure by the ratio of the squares of the anterior and posterior parts of the commissure ;

CH/TL is the ratio of the height to the length of the cardinal area, which is a parameter for the description of the shell inflation ;

TL(0)/TL (0.75) is the ratio of the length of the juvenile stage to the length of the completed adult shell, which describes the nature of the ontogenetic change in shell coiling shape ;

and TL is the length of the toothed portion of hinge line, which represents the absolute size of the shell.

Similarities and differences of ontogenetic change in taxonomic categories

The forgoing discussion has concentrated on the description of shell morphology from a strictly geometric viewpoint. As well as this, the complete morphological picture of a bivalve shell would include the many features of surface ornamentation, growth lines, internal structure, shell thickness, and so on. If the knowledge of ontogenetic change in shell shape is incorporated more thoroughly into the systematic description of *Anadara* species, the identification of taxonomic categories will be facilitated. Similarities and differences in ontogenetic change are analyzed here in the taxonomic categories proposed by Noda (1966).

(a) Similarities and differences in intraspecific variation

The specimens measured in this study are placed in the 15 species recognized by Noda (1966). Figures 4a, 4c, 5a, and 5c show the relationships of the parameters for *A.* (*H.*) *kakehataensis*. Each circle on the diagram represents data on one specimen. The distribution of the circles is restricted to a narrow region along the broken line. This narrow distribution suggests that these specimens have ontogenetic relationships in common for geometry, growth stage and absolute size. By contrast, the relationships of three species are illustrated in Figure 11b. The symbols are distributed over a wide region. The width of the distribution of points in these diagrams, therefore, is useful to examine whether the population analyzed is placed in a single species.

An important intraspecific variation is found in the AT/TL-TL relationship, which represents the ontogenetic relationship between the shape of the commissure and absolute size. Figure 8 shows variation in the shape of the commissure, and Figure 9 shows the distribution of AM/PM-TL data measured in *A.* (*H.*) *subcrenata* (Lischke). The circles are restricted to a narrow region along the line, so that the population is placed in a single species. Specimens 2 and 3 in Figure 8 are examples of intraspecific variations with respect to the AM/PM-TL relationship. Although these specimens possess almost the same size, specimen 2 is characterized by a smaller value of the ratio AM/PM than that of specimen 3 shown in Figure 9 ; specimen 2 has a more inequilateral commissure shape than that of specimen 3. Such an inequilateral shape also characterizes specimen 1, which is a younger than specimens 2 and 3 (Figures 8, 9). Therefore, wide intraspecific variation is recognized in the relationship between the commissure shape and absolute size in this species.

(b) Similarities and differences between allied species

Some workers have proposed that Japanese *Anadara* species could be divided into some groups of closely allied species. For example, Iwasaki (1964) recognized 9 groups: *Anadara daitokudoensis* group, *Anadara ninohensis* group, *Anadara amicula* group, *Anadara moriyensis* group, *Anadara ommaensis* group, *Anadara castellata* group, *Anadara valentula* group, *Anadara tricenicosta* group, and *Anadara granosa* group. Similarities and differences in ontogenetic change in shell form are examined here in 5 allied groups, as follows : *Anadara* (*Anadara*) *amicula elongata* group, *Anadara* (*Hataiarca*) *subcrenata* group, *A.* (*H.*)

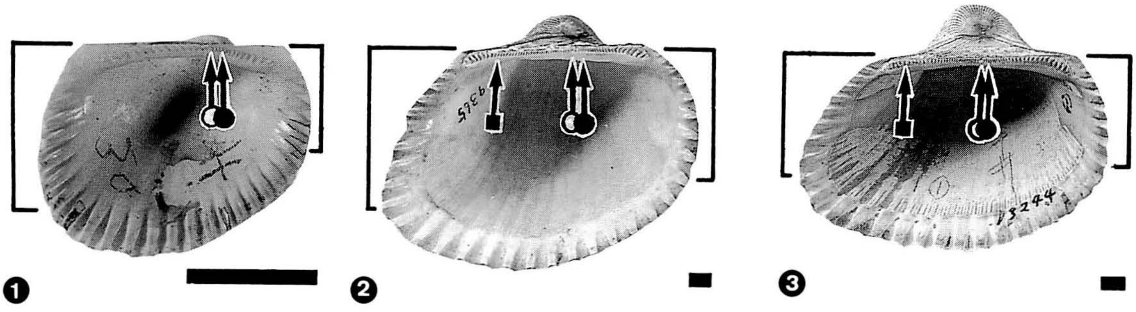


Figure 8. Ontogenetic and intraspecific variation in the shape of the commissure of *Anadara* (*Hataiarca*) *subcrenata* (Lischke) from the Narita Formation in Chiba Prefecture. Symbols as in Figure 1.

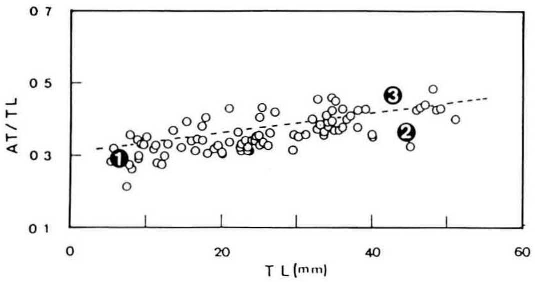


Figure 9. Distribution of ontogenetic and intraspecific variation in the relationship between AT/TL (the ratio of the lengths of the anterior teeth segments to toothed portion of the hinge line) and TL (absolute size) for *Anadara* (*Hataiarca*) *subcrenata* (Lischke). Numbers 1-3 on the diagram corresponds to numbers of specimens in Figure 8.

kakehataensis group, *Anadara* (*Scapharca*) *ommaensis* group and *A*. (*S*.) *ninohensis* group.

Figure 10 shows commissure shapes of three growth stages for *A*. (*H*.) *subcrenata* and its allied species *A*. (*S*.) cf. *satowi* (Dunker) and *A*. (*H*.) *pseudosubcrenata* Ogasawara. The relationships between EV/PT and AT/TL for these species are illustrated in Figure 11b. The symbols are restricted to a narrow region of the diagram ; the EV/PT and AT/TL relationships of these species are similar. The similarity of the relationships suggests that these species are closely similar in shell form at the same growth stage.

Figure 11a shows the relationships between EV/PT and the absolute size of these species. The distinct growth paths of these three species make it clear that the species have distinct EV/PT-TL relationships. Therefore, these three species are similar in shell shape but different in absolute size at the same growth stage.

Such interspecific variation with respect to the relationship between shell shape and absolute size was also observed in other groups of allied species. It has long been recognized that absolute size may not be a useful taxonomic criterion for mollusca species. It is only because that the basis of the spiral models, namely, that molluscan shells retain the same shape throughout growth, has been accepted. In a group of allied species, however, absolute size at the same growth stage is a useful character for the discrimination of the allied species.

(c) Similarities and differences between subgenera

The basic data used here comprise observations made on 15 species placed in 3 subgenera on the basis of Noda's (1966) systematics. These species are classified practically into two categories with respect to the ratio of the length of the juvenile stage to the length of the completed adult shell : one category of species is represented by TL(0)/TL(0.75) values less than 31%, and the other is represented by values greater than 46%. Three species placed in the subgenus *Anadara* (*Anadara*) are classified into the lower value category :

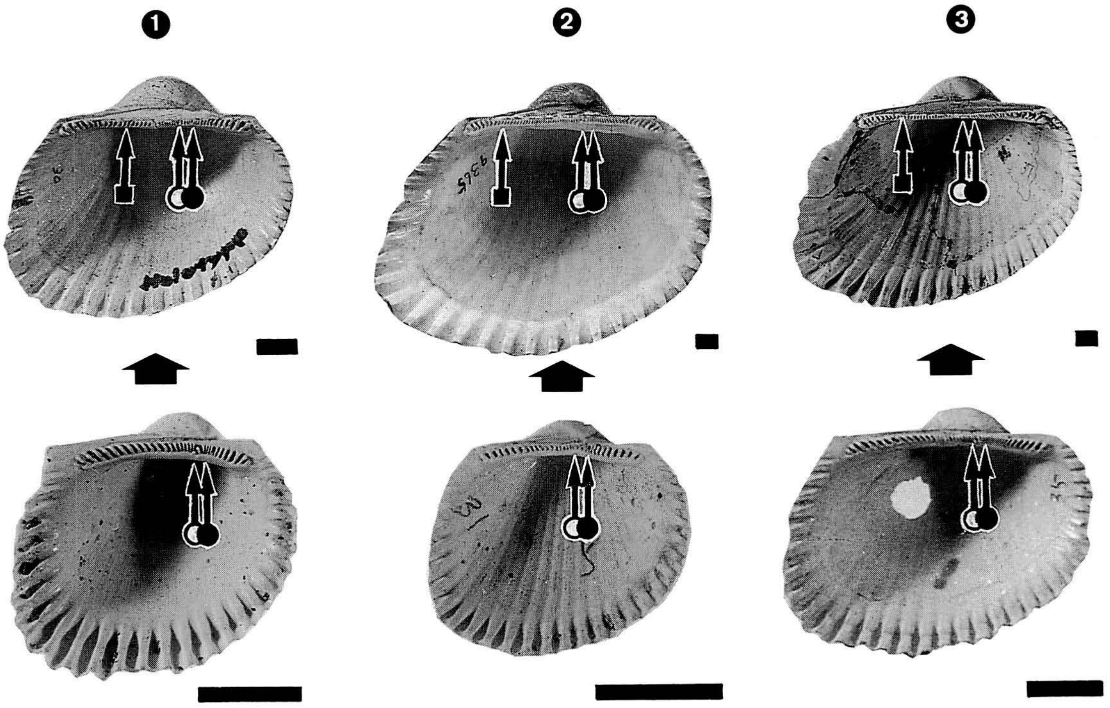


Figure 10. Ontogenetic and interspecific variation of the shape of the commissure of *Anadara* (*Hataiarca*) *subcrenata* (Lischke) and its allied species. Symbols as in Figure 1. **1**; *A.* (*H.*) *pseudosubcrenata* Ogasawara from the Omma Formation in Ishikawa Prefecture. 2; *A.* (*H.*) *subcrenata* (Lischke) from the Narita Formation in Chiba Prefecture. **3**; *A.* (*S.*) cf. *satowi* (Dunker) from the Omma Formation in Ishikawa Prefecture.

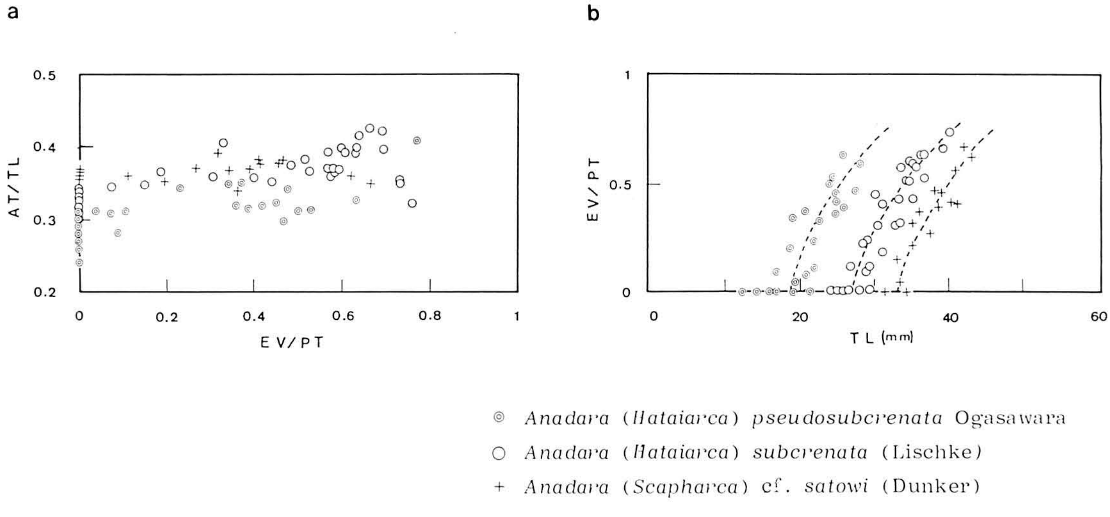


Figure 11. **a**; Comparison between the relationships of the shape of the commissure (AT/TL) and growth stage (EV/PT) for *Anadara* (*Hataiarca*) *subcrenata* (Lischke) and its allied species. **b**; Comparison between the relationships of growth stage (VE/PT) and absolute size (TL) for the same species.

A. (*A.*) *amicula elongata* Noda, *A.* (*A.*) *hataii* Noda, and *A.* (*A.*) *hokkaidoensis* Noda. Five species placed in the subgenus *Anadara* (*Hataiarca*), and 8 species placed in the subgenus *Anadara* (*Scapharca*) are classified into the higher value category: *A.* (*H.*) *kakehataensis* Hatai and Nisiyama, *A.* (*H.*) *kogachiensis* Noda, *A.* (*H.*) *subcrenata* (Lischke), *A.* (*H.*) *pseudosubcrenata* Ogasawara, *A.* (*S.*) cf. *satowi* (Dunker), *A.* (*S.*) *ommaensis* Otuka, *A.* (*S.*) *shizuokaensis* Noda, *A.* (*S.*) *taiwanica* Noda, *A.* (*S.*) *makiyamai* Hatai and Nisiyama, *A.* (*S.*) *ninohensis* (Otuka), and *A.* (*S.*) *tricenicosta* (Nyst), as shown in Table 2. Therefore, the subgenus *Anadara* can be discriminated from the other subgenera proposed by Noda (1966) by using the value of TL(0)/TL(0.75). Whereas, the subgenus *Hataiarca* can not be discriminated from the subgenus *Scapharca* by using this value.

The parameter TL(0)/TL(0.75), which describes the nature of ontogenetic change in shell coiling, corresponds to the relationship between W and D in Raup and Michelson's model. Considering the change in the relationship between W and D during ontogeny, which is exhibited by gastropods and ammonites, relative increase in the distance from the coiling axis to the generating curve (D) with respect to the whorl expansion (W) makes the shell form more evolute and more umbilicate. If the relationship changes during ontogeny by logarithmic growth, the shell will become more evolute as it grows. Therefore, the difference in relative size [TL(0)/TL(0.75)] between subgenera of the genus *Anadara* can be compared with the difference in degree to which the shell becomes evolute as it grows; lower value of TL(0)/TL(0.75) will produce a more evolute shell.

In summary, the criteria useful for the discrimination of taxonomic categories are as follows:

(1) Intraspecific variation: in a population placed in a single species, the relationships between descriptive parameters of shell growth (EV/PT, AT/TL, CH/TL and TL) are defined; particularly, the EV/PT-TL data are distributed in a narrow area of the diagram. Intraspecific variation is found in the relationship between the shape of the commissure (AT/TL) and absolute size (TL).

(2) Interspecific variation between allied species: allied species are similar in the relationship between the shell shape (AT/TL) and the growth stage (EV/PT), but differ in the relationship between the growth stage (EV/PT) and the absolute size (TL).

(3) Discrimination between subgenera of the genus *Anadara*: Species placed in the same subgenus are similar in the nature of shell coiling represented by the relative size [TL(0)/TL(0.75)]; the relative size of species in the subgenus *Anadara* is less than 31%, while that of species in the subgenera *Hataiarca* and *Scapharca* is greater than 46%.

Discrimination of *Anadara* (*Anadara*) *hataii* and *Anadara* (*Scapharca*) *ninohensis*

Anadara specimens from Kadonosawa in Iwate Prefecture and *Anadara* specimens from Kubota in Fukushima Prefecture are described by using the parameters defined above, and the proposed criteria are applied to discriminate their taxonomic categories.

(a) Review of the systematic problem

Anadara (Scapharca) ninohensis (Otuka) was originally described from the lower Middle Miocene Kadonosawa Formation by Otuka (1934). According to the original description, this species resembles *Anadara abdita* (Makiyama, 1926) but differs by having ungrooved radial ribs; *Anadara abdita* has a shallow median groove on each radial rib. Hatai and Nisiyama (1938) described *Anadara makiyamai* based upon the specimen from the Heiroku Formation in Northern Korea by Makiyama (1926) as *Arca abdita*.

Nomura and Hatai (1936) described the

Anadara specimens from the middle Middle Miocene Kubota Formation as *Anadara ninohensis*, and they pointed out that the Kubota specimens have a great range of variation in shell ornamentation and in shell form. Noda (1966) classified the specimens from the Kubota Formation into three species: *A.* (*A.*) *ninohensis*, *A.* (*A.*) *tanaguraensis* Noda, and *A.* (*A.*) *hataii* Noda. Iwasaki (1970) thought that the great range of variation of the Kubota specimens was intraspecific phenotypic variation of the single species *A. ninohensis*.

Despite this controversy over the systematic status of the Kubota specimens, Iwasaki (1964) and Noda (1966) agreed that *A. ninohensis* was the common ancestor from which the major Japanese *Anadara* lineages radiated. Iwasaki (1963) considered that *A. amicula* and its allied species, which flourished during Miocene and Pliocene time evolved from the *A. ninohensis* group, and that they were the ancestral species of the living *A. subcrenata* group. Noda (1966) thought that *A. ninohensis* and its allied species were placed in the subgenus *Anadara,* which may have been the ancestors of two major groups of subgenera *Anadara* that flourished during Miocene and Pliocene time: the *A.* (*A.*) *tatunokuchiensis* group evolved from *A.* (*A.*) *ninohensis,* and the *A.* (*A.*) *amicula* group from *A.* (*A.*) *makiyamai*.

(b) Observation on the specimens

(b)-1 *Anadara* (*Scapharca*) *ninohensis* (Otuka)

Stratigraphic records: Specimens of *Anadara ninohensis* were collected from the type locality of the Kadonosawa Formation at a small branch of the Shiratori River in Iwate Prefecture (Figure 12). The Kadonosawa Formation occupies the stratigraphically middle part of the Shiratori Group in the Ninohe area (Figure 13). The Shiratori Group is divided into the Yotsuyaku, Kadonosawa and Suenomatsuyama Formations in ascending order (Chinzei, 1966).

This group unconformably overlies the

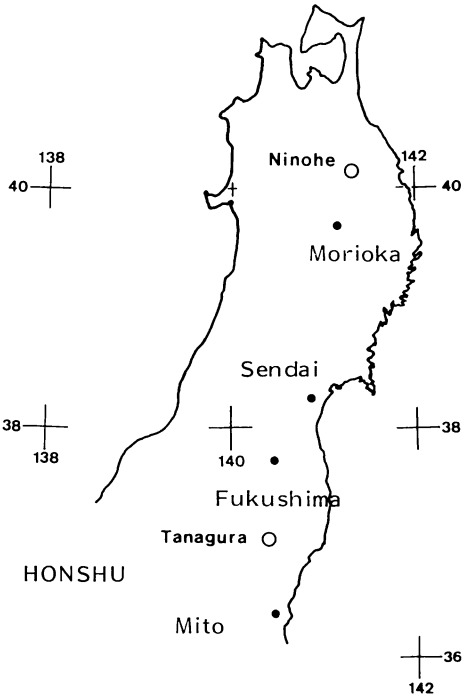


Figure 12. Index map of localities of specimens shown in Figures 14, 15. Ninohe: *Anadara* (*Scapharca*) *ninohensis* Otuka. Tanagura: *Anadara* (*Anadara*) *hataii* Noda.

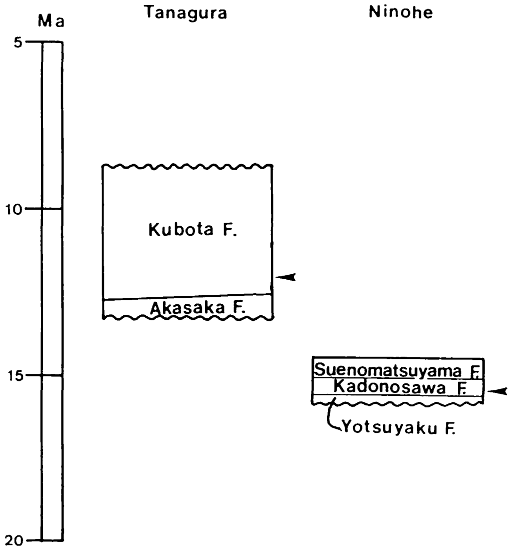


Figure 13. Stratigraphic occurrences of the Kubota and Ninohe specimens. Black arrows indicate shell-bearing horizons.

Nisatai Andesite. The diatom assemblage from the Kadonosawa Formation was correlated with the *Actinocyclus ingens* Zone by Maruyama (1984).

Synopsis : Shell medium in size, thick and inflated. Left valve slightly larger than right. Posterior margin slightly shorter than anterior margin. Umbonal area well developed. Beak prosogyrate. Shell surface sculptured with 26–30 (commonly 27–29) radial ribs. Surface of ribs finely undulated by intersecting commargiral growth lines on the left valve, but rather smooth on the right valve.

Shell morphology : Figure 14 shows the ontogenetic variation of this species. Figure 16a shows the CH–TL relationship for *Anadara* (*Scapharca*) *ninohensis*, and the EV/PT and TL data plotted as a scatter diagram are shown in Figure 16b. These diagrams show that the value of TL is 20 mm at the log size and 33 mm at an EV/PT value of 0.75. The value of CH/TL is 0.1 at the log size (EV/PT=0) and 0.152 at the adult size (EV/PT=0.75). Figure 16c shows the ontogenetic change in the ratio of the anterior and posterior teeth. The ratio is 0.32 at the log size and 0.38 at the adult size.

(b)-2 *Anadara* (*Anadara*) *hataii* Noda

Stratigraphic records : Specimens of *Anadara* (*Anadara*) *hataii* were collected from the Kubota Formation at Hanawa in Fukushima Prefecture (Figure 12).

The Kubota Formation occupies the upper part of the Higashi-Tanagura Group in the

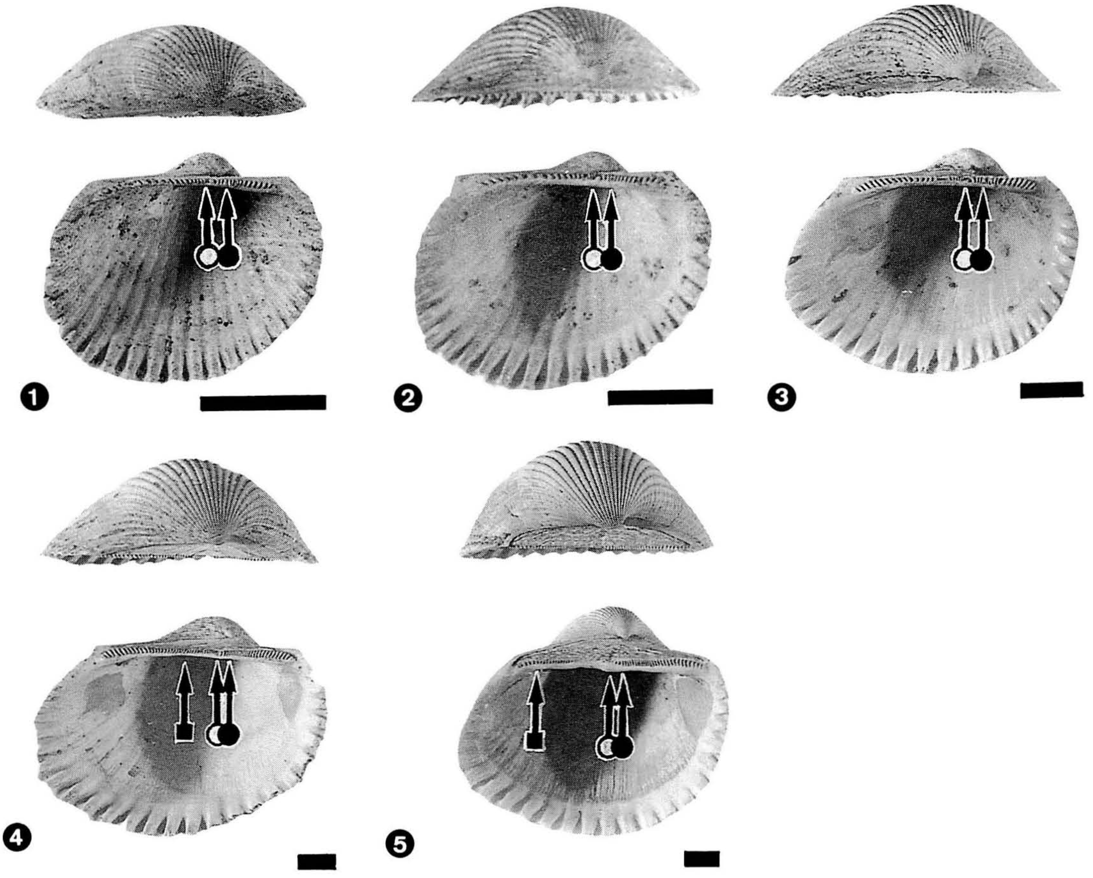


Figure 14. Ontogenetic variation of *Anadara* (*Scapharca*) *ninohensis* (Otuka) collected from the Kadonosawa Formation in Iwate Prefecture. Symbols as in Figure 1.

Tanagura area (Figure 13). The Higashitanagura Group is divided into the Akasaka and Kubota Formations in ascending order (Otuki, 1975). The geological age of the Kubota Formation is 8-12.5 Ma based on microfossil data (Otuki and Kitamura, 1986).

Synopsis : This species has a wide range of variation in shell form. These variations are classified into two variant types based on the inflation of the shell and on the rib sculpture, as follows :

Type A : Shell large, very thick, and weakly inflated. Shell surface sculptured with 26-32 (commonly 27-30) radial ribs. Radial ribs broad, flat-topped, and not subdivided by a groove in younger shells, but bipartite in many adult shells. Beak slightly prosogyrate, situated more anteriorly than that of Type B. Type A corresponds to the intraspecific variants Type 1, Type 2 and Type 5 of Iwasaki (1970). Also, the specimens that were identified as *A.* (*A.*) *ninohensis* by Noda (1966) are identical with Type A.

Type B : Shell large, very thick, and strongly inflated in adult. Radial ribs 26-32 (commonly 27-30). Ribs narrow, beaded-topped, and bipartite in most shells, both young and adult. Type B corresponds to Type 3 and Type 4 of Iwasaki (1970). The type specimen of *A.* (*A.*) *hataii* falls into Type B.

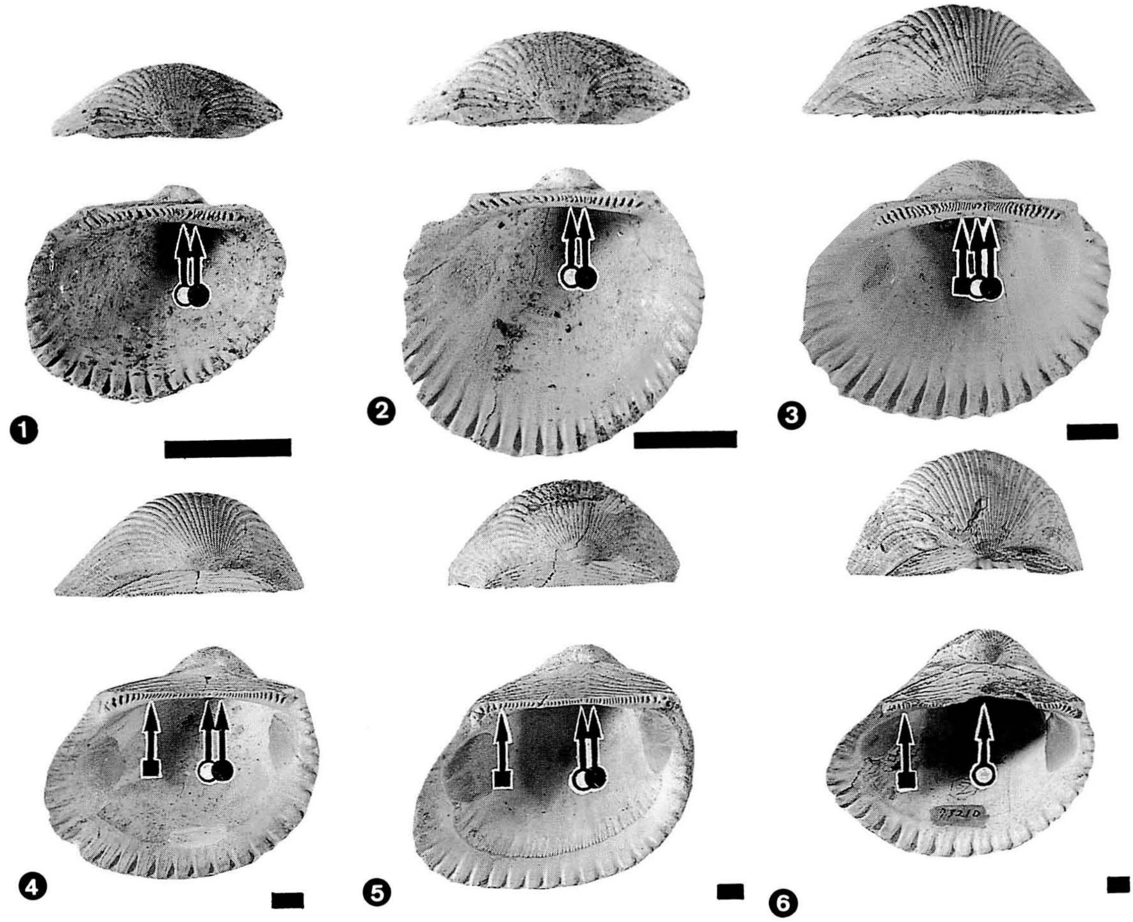
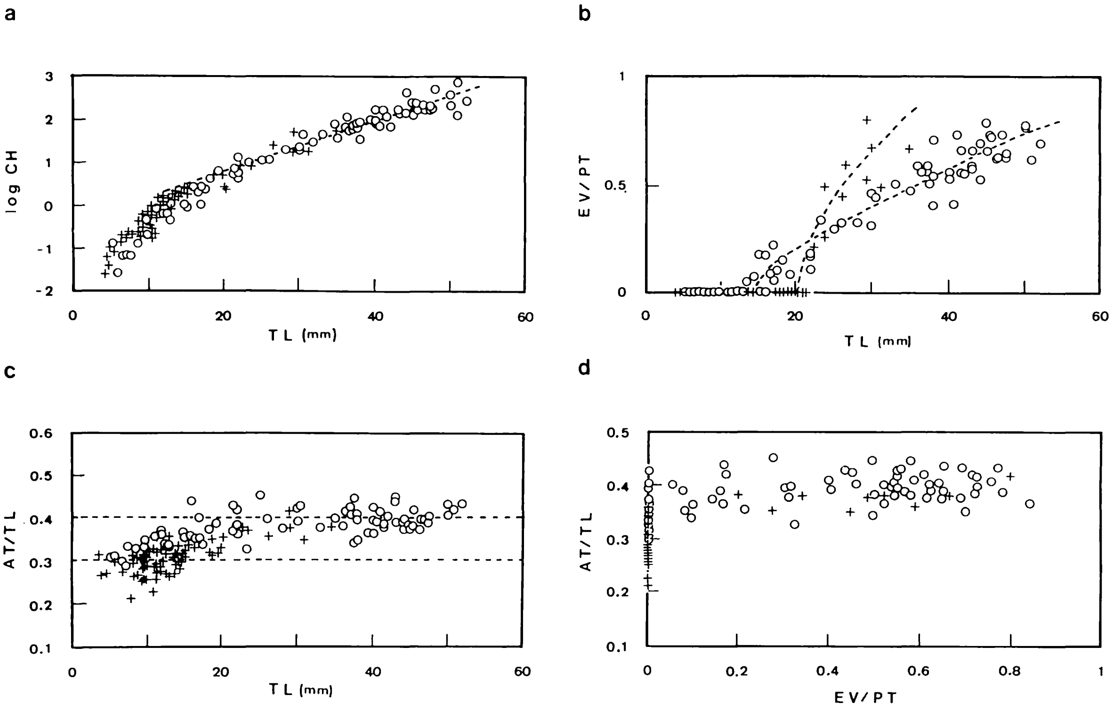


Figure 15. Ontogenetic and interspecific variation of *Anadara* (*Anadara*) *hataii* Noda from the Kubota Formation in Fukushima Prefecture. Symbols as in Figure 1. Specimens of the Type A variant are shown in numbers 4 and 5 ; a specimen of the Type B variant is shown in number 6.

Shell morphology : Figure 15 shows the ontogenetic and intraspecific variation of *A.* (*A.*) *hataii*. Figure 16a shows the CH-TL relation for *A.* (*A.*) *hataii*. The log size of this species is TL = 15 mm. The EV/PT-TL data, plotted as a scatter diagram, are shown in Figure 16b. At the adult size, the CH/TL ratio is 0.066, and at the log size, the CH/TL ratio is 0.256. Figure 16c shows the ontogenetic change in the ratio of the length of the anterior toothed portion to the length of the toothed portion of the hinge line. The ratio has a value of 0.35 at the log size and a mean value of 0.41 at the adult size. Variation in this ratio in adult shells is characteristic of this species. The proportion measured in the intraspecific variant Type A is distributed in the region of lower values (0.39), and that of variant Type B, by contrast, is distributed in the region of higher values (0.43).

(c) Discrimination of taxonomic categories

The Kubota specimens have a wide range of shell form. Because of this variation, Noda (1966) classified the Kubota specimens into three species, and Iwasaki (1970) recognized many intraspecific variant types. In spite of this variation, almost all specimens have common properties of ontogenetic change, as illustrated in the Figures. The EV/PT-TL data for this population, especially, are distributed in a narrow area of the diagram (Figure 16b), so that it is apparent that all the Kubota specimens belong in a



+ *Anadara (Scapharca) ninohensis* Otuka

O *Anadara (Anadara) hataii* Noda

Figure 16. Comparison between Kadonosawa and Kubota specimens in ontogenetic change of shell form. **a** : Distribution of ontogenetic variation in the log CH-TL plane. **b** : Ontogenetic change in the arrangement of hinge teeth. **c** : Ontogenetic change in the ratio between the anterior and posterior hinge lengths. **d** : Ontogenetic relationship between the values of AT/TL and EV/PT.

single species. The majority of the intraspecific variation of these specimens is found as a wide distribution of the relationship between AT/TL and TL, shown in Figure 16b. A similar type of variation can be found in *A*. (*H*.) *subcrenata,* as mentioned above.

The descriptive parameters measured for the Kadonosawa specimens [*A*. (*S*.) *ninohensis*] and for the Kubota specimens [*A*. (*A*.) *hataii*] are shown in Table 2. Comparison of the relative size of these specimens makes it clear that these specimens belong in different subgenera : the Kadonosawa specimens have a high value of the relative size (63%), thus they belong in either *Anadara* (*Scapharca*) or *Anadara* (*Hataiarca*) ; whereas the Kubota specimens have a lower value (30%), and thus belong in the subgenus *Anadara*. The subgenus *Hataiarca* was proposed by Noda (1966), based on the morphological character of a remarkably depressed area on the posterior margin. Because the Kadonosawa specimens have no depressed area, they can be placed only in the subgenus *Scapharca*.

Otuka (1934) and many other workers agreed that *Anadara* (*Scapharca*) *ninohensis* is allied to *A*. (*S*.) *makiyamai,* which was described from the lower Middle Miocene. *A*. (*S*.) *makiyamai* has a high value of the log size, as *A*. (*S*.) *ninohensis* has, and it has no depressed area. By contrast, the species allied to the Kubota specimens are *A*. (*A*.) *ogawai, A*. (*A*.) *watanabei*, and *A*. (*A*.) *amicula*, which constitute the *Anadara amicula* group of Iwasaki (1964). The Kubota specimens and their allied species are assignable to the subgenus *Anadara*, which has low values of the relative size. In the light of the ontogenetic change in shell shape, the Kadonosawa population of *A*. (*S*.) *ninohensis* has a remote relationship to the Kubota population of *A*. (*A*.) *hataii* as the other *A*. (*S*.) species have to *A*. (*A*.) species. The phyletic relationship of the Japanese *Anadara* species, which was proposed by Iwasaki (1964) and Noda (1966), was constructed on the assumption that the Kubota specimens belong to *A*. (*S*.) *ninohensis*. The evidence presented here shows that the phyletic relationships of Japanese *Anadara* species need reconsideration.

Conclusions

1 : Ontogenetic variation in teeth characters and shell morphology occur in *Anadara* species. Relational changes between teeth characters and shell geometry are recognized ; tooth arrangement change (EV/PT) is related to a change in the shape of the cardinal area (CH/TL), and the ratio of the anterior and posterior hinge lengths (AT/TL) is related to the proportion of the heights between the anterior and posterior commissural margins (AM/PM).

2 : The shape of the *Anadara* shell can be described dynamically by using sets of 5 parameters : EV/PT, AT/TL, CH/TL, TL(0)/TL(0.75) and TL. The EV/PT value is a measure of the growth stage. The ontogenetic change in the AT/TL value represents a change in the shape of the commissure. The change in the CH/TL value corresponds to the D-W relationship of Raup (1966), which represents a change in shell inflation. The relative size [TL(0)/TL(0.75)] represents the ratio between the lengths of the juvenile and adult stages. TL represents the absolute size of shell.

3 : Taxonomic criteria for the discrimination of *Anadara* subgenera, groups of allied species, and species are proposed based on similarities in the ontogenetic change in shell shape. Intraspecific variation is found in the relational change between AT/TL and TL. Allied species are similar in the relationship between EV/PT and AT/TL, but are different in the relationship between EV/PT and TL. The subgenus *Anadara* differs from the subgenera *Scapharca* and *Hataiarca* in the relative size [TL(0)/TL(0.75)], which represents the degree to which the shell

becomes evolute.

4 : *Anadara* specimens from the Kadonosawa and Kubota were discriminated by using the criteria proposed above, so that the specimens form the Kadonosawa are placed in the subgenus *Scapharca,* and the specimens form the Kubota are placed in the subgenus *Anadara*. Therefore, the analysis of ontogenetic change in shell form is a useful method for the discrimination of *Anadara* taxonomic categories.

The purpose of this paper has been to isolate some of the different elements involved in the growth of the *Anadara* shell. It has been suggested at several points that the use of such an analysis may serve to reveal similarities and differences that would be less easily recognized from more conventional modes of description.

In order to illustrate each factor in turn without complications, the analysis has been concerned chiefly with shell form. Most actual shells are the products of extremely complex interactions between many or all of the features of surface ornamentation, internal structure and so on. The interactions between them suggest that the ontogenetic change in form cannot be ignored in systematic description and some attempts should be made to describe the ontogenetic changes.

Since the shell is the cumulative product of these varied factors, its form should be described "dynamically", in such a way that the description emphasizes the sequence of stages that brought the shell to its final form ; and it should be analyzed into its formally independent elements.

In the light of logic, the nested set structure that taxonomic categories consist of represents logical relationships between the criteria for the discrimination of these taxonomic categories. This is an important reason why the taxonomic categories should be represented by using the features of ontogenetic change ; the criterion used to define subgenera expresses a more essential feature of similarities between shell shapes than the criterion used to define species expresses.

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Hanawa 塙, Kadonosawa 門の沢, Ninohe 二戸, Kubota 久保田, Tanagura 棚倉.

Anadara 属の殻形態記述のための計数：殻形質の成長変化を4組の体格比率と殻サイズの関係として解析した。これらの成長変化を表す関係は，Raup and Michelson (1965) などの殻形態螺管モデルの形態計数間の関係に等しい。そこで，Noda (1966) によって提案された分類群について，殻の成長変化についての差異と相同を調べ，種内類似種間，あるいは亜属間における形態の差異の現れ方を，螺管モデルに基づいて検討した。その結果から，殻の成長変化に基づいて亜属，類似種，種に分類するための判別基準を考察した。これらの判別基準に基づいて *Anadara ninohensis* とされていた2つの標本集団，門の沢標本集団と久保田標本集団の成長変化を判別した結果，これらの標本集団はそれぞれ異なる亜属に属する種と考えられる。

佐々木 理

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 158, pp. 535-539, 1 Figs., June 30, 1990

902. A NEW GENUS OF THE MIOGYPSINID FORAMINIFERA FROM SOUTHWEST JAPAN*

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Abstract. A new genus of the miogypsinid foraminifera, *Tania* is proposed from the Miocene *Miogypsina* Sandstone of the Lower Formation, Bihoku Group, Okayama Prefecture. *Tania inokosiensis*, n. gen. and n. sp. is selected as the type species.

Key words. *Tania inokoshiensis, Miogypsina* Sandstone, Bihoku Group, Miocene, Okayama Prefecture.

Introduction

Scince Yabe and Mabuchi (1934) described *Miogypsina* cf. *kotoi* Hanzawa in addition to *Operculina* cf. *complanata* Defrance from the *Miogypsina* Sandstone, of the Lower Formation, Bihoku Group exposed at Inokoshi, Koyamaichi Village, Okayama Prefecture, our knowledge of *Miogypsina* from Inokoshi has been extended by Hanzawa (1935), Tan (1937a), Ujiié (1966) and Matsumaru (1973). Most specimens of *Miogypsina* from Inokoshi are identical in every respect with those from many localities of Japan, and have been classified as *Miogypsina kotoi* Hanzawa. *Miogypsina kotoi* containing beds in the Kanto Region, Central Japan was referred to N 8 Zone of the planktic foraminiferal Zone of Blow (1969) by Matsumaru (1977), Takayanagi *et al.* (1978), Chiji and Konda (1978), and Matsumaru and Hayashi (1980), hence the *Miogypsina* Sandstone exposed at Inokoshi may safely be assigned to N 8 Zone, which is considered to Early Miocene of Blow (1969).

Recently, the present author discriminated a new type of *Miogypsina* from the *Miogypsina* Sandstone at Inokoshi, which shows peculiar characteristics intermediate between the genera *Miogypsinoides* Yabe and Hanzawa (1928) and *Miogypsina* Sacco (1893) or *Lepidosemicyclina* Rutten (1911). The author should, therefore, like to propose a new genus name *Tania* for these forms, taking *Tania inokoshiensis*, n. sp. as the type species.

Family Miogypsinidae Vaughan, 1928
Genus *Tania* Matsumaru, n. gen.

Type species: —*Tania inokoshiensis* Matsumaru, n. sp.

Diagnosis: —Test large, laterally flabelliform to somewhat digitate-form, longitudinally biconvex in outline, exterior surface studded with large raised papillae directly over periembryonic chambers and with small ones arranged in apical portion; composed of layers of flattened lateral chambers on each side of equatorial layer. Embryonic chambers of spherical protoconch and reniform deuteroconch in megalospheric generation apically placed, with no nepionic and equatorial chambers on place between protoconch and marginal fringe of apical portion. Two inequal sets of spiral nepionic chambers are situated along the outer side of deuteroconch,

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which is always situated on place between protoconch and normal equatorial chambers of frontal margin. Microspheric generation with spire of nepionic chambers situated apically. Adult equatorial chambers are arcuate, lozengic, hexagonal and spatulate; chambers connected by proximal and distal foramina, and by a system of diagonal and concentric stolons; intraseptal and spiral canal system, and pillars present in central portion of test.

Comparison: —This new genus resembles *Miogypsinoides* in respect to the arrangement of embryonic chambers in the apical portion of test, but it can be distinguished from the latter by having well-developed lateral chambers. Also, *Tania* resembles *Miogypsina* without nepionic and equatorial chambers on place between the embryonic chambers and apical fringe. However, the former is distinguished from the latter by both the arrangement of embryonic chambers in the apical portion, and development of hexagonal to spatulate equatorial chambers. *Tania* resembles *Lepidosemicyclina* in having the hexagonal to spatulate equatorial chambers, but it is distinguished from the latter by the arrangement of embryonic chambers. *Miolepidocyclina* A. Silvestri (1907) and *Miogypsinita* Drooger (1952) resemble *Tania*, but they are distinguished from the latter by having normal nepionic and equatorial chambers on place between the embryonic chambers and marginal to apical fringe.

Etymology: —*Tania* is named in honor of Tan Sin Hok, who introduced the nepionic acceleration theory of the miogypsinid foraminifera (Tan Sin Hok, 1936, 1937b) and is originated with his family name, Tan.

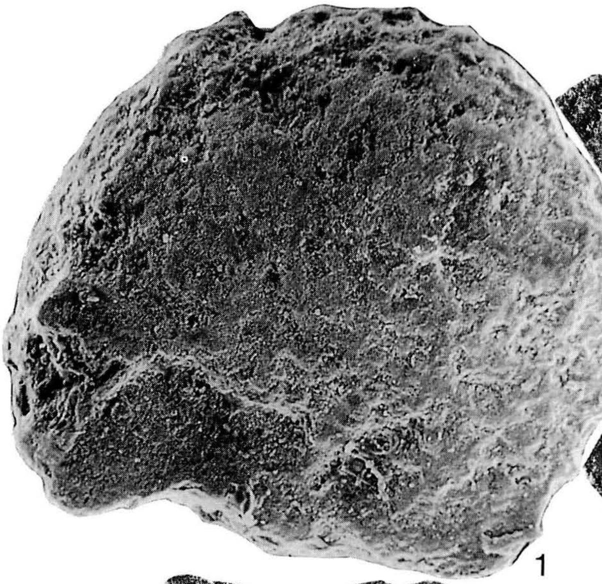
Tania inokoshiensis Matsumaru, n. sp.

Figures 1-1—6

Type material: —Holotype, equatorial section, Saitama University Coll. no. 8803 (Figures 1-4, 6); Paratype specimen, Saitama University Coll. no. 8804 (Figure 1-1); Paratype, equatorial section, Saitama University Coll. no. 8805 (Figures 1 - 2, 3); Paratypes, vertical section, Saitama University Coll. no. 8806 (Figure 1-5).

Description: —Test large in size measuring 2.3 to 2.5 mm., 2.3 to 2.8 mm. and 0.9 to 1.1 mm. in largest diameter, smallest diameter and thickness, respectively, from 12 specimens. Test usually flabelliform (Figure 1-6), but sometimes with digitate-form (Figure 1-1), and biconvex in vertical section (Figure 1-5). Large raised papillae measuring from 65 to 80 μm are distributed at thickest portion over periembryonic chambers with respect to apical parts of test. Outer and inner diameters of protoconch being 268 to 313 μm and 214 to 264 μm, respectively, from 4 specimens in equatorial section. Outer and inner diameters of deuteroconch being 211 to 398 μm and 170 to 313 μm, respectively, from 4 specimens. Proportion between protoconch and deuteroconch diameters given 0.92 to 1.22 and 1.10 to 1.23 in outer and inner diameters, respectively. Angle ($=\gamma$) between axis of two embryonic chambers and apical frontal line giving 135 to 140 degrees. Number of primary and secondary protoconchal nepionic chambers giving 5 to 6 and 3 to 4, respectively, until both nepionic chambers attaining to a stout wall on place between protoconch and marginal fringe of apical portion. Number of primary and secondary deuteroconchal chambers and counting 1/2 for closing chamber are 2.5 to 3.5 and 2.5 to 4.5, respectively. Equatorial chambers in equatorial section arcuate to ogival, lozengic, and hexagonal to spatulate in shape, with dimensions of 108×67 μm to 135×102 μm, 122×135 μm to 139×178 μm, and 104×157 μm to 113×178 μm, respectively. Lateral chambers differentiated from equatorial chambers, arranged in 7 to 10 regular layers in adult specimens. Lateral chambers with dimension of 82×47 μm to 129×65 μm in width and height.

Locality: —Inokoshi, Koyamaichi Vil-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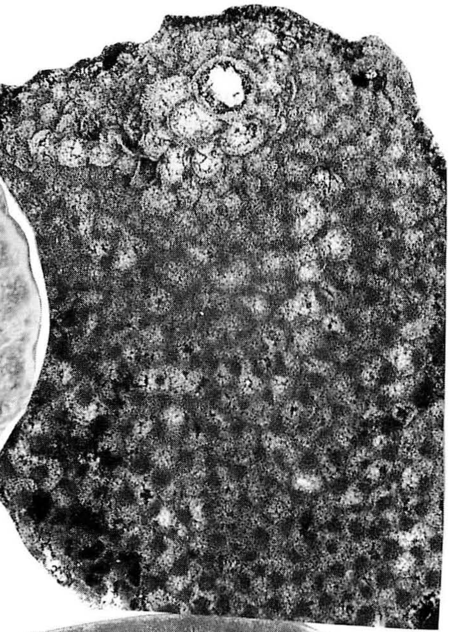
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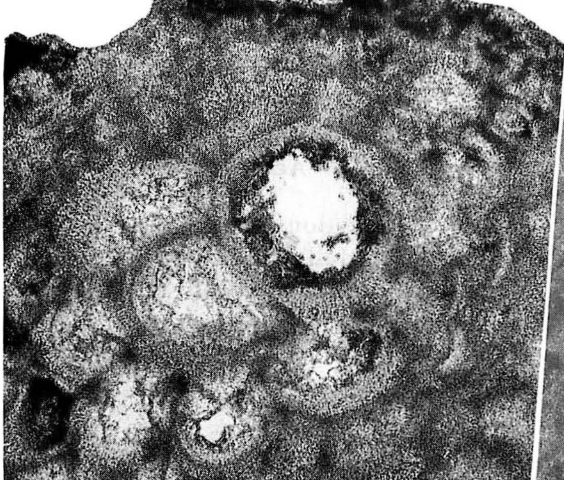
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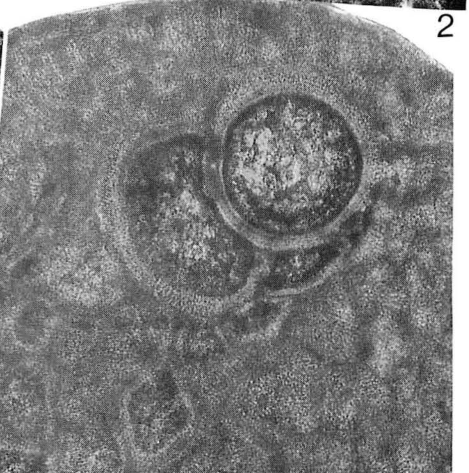
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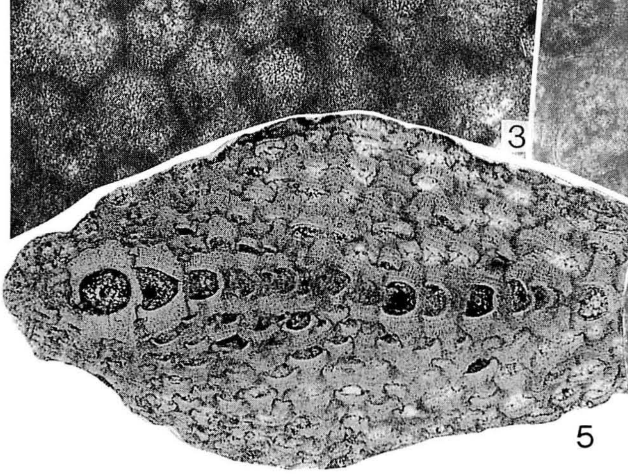
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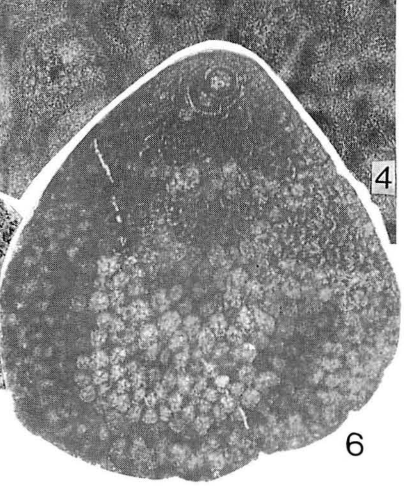
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lage, Kawakami-Gun, Okayama Prefecture (34°45′N. Lat., 133°24′E. Long.).

Stratigraphic horizon: —*Miogypsina* Sandstone, Lower Formation, Bihoku Group.

Geological age: —Early Miocene of Blow, (1969).

Remarks: —*Tania inokoshiensis*, n. sp. represents more primitive arrangement of embryonic chambers and more advanced hexagonal to spatulate equatorial chambers than each one of *Miogypsina kotoi* Hanzawa, respectively. The present new species represents the same hexagonal to spatulate equatorial chambers as *Lepidosemicyclina thecidaeformis* (Rutten) which has more advanced equatorial chambers than *Miogypsina kotoi*. However, this new species has more primitive arrangement of embryonic chambers than *L. thecidaeformis*. Also, *Tania inokoshiensis*, n. sp. has the same arrangement of embryonic chambers as *Miogypsina gunteri* Cole from the Oligocene bed at Port St. Joe, Florida (Cole, 1938) that has its deuteroconch situated on place between the protoconch and main equatorial chambers in frontal margin. However, the latter is distinguished from the former by the arrangement of nepionic chambers in a single spiral. Thus, *Tania inokoshiensis*, n. sp., whose arrangement of embryonic chambers is characterized in having more than 135 degrees in γ value, is considered to be more rationary close to *Miogypsina gunteri* than to *Lepidosemicyclina thecidaeformis*.

In the Pacific Region, *Miogypsina gunteri* Cole is found from the Late Oligocene to Early Miocene Tagpochau Limestone at Locality M107, Saipan, Micronesia by Matsumaru (1976, pl. 4, figs. 1, 9). Also, the present author (in Hashimoto *et al.*, 1977) identified *Miogypsina gunteri* from the limestone of sample 11413 collected at around Bugton Point, Mindoro, Philippines. This limestone is known as the Early Miocene Paclasan Limestone by Hashimoto and Matsumaru (1984, p. 158). Matsumaru (in Hashimoto *et al.*, 1982, pl. 10, figs. 9, 10) described *Miogypsina gunteri* in association with *Nephrolepidina praetournoueri* H. Douville from limestone sample of the Escalante Formation at Locality 7682906, Negros, Philippines. Though Hashimoto *et al.* (*op. cit.*) regarded this limestone sample to be probably Early Miocene, the age of the limestone at Loc. 7682906 is thought probably to be Late Oligocene, based on the occurrence of *Nephrolepidina praetournoueri*. As a result of the present study, it is concluded that *Tania inokoshiensis*, n. sp. may have a close phylogenetic relationship to *Miogypsina gunteri*, based on both the arrangement of embryonic chambers and the relationship of the occurrence between both species.

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← **Figure 1.** *Tania inokoshiensis* Matsumaru, n. gen. and n. sp. **1.** Equatorial view of a paratype, Saitama University Coll. no. 8804, ×30. **2—4, 6.** Equatorial sections, **2.** ×37, paratype, Saitama University Coll. no. 8805. **3**, enlarged from **2**, ×93, showing the arrangements of embryonic chambers, and nepionic and equatorial chambers in the apical portion. **4.** Holotype, Saitama University Coll. no. 8803. enlarged from **6**, ×70, showing the arrangements of embryonic, nepionic and equatorial chambers. **6.** ×23, showing the whole test of the holotype with the hexagonal to spatulate equatorial chambers. **5.** Vertical section, paratype, Saitama University Coll. no. 8806, ×43.

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西南日本産の Miogipsinid 有孔虫の新属：岡山県川上郡高山市村飯越の中新世備北層群下部層 *Miogipsina* 砂岩から *Tania inokoshiensis* を記載した。この新属・新種は *Miogypsina gunteri* Cole に近い系統のものと推察される。 松丸国照

Errata

No. 896. Hiromichi Hirano, Takashi Okamoto and Kohji Hattori: Evolution of some Late Cretaceous desmoceratine ammonoids.

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